

Comprehensive Summaries of Uppsala Dissertations  
from the Faculty of Science and Technology 915



# Plumage Colours and the Eye of the Beholder

*The Ecology of Colour and its Perception in Birds*

BY

OLLE HÅSTAD



ACTA UNIVERSITATIS UPSALIENSIS  
UPPSALA 2003

Dissertation presented at Uppsala University to be publicly examined in Friessalen, EBC, Uppsala, Friday, December 19, 2003 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

**Abstract**

Håstad, O. 2003. Plumage Colours and the Eye of the Beholder. The Ecology of Colour and its Perception in Birds. Acta Universitatis Upsaliensis. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 915. 34 pp. Uppsala. ISBN 91-554-5824-6

Virtually all diurnal birds have tetrachromatic vision based on four different colour receptors. As a result, birds are potentially able to perceive their environment in twice as many colours as humans and four times as many colours compared to most other mammals, which are dichromatic. In addition to the spectrum visible to humans, birds are able to detect ultraviolet (UV) light. Signals with a UV component have been shown to be important to birds both in foraging and colour signalling. Because of the superior colour discrimination of the avian eye, UV sensitivity, but especially owing to its tetrachromacy, we cannot know what birds look like to those that matter, i.e. other birds.

In my thesis I describe a new molecular method with which it is possible to identify the vision system of birds only using a small amount of DNA, without the need to keep or sacrifice the animal. It thereby facilitates large screenings, including rare and endangered species. The method has been used to increase the number of species with identified vision system type from 19 to 66. I show that raptors and songbirds have different vision systems, giving songbirds the possibility of a secret channel for colour signalling, and that male songbirds in coniferous forest take advantage of this to be significantly more cryptic to raptors than to females songbirds. I show that gulls have gained a vision system enabling them to detect the UV signals of fish when the fish swim close to the surface.

Even though we tend to be rather self-satisfied with the quality of our colour vision, we are colour-blind when compared to birds. My work shows that human colour vision is inadequate for judging animal coloration, and that there is much more going on in bird colour signalling than meets our eye.

*Keywords:* ultraviolet, colour vision, opsin

*Olle Håstad, Department of Evolutionary Biology, Animal Ecology, Norbyv. 18D, Uppsala University, SE-75236 Uppsala, Sweden*

© Olle Håstad 2003

ISSN 1104-232X

ISBN 91-554-5824-6

urn:nbn:se:uu:diva-3864 (<http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-3864>)

*To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree. When it was first said that the sun stood still and the world turned round, the common sense of mankind declared the doctrine false; but the old saying of Vox populi, vox Dei, as every philosopher knows, cannot be trusted in science.*

*– Charles Darwin*

*Sequencing – how hard can it be? They are doing  
it at the other department!*

*– Mats Björklund*

---

The thesis is based on the following articles, which are referred to by their Roman numerals in the text

---

- I** Rintamäki P T, Håstad O, Ödeen A, Alatalo R V, Höglund J and Lundberg A. (2002) Sexual selection, colour perception and coloured leg rings in grouse (Tetraonidae). *Avian Science* 2(3):145–152
- II** Ödeen A and Håstad O. (2003) Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution*. 20(6):855-861.
- III** Håstad O, Ödeen A and Ekstrand M. Have colour vision and sexual signals co-evolved in birds? Manuscript
- IV** Håstad O, Ödeen A and Victorsson J. Crypsis is in the eye of the beholder: Differences in perception of songbird plumage colours between predator and prey. Manuscript
- V** Håstad O, Ernstdotter E and Ödeen A. UV biased colour vision in piscivorous dip and plunge diving birds. Manuscript

---

Article I and II was printed with permission from the publishers.

The order of the authors reflects their involvement in the papers.

- I** AÖ and OH did all work related to vision function including writing those sections of the paper.
- II+III** OH and AÖ contributed equally to the papers apart from data collection in III by ME and calculations by OH.
- IV** Equal contribution apart from calculations by OH and ornithological background by JV.
- V** Equal contribution apart from sequencing by EE supervised by OH.

# Contents

Introduction .....	7
Animal colour vision .....	7
Ultraviolet sensitivity .....	8
Eye physiology .....	9
Aims of the present investigation .....	13
Results and discussion .....	14
Paper I: Sexual selection, colour perception and coloured leg rings in grouse (Tetraonidae) .....	14
Paper II: Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA .....	16
Paper III: Have colour vision and sexual signals co-evolved in birds? .....	18
Paper IV: Crypsis is in the eye of the beholder: Differences in perception of songbird plumage colours between predator and prey .....	20
Paper V: UVS as a foraging tool for dip and plunge divers .....	24
Conclusion .....	27
Acknowledgements .....	28
Computer programs .....	29
Errata .....	29
References .....	30



# Introduction

We would be hard pressed to find a group of animals more visually competent than birds. Their eyes commonly occupy at least 50% of the cranial volume as compared to approximately 5% in humans (Waldvogel 1990), and birds have been found to possess high visual acuity, e.g. peregrine falcons frequently detect and approach prey the size of robins from distances of up to 1500 m (Tucker *et al.* 2000). Birds are colourful animals displaying a great variety of patterns, contrasts, colours, hues and shades. They also have a retinal design that allows them to perceive the world in a diverse set of colours.

Until the turn of the last century we did not recognise that the sensory perception of animals differed from our own. The first to do so was Jacob Johann von Uexküll who coined the term “*umwelt*” to describe the sensory experience of a species (Waldvogel 1990). When imagining the *umwelt* of animals we often extrapolate from our own sensory experience of the world, giving the animals only a quantitative difference in perception from our own. This may or may not be true, however, stating that bats only hear higher frequencies and dogs just have a more accurate sense of smell than we do may lead us to underestimate or miss important qualitative differences in the function of the senses. This will also limit our ability to understand the connection between behavioural responses and what special qualities of the signal that induced it. A basic insight to animal perception is therefore crucial to our understanding of animal behaviour and ecology.

In this thesis I focus on aspects of the colour perception of birds with special emphasis on the differences between species regarding their colour vision system and colour signalling.

## **Animal colour vision**

The human colour vision is of an uncommon type, only shared by old world monkeys and apes (Jacobs 1993), and is therefore unfit to evaluate the colour perception of most other animals. Our colour vision is based on the signals from three distinct classes of cones in the retina (blue, green and red) and gives us a trichromatic vision system. Virtually all diurnal birds have tetrachromatic vision (Osorio *et al.* 1999; Hart 2001b) based on four single cone types (SWS1, SWS2, MWS and LWS: short, medium and long wavelength sensitive). This adds an extra dimension to potential colour space (Bennett *et al.* 1994). As a result, birds are potentially able to perceive their environ-

ment in twice as many distinct colours as humans and four times as many colours compared to most other mammals, which are dichromatic (Jacobs 1993). A retina with four classes of cones involved in colour perception (tetrachromatic vision) appears to be a basal character in vertebrates (Shi and Yokoyama 2003) and has been reported in birds (Goldsmith 1990), fish (Palacios *et al.* 1998) and reptiles (Fleishman *et al.* 1993). We may not just perceive slightly different hues compared to other animals, but might possibly be missing major components of animal colouration. Humans may hence be blind to many critical aspects of animal coloration and perception (Losey *et al.* 1999).

### **Ultraviolet sensitivity**

The sensitivity of the SWS1 cone type is located near, or in, the ultraviolet (UV) range of the spectrum. The UV waveband is not perceivable for humans, but it has been shown to be important in several aspects of bird ecology.

The ancestral state in vertebrates seems to be with SWS1 opsin being mainly sensitive in the UV range. However, among birds the more long-wavelength sensitive type (violet sensitive: VS, Hart *et al.* 2000b) is likely the basal type with a shift of the sensitivity into the UV range (UV sensitive: UVS, Hart *et al.* 2000b) having been secondarily derived from VS ancestors (Shi and Yokoyama 2003). This classification is somewhat simplified as there is variation in sensitivity maximum ( $\lambda$ -max) within the groups (reviewed in Hart 2001b), nevertheless the difference between the groups is distinct enough to make it possible to classify sensitivity of a bird into either group. The most pronounced difference is in the  $\lambda$ -max of the SWS1 cone where UVS possess a  $\lambda$ -max ranging from 355 to 376 nm, while the  $\lambda$ -max of VS is located between 402 to 426 nm (Cuthill *et al.* 2000). There is also a co-occurring change in the same direction of the  $\lambda$ -max of the second short-wavelength sensitive cones (SWS2).

The VS system has been demonstrated throughout avian phylogeny: in mallard (*Anas platyrhynchos*) (Jane and Bowmaker 1988), chicken (*Gallus gallus*) (Bowmaker *et al.* 1997), Humboldt penguin (*Spheniscus humboldtii*) (Bowmaker and Martin 1985), Japanese quail (*Coturnix japonica*) (Bowmaker *et al.* 1993), domestic turkey (*Meleagris gallopavo*) (Hart *et al.* 1999), common peafowl (*Pavo cristatus*) (Hart 2002), Manx shearwater (*Puffinus puffinus*) (Bowmaker *et al.* 1997) and ostrich (*Struthio camelus*) (Wright and Bowmaker 2001). The UVS system has traditionally been found only in birds of the orders Passeriformes and Psittaciformes: pekin robin (*Leiotrix lutea*) (Maier and Bowmaker 1993), budgerigar (*Melopsittacus undulatus*) (Bowmaker *et al.* 1997), starling (*Sturnus vulgaris*) (Hart *et al.* 1998), canary (*Serinus canaria*) (Das *et al.* 1999), blue tit



(*Parus caeruleus*), Eurasian blackbird (*Turdus merula*) (Hart *et al.* 2000b), zebra finch (*Taeniopygia guttata*) (Bowmaker *et al.* 1997) and four species of estrildid finches (Hart *et al.* 2000a)

Experimental alteration of the ultraviolet part of the spectrum has been shown to affect both foraging efficiency in several species (Goldsmith 1990; Viitala *et al.* 1995; Church *et al.* 1998b; Siitari *et al.* 1999) and sexual signals (Bennett *et al.* 1996, 1997; Andersson and Amundsen 1997; Hunt *et al.* 1997, 1998, 1999). To humans it is in many cases difficult to understand which part of the signal is detectable by birds and, even more so, which qualities of the signal convey important information. Behavioural experiments on birds indicate that no part of the spectrum is of special importance to avian receivers (Hunt *et al.* 2001; Maddocks *et al.* 2001), but see Hausmann *et al.* 2003. Most behavioural studies in recent years have however only focused on UV as a separate communication channel and may have missed potentially important differences in colour perception arising from tetrachromacy. Given the highly-developed ability of birds to send and receive colour signals, it is probable that the tetrachromatic colour vision system plays an important part in avian ecology.

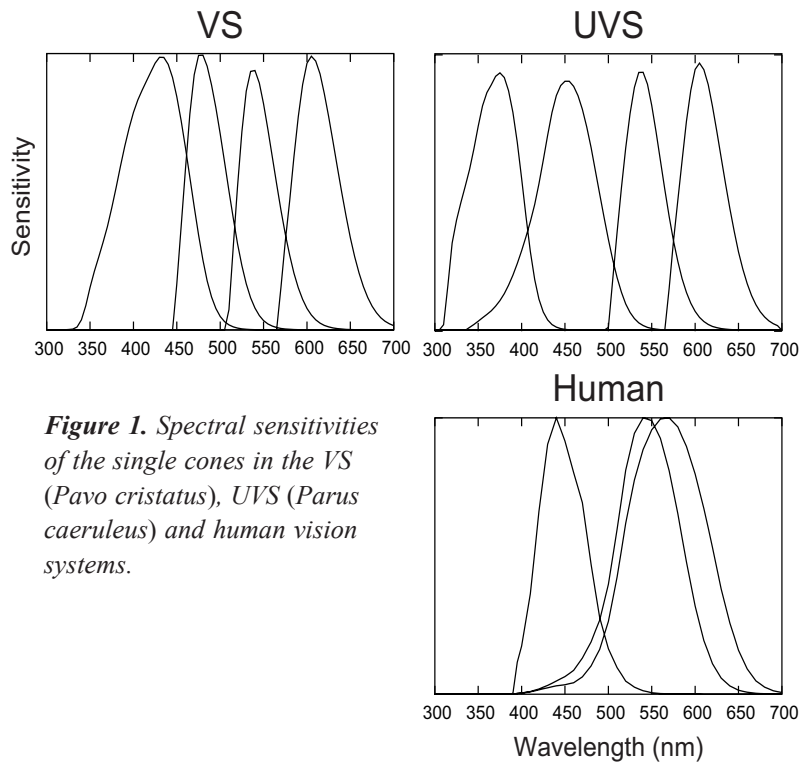
### Eye physiology

The anatomy and histology of a typical bird's eye is very similar to that of ours but differs in some important aspects.

For the light to reach the retina it has to pass through the cornea, aqueous humour in the anterior chamber, lens and vitreous humour. Henceforth I will refer to these structures as the *ocular media*.

The retina is a two dimensional light detector array consisting of six types of photo receptors (Hart 2001b). Of these receptors are four single cones with sensitivity maxima located at 543-571 nm (LWS), 497-509 nm (MWS), 430-463 nm (SWS2) and the above mentioned SWS1 (figure 1). Birds also have rods for use under low light conditions ( $\lambda$ -max 501-509 nm) and double cones, a receptor type consisting of a pair of differently sized cones carrying the LWS pigment (Cuthill *et al.* 2000). The double cone is the most abundant receptor type in the avian retina (Bowmaker *et al.* 1997); they are most likely not involved in colour vision, but in achromatic tasks such as movement detection (Campenhausen and Kirschfeld 1998; Vorobyev *et al.* 1998).

The vertebrate visual pigments are a family of membrane bound G-protein-linked-receptors (opsins) to which the aldehyde of vitamin A, the chromophore 11-cis retinal, is bound (Applebury and Hargrave 1986). It is the molecular properties in the area of the chromophore binding site that determines the maximum



**Figure 1.** Spectral sensitivities of the single cones in the VS (*Pavo cristatus*), UVS (*Parus caeruleus*) and human vision systems.

sensitivity wavelength of the complex. In the avian SWS1 opsin only six amino acid positions out of ~300 are responsible for the wavelength sensitivity tuning (Zhang 2003). A single point-mutation in amino acid 90 from cysteine (C) to serine (S) (C90S), shifts  $\lambda$ -max by 35 nm and effectively accounts for the difference between UVS and VS (Wilkie *et al.* 2000; Yokoyama *et al.* 2000). While the molecular properties of the opsin could be considered to facilitate volatile character states, there are changes associated with the shift between UVS and VS in the spectral transparency of the ocular media and cone oil droplets (Hart 2001b), which suggest an adaptive background for transitions between the main sensitivity types.

At the distal end of the inner segment of the cone, birds have a pigmented oil droplet filtering the light before it reaches the outer segment where the visual pigments are located. The oil droplets are differently coloured depending on cone type and function as a cut-off filter reducing the sensitivity overlap of adjacent

cones, but in doing so they also reduce the absolute sensitivity of the cone (for a review see Hart 2001b). The smaller overlap between the sensitivity peaks are predicted to increase the dispersion of spectra in receptor space and improve colour constancy (Goldsmith 1990; Vorobyev *et al.* 1998).

The spectral sensitivity may also be changed by varying the relative proportion of cone types (Vorobyev and Osorio 1998). The distribution in the variation of cones among birds appears to be mainly governed by the birds' life styles rather than their phylogenetic relationships, even though the results are not conclusive (Hart 2001a).

UV-sensitivity in birds and other vertebrates is primarily a function of UV transparency of the ocular media (Cuthill *et al.* 2000). The larger the eye, the longer the pathway light has to cross and the less UV will reach the retina. The UVS vision system may have evolved as a side effect of a decrease in body size resulting in more UV reaching the retina (Hart 2001b) and has been maintained because of advantages in foraging efficiency (Church *et al.* 1998a-b). If the main adaptive reason for the change in vision system from VS to UVS is foraging, any adjustments of the plumage coloration to fit the new system could represent a case of sensory exploitation in the signal-perception evolution (Endler and Basolo 1998).

There are however adverse effects associated with a spectral sensitivity that extends into UV. UV light is absorbed by DNA and other organic molecules and may damage the retinal tissue, something that animals may protect themselves against by having UV-opaque ocular media. This option is not available to animals relying on the ability to detect UV. Furthermore, the optical properties of light from a wide range of wavelengths may result in an unfocused image on the retina through chromatic aberration and the higher scattering of shorter wavelengths within the eye (Siebeck and Marshall 2001). To maintain a vision system sensitive to UV despite these costs indicates that it carries a significant advantage to the animal (Bennett and Cuthill 1994).

How an animal perceives the colour of the light entering its eyes is thus initially governed by the relative absorbance of different wavelengths by the colour receptors of the retina. This in turn depends on the chromatic ocular disposition (COD) of the eye, i.e. the composite effect of

- I the wavelength of maximum absorbance ( $\lambda$ -max) of the cone visual pigments
- II the filtering effect of the ocular media (cornea, lens, vitreous and aqueous humour) and that of the oil droplets
- III the relative proportion of different cone types

The apparent integration of at least the first two of these tuning components in the colour vision of birds opens a possibility for identifying the visual tuning of a

species into one of the two major classes if only one of the tuning components is known. Three methods for this have traditionally been used.

Microspectrophotometry (MSP) has been the standard method to examine the photo receptor properties of animals. It is used to measure the absorption of individual cells in their native state in the retina. To prepare retinas for MSP, the live subjects are held in darkness for several hours prior to being sacrificed and having their eyes dissected (Hart *et al.* 1999). Owing to the complexity of the method, the absorbance of visual pigments has only been examined in a limited number of species. Another method is electroretinographic (ERG) flicker photometry with which the animal's sensitivity to different wavelengths is measured *in vivo* (Jacobs 1998). The molecular sequence of the SWS1 opsin has been described, and 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. Substitutions in four of the sites described by Wilkie *et al.* (2000) only lead to minor or no shifts in  $\lambda$ -max. A change from cysteine (C) to serine (S) in position 90, however, causes a substantial change in  $\lambda$ -max (35 nm). Hence a C in position 90 characterizes the UVS group, while the VS group has an S in the same position (Yokoyama *et al.* 2000). These studies used RNA from retinas to produce cDNA. The main disadvantage of these methods is that they require either a fresh eye or living animal for use in the examination.

## Aims of the present investigation

It has been my aim with this study to investigate how differences in colour perception among birds affect their ecology. I especially focused on the interaction between colouration and colour perception (papers I, III and IV) and the effects of vision system on foraging (papers IV and V). To be able to carry out cross species comparisons, more information on the phylogenetic distribution of vision systems was needed, for which a method of vision system typing was required (papers II and V).

## Results and discussion

### **Paper I: Sexual selection, colour perception and coloured leg rings in grouse (Tetraonidae)**

Black grouse (*Tetrao tetrix*) males have distinct reddish supra-orbital eye-combs, which have presumably evolved through sexual selection. When studying the lek-behaviour of black grouse, differently coloured leg rings are often used. Because birds sometimes may use colour cues other than the partner's plumage in mate choice, we postulated that this leg ring might affect the choice by females, especially if it is of a colour close in appearance to the supra-orbital eye-combs colouration.

Studies on birds have suggested that coloured leg rings, resembling male feather or bare part ornaments, may increase male attractiveness to females or may be important in intrasexual interactions between males. Most of these studies, however, have not considered that the physiology of avian vision is different from the human. In consequence, colours that are perceived as similar by a researcher may be seen as different by a bird.

In this study we set out to investigate if the identification markings used affected mate choice and to see if it was likely that the grouse may confuse the colour of the bands with the sexual signal of males.

Several studies on birds have documented that females use conspicuous male colours in their mate choice and favour males that express the most elaborated plumage or bare part ornaments (Andersson 1994). In the context of sexual selection it has been suggested that coloured leg rings originally used for individual identification in field studies may attract prospecting females, as well as leading to escalated fights between males (Burley *et al.* 1982; Holder and Montgomerie 1993; Metz and Weatherhead 1993; Cuthill *et al.* 1997). These observations have induced a suite of empirical and experimental studies that have demonstrated that leg rings of an ornament-resembling colour may increase male attractiveness (e.g. Burley *et al.* 1982; Brodsky 1988 but see Ratcliffe and Boag 1987; Holder and Montgomerie 1993; Zann 1994; Jennions 1998) and change the fighting behaviour of territorial males (Holder and Montgomerie 1993; Metz and Weatherhead 1993). A plausible explanation for these results is that leg rings reinforce the effect of the ornament.

We quantified the colour difference between leg rings and the eye-combs of

black grouse as perceived by birds and humans, and compared this with data on male attractiveness and mating success.

The colour as perceived by any viewer is initially a combination of the reflectance spectrum reaching the retina and the sensitivities of the photoreceptors involved in colour perception (cones). To measure the reflectance of the leg rings and supra-orbital combs we used a spectrometer with a fibre optic probe and a combined deuterium-halogen light source.

Black grouse is a Galliform bird i.e. it is related to the domestic chicken. We therefore assumed that their vision system was of the same type. As the sensitivity curves of the chicken are known it was possible to calculate the strength of the signal from each of the chicken's cone types when exposed to the measured reflectance spectrum. The human cone sensitivities are also known, so we did the same calculation using these. The output signal from the different cone classes can be treated as coordinates in a colour space with the same number of dimensions as the number of cone types. For humans this is a three dimensional colour space and for the birds a four dimensional one. To compare two colours it is then possible to calculate the distance between their positions in colour space. We calculated the distance between all eye-combs and the rings and the eye-combs for both human and chicken. After normalising the distances to have a maximum of one, the average distance for the red leg ring and the eye-comb was 0.074 (s.d. 0.037) for chicken and 0.068 (s.d. 0.018) for human. The average distance for the orange leg ring and the eye-combs was 0.039 (s.d. 0.028) for chicken and 0.025 (s.d. 0.012) for human.

To test if the distances were significant we performed a randomisation test. For human the mean distances from the randomisations did not deviate significantly from the observed mean among eye-combs ( $P = 0.35$  for red leg ring and 0.13 for orange leg ring), roughly coinciding with visual observations by the authors; both the leg rings were perceived as being rather close in colour to the combs, the red a little closer than the orange. For chicken however the situation was the opposite with the red leg ring and eye-comb significantly different ( $P = 0.012$ ) but not the orange leg ring and eye-comb ( $P = 0.80$ ). This implies that a black grouse is not likely to perceive the colour of the red leg ring as that of an eye-comb, but it may confuse the colour of the orange leg ring with that of an eye-comb. Coloured leg rings corresponding to ornament colour did not improve male mating success in the black grouse but instead reduced it, a result also suggested by meta-analysis of lekking grouse species. The fighting behaviour of black grouse males equipped with reddish or other leg rings did not vary significantly.

The model based on the spectral reflectance data suggests that grouse perceive colours differently from humans. These results confirm the importance of taking

the study species vision system into account, and the importance of not using human vision as a proxy for bird perception.

To calculate the black grouse values we used the eye design of chicken (*Gallus gallus*). As the chicken belongs to the same order (Galliformes) as the black grouse we assumed that the chicken eye design also applies to black grouse. We did not find this satisfying, and saw a need for a simple method for identifying the vision system of birds.

### **Paper II: Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA**

Although the existing methods for examining the vision system of birds provide all necessary information and are well known they are not easily accessible to the ecologist who wants to examine the vision system of his study species. The traditional methods also require a living animal for study, something not always available.

As previously described, the type of SWS1 opsin possessed by a bird is indicative of its vision system. In this study we developed a molecular method that can be used to quickly, easily and cheaply assess the vision type in almost any bird by sequencing the part of the SWS1-opsin including the C90S mutation site from small samples of total DNA. By using total DNA it is possible to use almost any tissue for the analysis, e.g. blood, skin or feathers, even from preserved specimens.

We used degenerate primers to amplify the target sequence in a total of 45 species of which the spectral tuning was previously unknown in 37. The results of the remaining eight and comparisons between closely related species were consistent with MSP examinations and in vitro observations of cloned genes (Wilkie *et al.* 2000). We found five new mutations at spectral tuning position 86 and one at 93, i.e. 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 suspect the new mutations to have any drastic effects on the spectral tuning of the SWS1-opsin.

Our results confirm that the UV-tuned vision system 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. As we expect the change from UVS to VS to be adaptive these are intriguing results that call for further study.



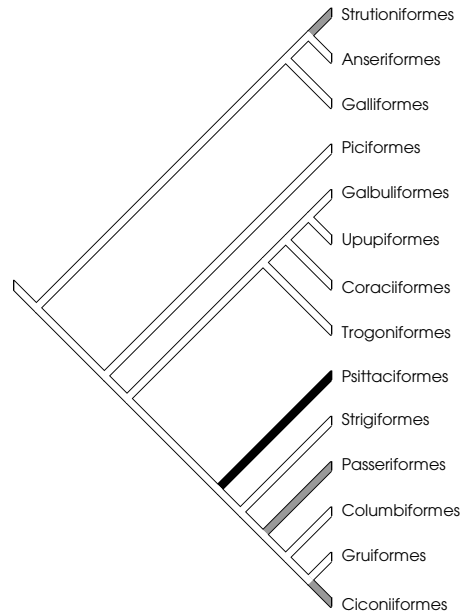


Figure 2. Type of vision system mapped onto phylogenetic relationship among avian taxa: (a) Phylogeny of orders based on DNA-DNA hybridization analysis (Sibley and Ahlquist 1990). The passeriform families are combined. White denotes violet sensitive (VS), black ultraviolet sensitive (UVS) and grey is taxa including both systems.

The distribution of the UVS/VS character in the avian phylogeny has been considered to reflect the degree of relatedness of avian taxa and 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, the presence of UVS in at least nine families from four orders, inter-dispersed with VS taxa (figure 2) strongly indicates that the UVS character has been acquired independently in each of these groups from a VS ancestor and that its distribution does not reflect the degree of relatedness between avian species.

We can expect intriguing effects on the evolution of colour signals from interactions between raptors (Ciconiiformes) and their passeriform prey. Trade-offs between foraging and mating benefits against predation costs may explain the presence of UVS in Laridae and Passeriformes.

For the purpose of identifying the vision system of a bird in the context of a

ecological study, our method offers a considerably more practical tool than does MSP. We however, do not imply that our method should replace the latter; MSP is undeniably more direct and informative. 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.

### **Paper III: Have colour vision and sexual signals co-evolved in birds?**

Arguably, the VS and UVS vision systems can produce significantly different colour signals from the retina to the visual cortex when exposed to the same spectrum of light. In intraspecific colour signalling we would expect co-evolution of plumage colour and vision system. A correlation between plumage reflectance and sensitivity maxima of the cones would thus maximise the strength of the colour signal, thereby improving the social and sexual aptitudes of both the signaller and the receiver, and in so doing increase the fitness of both.

In paper II we identified the vision system of a large number of taxa. This information gave us the opportunity to do a broad test of correlation between sexual signal and vision system among birds. Given the highly-developed ability of birds to send and receive colour signals, interspecific differences in colour vision should play an important part in avian ecology. We tested this using data from reflectance spectrophotometry on museum skins in combination with published data of  $\lambda$ -max from microspectrophotometry or SWS1 opsin sequences to identify the vision system of the species. We constructed a simple retinal model to estimate the match between reflectance and sensitivity measured as the chromatic content of the colour signal and used it to test if there is a correlation of plumage reflectance to spectral sensitivity of two different types of avian colour vision.

In this study we used a slightly different distance measure than the one used in paper I to isolate better the effect of plumage reflectance peak position from effects such as the number of cones stimulated. We therefore used the distance from the plumage reflectance receptor signal to the closest achromatic point in receptor space ( $\Delta A$ ) of the same signal intensity, i.e. with the same vector sum.

We were interested in sexual signals and needed to objectively to choose a single plumage patch from each species that most likely was used as such signal. As our results from paper I showed, the human vision system is inadequate for this task. We therefore used a criterion of high colour information content regard-

less of the viewer's vision system for the selection process. To keep the selection process independent of bias related to differences in colour vision, including human vision, we selected patches based on variation in reflectance within the spectrum using a modified variance measure.

To check if the smaller overlap between the sensitivity peaks of the cones caused by the filtering effects of the oil droplets and the larger spacing between the short-wavelength sensitive opsins of the UVS COD to increase the dispersion of spectra in receptor space we measured reflectance spectra of 25 mineral samples at The Museum of Evolution at Uppsala University, and used these as a control for colour dispersion.

Our results confirmed that the UVS retina delivers a more chromatic signal, i.e. more saturated "colours", to the later part of the vision pathway when exposed to light reflected from either type of plumage or minerals than will the VS retina. This difference between CODs is not due to a specific tuning to plumage but a general increase in chromatic resolution for UVS, as predicted by Goldsmith 1990 and Vorobyev *et al.* 1998. We also found a stronger chromatic signal for UVS CODs than for VS, viewing UVS plumage, which supports a possible plumage and vision system co-evolution for UVS birds.

UVS also produced a significantly stronger chromatic signal from UVS plumage than from VS, this result supports the notion that the plumage of the UVS birds has been subjected to co-evolution with the COD and that UVS birds will deem their own plumage as particularly chromatic. When performing the same test on VS we however detected a stronger chromatic signal from UV-plumage than from their own plumage.

Our results show that the UVS birds have plumage colours better tuned to the shared properties of both COD types than VS birds have. We also saw a better ability within the UVS for detecting and separating colours. This suggests that chromatic signalling plays a more important role for UVS than for VS birds. Spectral tuning of the plumage will increase the contrast of the coloration to the foliage of the background. Although this might be desired for sexual selection it will carry the cost of an increased risk of detection by predators. A plausible scenario is that the transition from VS to UVS granted an ability to determine better the quality of a potential mate by his coloration, in a way which increased the reward for accurate plumage reflectance tuning more than it did the risk of detection in these species.

**Paper IV: Crypsis is in the eye of the beholder: Differences in perception of songbird plumage colours between predator and prey**

Birds have to make a trade-off between conspicuous sexual signalling enhancing their attractiveness and crypsis prolonging their life. Sexual selection favours brighter and bigger traits (Andersson 1994), but chromatic exaggeration may increase conspicuousness to predators. If possible, signalling with colours that are inconspicuous to predators should reduce the predation cost of signalling, and therefore facilitate the evolution of stronger sexual and social signals.

Our results from paper III suggest that this may have been the case during the evolution of UVS plumage colours.

Guilford and Harvey (1998) proposed that SWS1 (ultraviolet (UV) vision) functions as a private avian communication channel lowering the risk of predation, as mammalian predators are blind to UV (Jacobs 1993; Bowmaker 1998). This idea is however contradicted by the fact that predation on small birds is at least equally likely to be by raptors (Banks 2001). Raptors (i.e. kestrels *Falco tinnunculus*) have been shown to use UV cues while foraging (Viitala *et al.* 1995), and therefore UV signals will be visible to at least some predators. These arguments however rest on the assumption that avian predators and prey are tuned to the same part of the UV range, while molecular and retinal studies suggest otherwise.

In paper II we showed that the Passerida (sparrow- and thrushlike songbirds, henceforth called songbirds) have the UVS type and that their main avian predators, raptors and the passeriform group Corvida, have the VS type. The raptors include the sparrowhawk (*Accipiter nisus*) and goshawk (*A. gentiles*) which forage primarily in forested environments and are specialised at capturing birds. When the prey is perching or in the nest, crypsis should be its main defence. The corvids hooded crow (*Corvus corone*), common raven (*C. corax*) and European jay (*Garrulus glandarius*) (Andrén 1992) are important nest predators on songbirds. There is a positive correlation between parental activity (such as chick provisioning) and nest predation in some birds (Martin *et al.* 2000; Eggers 2002), likely because nest predators can find nests by detecting parents provisioning their chicks (Alerstam and Högstedt 1981). If adult songbirds were cryptic to corvids, the risk of nest detection/predation would therefore be lowered.

As songbirds differ in vision from their predators, do they preferentially signal with colours that are conspicuous to members of their own species, but dull or cryptic to predators like hawks and corvids? To be useful indicators of quality, colour signals need to be controlled for honesty, either through predation or social interaction (Andersson 1994). Predation will select against conspicuous colouration in both males and females, while sexual selection will force males to provide a

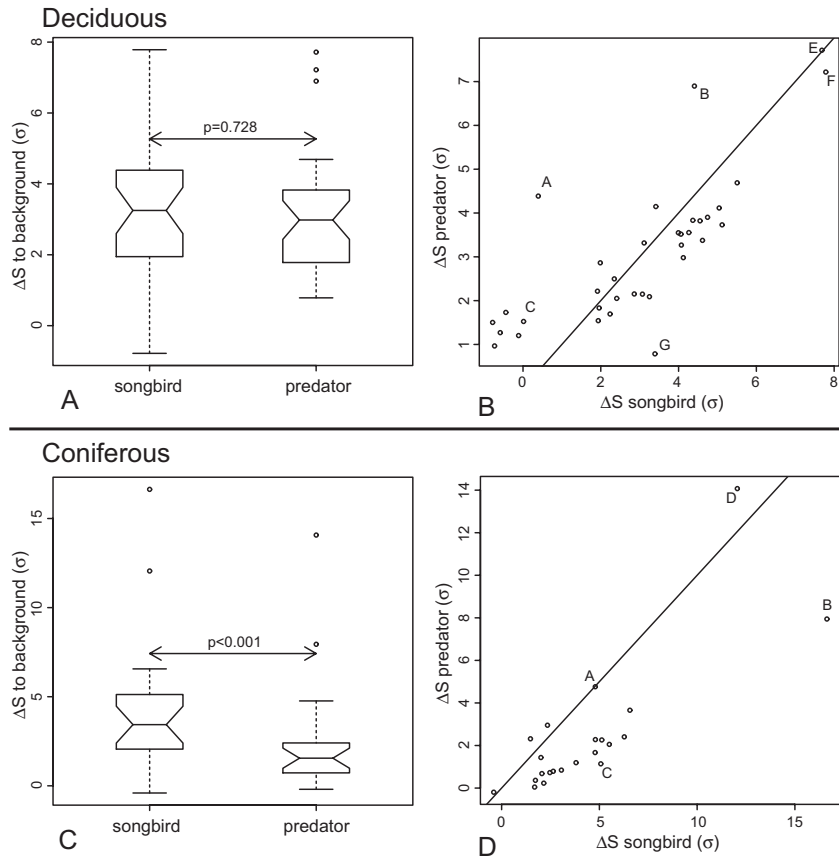
strong signal of quality. Females can only rely on their own vision for assessing a male's quality. Males are thus able to reduce their signal-colour conspicuousness to predators, as long as the attractiveness of the colouration to conspecific females does not decline. We therefore predicted that the colour signals of male songbirds will be perceived as more different from the background when viewed by a songbird (UVS) than by a predator (VS). This was tested by using plumage reflectance data from the head and chest of Swedish songbirds and compared to the backgrounds of deciduous and coniferous forests using natural light regimes.

We selected 18 species of songbirds that chose breed in Sweden and spend much of their time in the foliage of trees during the breeding season. For each species the forest type used during breeding-season was classified according to the dominating tree species as: 1) deciduous; 2) coniferous; 3) mixed deciduous and coniferous. Some species may expand their ranges to breed in non-preferred types of forest during periods of increasing population size. In these cases the species was classified as belonging to the habitat where it is present when the population is small.

The background against which the forest-living birds are to be detected is very heterogeneous, consisting of differently coloured leaves and branches exposed to ever-changing light conditions. To simulate this temporally and spatially heterogeneous background for the deciduous habitat we used averaged measurements of leaves from each of eight species of deciduous trees and twigs from four and averaged measurements from needles and twigs of Norway spruce and Scots pine for the coniferous habitat. We collected ambient light measurements in late mornings to noon during summer on the surface, in the middle of the foliage and close to the trunk, both on trees standing in direct sunlight and in the shade. We then calculated the signal from the cones as in paper I by multiplying the reflectance of a surface with a light spectrum and the cone sensitivities of a vision system. The resulting vector defines a position in receptor space. We constructed a background cloud in receptor space by using all combinations of surfaces and lights for that habitat to represent the variable colour environment of the songbirds. From the background cloud we calculated a distribution of background colour distances.

The position in colour space of each feather patch was calculated as if the bird was perching in the middle of the foliage of a sun-exposed tree, using the averaged light from the mid foliage measurements. We calculated the colour distance ( $\Delta S$ , Vorobyev *et al.* 1998) to all background colours and compared this distribution to the background distribution.

We repeated this procedure with the cone sensitivities from blue tit, *Parus caeruleus*, (Hart *et al.* 2000b) and peafowl, *Pavo cristatus*, (Hart 2002), representing birds of the UVS and VS system respectively.

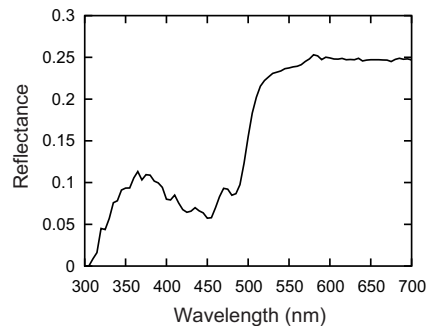


**Figure 3.** A and C) Distributions of the averaged colour distance to background for UVS and VS birds. Differences tested with Wilcoxon's paired sample test.

B and D) Colour distance measured in standard deviations of the background viewed with VS and UVS eyes. A: common redstart chest, B: robin chest, C: brambling chest, D: goldcrest crown, E: blue tit crown, F: bluethroat chest and, G: blue tit yellow chest. The solid line in the figure represents equal distances from the background for both vision systems. Points falling below the line are more different from the background to songbirds than to their predators.

The distributions of the averaged colour of birds' feathers in the coniferous habitat were significantly more cryptic to raptors than to other songbirds ( $P < 0.001$ )

**Figure 4.** Spectrogram of a blue tit chest (figure 3B point G). An example of a colour cryptic to predators while conspicuous to songbirds.



(See figure 3). In the deciduous forest the distances were not significantly different ( $P=0.728$ ) (figure 3).

Interestingly we also found that the relative visibility of some colours changed greatly between biotopes. These have been marked as A, B and C in figure 3, and are all perceived as being red by the human eye.

We found the colours of forehead, crown and chest in a number of Swedish songbirds to be significantly more conspicuous to other songbirds than to avian predators in coniferous but not in deciduous forests. The result from the coniferous forest shows that songbirds use colour signals that their vision system is better at detecting than is that of their predators. This ability may allow a private communication channel for displaying male quality. Although this possibility for secret signalling thus exists, few species seem to take full advantage of it. The yellow colour of the blue tit chest (figure 3:B point G, spectrogram in figure 4) is one example of a species fully exploiting the fact that its main predators have a different vision system. In coniferous forest the blue tit chest is highly conspicuous to other blue tits but at the same time cryptic to predators. The signal is probably more visible to songbirds because the position of the UV component corresponds to their vision system's UV-sensitivity while it is positioned too far into UV for the VS system.

Our results indicate that male songbirds tune their signals to the vision system of the intended receiver, while reducing colour contrast to the background in spectral parts to which their predators are most sensitive. It is important to acknowledge that crypsis is not absolute but relative. The songbird signals that we analysed are not invisible to their predators, only less conspicuous. Prey do not have to be totally invisible to predators to be cryptic, just cryptic enough to minimise predation (Endler 1991).

One possible explanation to the nonsignificant result in deciduous forest is that several of the colours that are more visible to raptors differ very little from the

background. Six patches deviate as much or less from the background as the average leaf do when viewed with a songbird's eyes, while having very low distance values even for raptors. These colours are five brown crowns and one rusty red chest (figure 3 point C) and could be considered cryptic or at least not to be colour signals.

Two of the data points in deciduous forest stand out as being much more visible to predators than to songbirds (figure 3 point A and B). One is the red chest of the common redstart, the other is the red chest of the robin. These two species, the robin and the common redstart, start to sing very early at dawn (Thomas *et al.* 2002). This could be an adaptation to displaying their signals at a time when predation risk is very low.

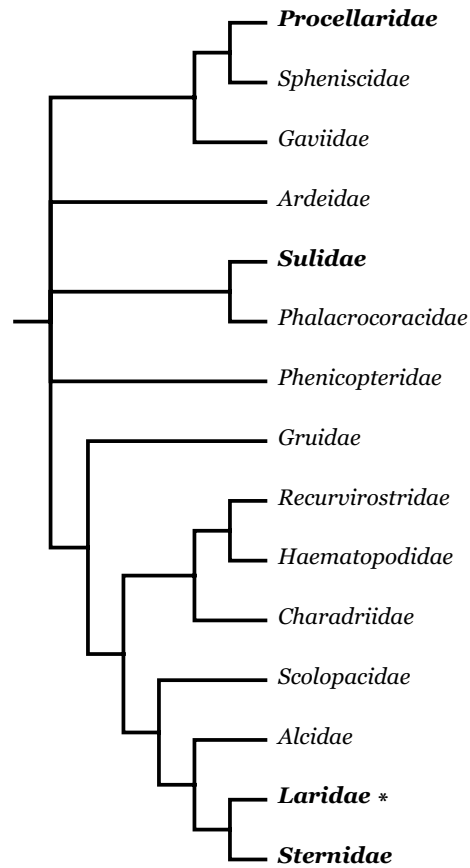
The red colours of the robin and the common redstart were however much less apparent to predators in the coniferous habitat (figure 3:D), raising the possibility of these species not having been assigned to the right forest type. However, we only know where to find the species today; the forest type where individual species evolved their colours is seldom known, because reliable palaeontological evidence is often missing. Given that the Quaternary period has seen large and rapid variation in the size and position of ecozones, it is possible that the red signals of the common redstart and the robin evolved primarily in coniferous forest and that the species have so recently spread to other forest habitats that the colour signals have not had time to adapt.

### **Paper V: UVS as a foraging tool for dip and plunge divers**

In paper II we found that some gulls of the genus *Laridae* were of the UVS vision type while all other species within this diverse order had the VS type. Arguably, the most plausible explanation would be that UVS has evolved in gulls as a foraging specialisation. We felt it necessary to further investigate the distribution of vision systems among seabirds and possible correlations with the foraging mode of the species.

We surveyed the vision system of four families of dip or plunge divers (Laridae, Sternidae, Procellariidae and Sulidae) and compared the results with both related and unrelated taxa of varying foraging methods. The four families of dip or plunge divers form three monophyletic groups (figure 5), each of which has a sister group consisting of swimming piscivorous birds. In addition to providing a better resolution in vision system distribution among seabirds the phylogenetic relationship allowed for a pair wise comparison of vision specialisation in relation to foraging method. This approach might bring order to the entangled interspecies relationships in spectral sensitivity of piscivorous birds.





**Figure 5.** Phylogeny of seabirds within the order Ciconiiformes (Van Tuinen et al. 2001; Paton et al. 2003). Families of mainly dip or plunge divers are marked in bold. Laridae, the only family that is predisposed for UVS colour vision, is marked with an asterisk.

UV vision has been shown to play a part in fish communications (Carleton *et al.* 2000). Many of the markings on fish that reflect UV light are situated on parts of the body that are usually displayed in courtship behaviours, such as the face or the fins, suggesting a role of the UV patterns in social communication (Siebeck and Marshall 2001).

Light differ in physical properties depending on wavelength, causing the available spectrum of light in water to change with depth. Long wavelengths are absorbed more than intermediate wavelengths, and short wavelengths are scattered more than those in the middle of the spectrum (Lythgoe 1979). UV is assumed to be available down to 200 m in clear sea, but scattering will prevent light in these wavelengths from being effectively used at distances of more than 5 m (Losey *et*

*al.* 1999). In order to utilise reflected UV light for signalling purposes, a fish needs to be close to the intended receiver, as scattering otherwise would blur the signal. UV cues are therefore arguably of little use to underwater predators such as fish and diving birds. To avian predators foraging close to the surface, however, these signals could be of substantial value. The UV scattering between fish at shallow depths and the surface is minor and the scattering in air is negligible. Fish swimming close to the surface may thus expose their private UV signalling to dip and plunge diving birds.

The interspecific variation of enhanced long-wavelength and short-wavelength sensitivities in surface-feeding aquatic birds and what, if any, adaptive significance they have remains to be determined (Hart 2001a-b). As previous studies, devoted to studying the relative proportions of cone types, have yielded inconclusive results (Hart 2001a-b) we have concentrated on the distribution of SWS1 spectral sensitivities among the seabirds of the order Ciconiiformes, and placed the results in a phylogenetic context. If UVS is a foraging adaptation in birds, this derived trait should be more strongly associated with foraging tactic than phylogenetic relationship. We would therefore expect to find it in dip and plunge divers regardless of whether their close relatives with other feeding modes have the ancestral VS system.

We amplified 74 bp SWS1 opsin sequence using the same method as in paper II from common sandpiper (*Actitis hypoleucos*), (*Fulmarus glacialis*), common snipe (*Gallinago gallinago*), Hartlaub's ull (*Larus hartlaubii*), sooty gull (*Larus hemprichii*), black-headed gull (*Larus ridibundus*), northern gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), artic tern (*Sterna paradisaea*) and sandwich tern (*Sterna sandvicensis*). Our results confirm earlier results obtained by Ödeen and Håstad 2003, that among seabirds UVS is restricted to the monophyletic group of gulls. The gulls' closest relatives, the terns, which share feeding habits with gulls, did not have the UVS system. The closest relatives of the clade including the families Laridae, Sternidae and Alcidae are the waders (families Charadriidae, Haematopodidae, Recurvirostridae and Scolopacidae) (Paton *et al.* 2003). Three of the families were previously known to be VS (Ödeen and Håstad 2003) and the two species of Scolopacidae examined in the present study confirmed that this fourth family is of the VS type as well.

These results show that the differences in tuning of the SWS1 cone show a distinct phylogenetic pattern of distribution among the seabirds, as opposed to the complex interspecies differences in cone frequencies. Surprisingly, the highly specialised dip diving terns turned out to be VS and not UVS like their sister group, the gulls. For a perfect association between foraging method and vision system we would have expected to also find UVS in Sulidae and Procellariidae. Instead our

results suggest that tuning of colour vision among piscivorous birds is closely associated with phylogeny and not differences in foraging tactics.

There are different ways of optimising the ability to find prey through the water surface. Optimisation of the vision system for prey detection in dip or plunge diving birds is apparently achieved by different mechanisms in different taxa. Our results show that gulls are monomorphic for UVS and the only group within the order to have evolved this vision system. This result may help to gain a deeper understanding of the visual interactions that take place between socially signalling fish and their avian predators. To be able to further investigate this issue, more information on the retinal composition and ocular media in the piscivorous groups of birds is needed.

### **Conclusion**

All studies quantifying colour signals in non-human species suffer from difficulties of identifying the signals without resorting to anthropocentric criteria. The focus on UV as a separate communication channel that has imbued behavioural studies in recent years ignores the importance of differences in colour perception arising from tetrachromacy, differently positioned absorbance maxima of the cone pigments and the oil droplets. “UV-vision” is an anthropocentric characterisation of disparate visual sensitivities below 400 nm, and has nothing to do with avian biology. We have shown here that there is a possibility of a private communication channel in songbirds, not because of the absence or presence of UV-sensitivity but because songbirds and their predators have differently-tuned colour receptors. The results from this thesis emphasise the importance of taking the sensory system of the study organism into account when studying animal signalling. There may not be an obvious adaptive link between the reflectance of an animal and its ability to detect said reflectance, as indicated by paper III. Studies restricted to the reflective properties of bird plumage may indeed find a correlation with the quality of the studied individual, but not measure to what degree this information can be detected by various receivers. These results emphasize the importance to future ecological studies of taking the vision system of the study species into account. In this thesis we have provided another tool for that task.

## Acknowledgements

I have had a great time at Zootis and EBC and many people have contributed to that experience. First of all I want to thank Staffan for giving me this opportunity even though I apparently only talked about impractical things during the interview. Mats, for letting us go where our interest took us. If not, you would all have read 25 pages about dung beetles by now. You did read the theses summary before looking at the acknowledgements, didn't you? No, of course you didn't. Ingela and Marianne for saving my butt more than once. Having the organizing capabilities of a coati you made it possible for me to focus on what I found really important. Anders – If I could fake being interested in half the things you gets get enthusiastic about, you would still twice as hyperactive. It has really been a pleasure working with you. My other collaborators Måns (the other tall guy who badly needed a zap-a-grad-cap), Jonas (thanks for washing my desk, it was badly needed), Emma (there is no bird called flamongo) and Malin (I don't dare write anything after the "how's it going" e-mail). Graham and Lennart for being good mentors in the harsh world of international science. I have really enjoyed your company. Rolf. Martin really pitched in these last weeks. I'm really grateful for all your help. I also want to thank Annika, Gunilla and Magnus for helping us figure out what was wrong with our lab-work. I want to thank everyone that offered to help me in all kinds of ways the last couple of weeks. I hope I deserved it. Everybody in the spex group. The happy crowd, you know that I mean you. UJJK, RA, JO. The zoomorphology crowd, Lennart (again), Carina och Calle. Every student who faked an interest in whatever I was trying to teach. Lambi and Kleenex, Mountain dew, PhD comics and Pärsonsoda.

*To all those who suffered because of my absentmindedness*

Finacial support was provided by Zoologiska stiftelsen, Helge Ax:son-Johnsons Stiftelse and Anna Maria Lundins stipendiefond.

**Computer programs**

All programs written for this thesis are available under the GNU GPL from <http://www.ebc.uu.se/files/hastad/thesis.tgz>

**Errata**

Published paper II

p. 857 *Taeniopygia guttata* has the UVS vision system.

Fig. 1A Passerformes should read Passeriformes.

## References

- Alerstam, T., and G. Högstedt. 1981. Evolution of hole nesting in birds. *Ornis Scandinavica* 12:188-193.
- Andersson, M. B. 1994. *Sexual selection*. Princeton University Press, New Jersey.
- Andersson, S., and T. Amundsen. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond. B Biol. Sci.* 264:1587-1591.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* 73:794-804.
- Applebury, M. L., and P. A. Hargrave. 1986. Molecular biology of the visual pigments. *Vision Res.* 26:1881-1895.
- Banks, A. N. 2001. For your eyes only? The role of UV in mate choice. *Trends Ecol. Evol.* 16:473-474.
- Bennett, A. T. D., and I. C. Cuthill. 1994. Ultraviolet vision in birds: What is its function? *Vision Res.* 34:1471-1478.
- Bennett, A. T. D., I. C. Cuthill, and K. J. Norris. 1994. Sexual selection and the mismeasure of color. *American Naturalist* 144:848-860.
- 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. U. S. A.* 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 (London)* 380:433-435.
- Bowmaker, J. K. 1998. Evolution of colour vision in vertebrates. *Eye* 12:541-547.
- 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.
- Brodsky, L. M. 1988. Ornament size influences mating success in male Rock Ptarmigan. *Animal Behaviour* 36:662-667.
- Burley, N., G. Krantzberg, and P. Radman. 1982. Influence of color-banding on the conspecific preferences of Zebra Finches (*Poephila guttata*). *Animal Behaviour* 30:444-455.

- Campenhausen, M. v., and K. Kirschfeld. 1998. Spectral sensitivity of the accessory optic system of the pigeon. *J. Comp. Physiol. [A]* 183:1-6.
- Carleton, K. T., F. I. Hárosi, and T. D. Kocher. 2000. Visual pigments of African cichlid fishes: evidence for ultraviolet vision from microspectrophotometry and DNA sequences. *Vision Res.* 40:879-890.
- Church, S. C., A. T. D. Bennett, I. C. Cuthill, S. Hunt, N. S. Hart, and J. C. Partridge. 1998a. Does lepidopteran larval crypsis extend into the ultraviolet? *Naturwissenschaften* 85:189-192.
- Church, S. C., A. T. D. Bennett, I. C. Cuthill, and J. C. Partridge. 1998b. Ultraviolet cues affect the foraging behaviour of blue tits. *Proc. R. Soc. Lond. B Biol. Sci.* 265:1509-1514.
- Cuthill, I. C., S. Hunt, C. Cleary, and C. Clark. 1997. Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). *Proc. R. Soc. Lond. B Biol. Sci.* 264:1093-1099.
- Cuthill, I. C., J. C. Partridge, A. T. D. Bennett, S. C. Church, N. S. Hart, and S. Hunt. 2000. Ultraviolet Vision in Birds. *Advances in the Study of Behavior* 29:159-214.
- Darwin, C. 1859. *On the origin of species*. John Murray, London.
- 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.
- Eggers, S. 2002. Behaviour and life-history responses to chick provisioning under risk of nest predation, Ph. D. Thesis. Uppsala University, Uppsala.
- Endler, J. A. 1991. Interactions between predators and prey. in Krebs, J.R. and Davies, N.B., eds. *Behavioural ecology: an evolutionary approach*. 3rd ed. Blackwell Science.
- Endler, J. A., and A. L. Basolo. 1998. Sensory ecology, receiver biases and sexual selection. *Trends. Ecol. Evol.* 13:415-420.
- Fleishman, L. J., E. R. Loew, and M. Leal. 1993. Ultraviolet vision in lizards. *Nature* 365:397
- Goldsmith, T. H. 1990. Optimization, constraint, and history in the evolution of eyes. *Q. Rev. Biol.* 65:281-322.
- Guilford, T., and P. H. Harvey. 1998. The purple patch. *Nature* 392:867-869.
- Hart, N. S. 2001a. Variations in cone photoreceptor abundance and the visual ecology of birds. *J. Comp. Physiol. [A]* 187:685-6697.
- Hart, N. S. 2001b. The Visual Ecology of Avian Photoreceptors. *Progress in Retinal and Eye Research* 20:675-703.
- Hart, N. S. 2002. Vision in the peafowl (Aves: *Pavo cristatus*). *J. Exp. Biol.* 205:3925-3935.
- 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.
- Hart, N. S., J. C. Partridge, and I. C. Cuthill. 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.
- Hausmann, F., K. E. Arnold, N. J. Marshall, and I. P. F. Owens. 2003. Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. B Biol. Sci.* 270:61-67.
- Holder, K., and R. Montgomerie. 1993. Red colour bands do not improve the mating success of male Rock Ptarmigan. *Ornis Scandinavica* 24:53-58.
- 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. Bennett, and R. Griffiths. 1999. Preferences for ultraviolet partners in the blue tit. *Animal Behaviour* 58:809-815.
- 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, J. P. Swaddle, and A. T. D. Bennett. 1997. Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*. *Animal Behaviour* 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.
- Jacobs, G. H. 1998. Photopigments and seeing-Lessons from natural experiments: The Proctor Lecture. *IOVS* 39:2205-2216.
- 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.
- Jennions, M. D. 1998. The effect of leg band symmetry on female-male association in Zebra Finches. *Animal Behaviour* 55:61-67.
- 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. *Journal of Fish Biology* 54:921-943.
- Lythgoe, J. N. 1979. *The ecology of vision*. Oxford University Press, Oxford.



- 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.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. Lond. B Biol. Sci.* 267:2287-2293.
- Metz, K. J., and P. J. Weatherhead. 1993. An experimental test of the contrasting-color hypothesis of redband effects in Red-winged Blackbirds. *Condor* 95:395-400.
- Osorio, D., M. Vorobyev, and C. D. Jones. 1999. Colour vision of domestic chicks. *J. Exp. Biol.* 202:2951-2959.
- 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.
- Paton, T. A., A. J. Baker, J. G. Groth, and G. F. Barrowclough. 2003. RAG-1 sequences resolve phylogenetic relationships within Charadriiform birds. *Molecular Phylogenetics and Evolution* 29:268-278.
- Ratcliffe, L. M., and P. T. Boag. 1987. Effects of color bands on male competition and sexual attractiveness in Zebra Finches (*Poephila guttata*). *Canadian Journal of Zoology* 65:333-338.
- Shi, Y., and S. Yokoyama. 2003. Molecular analysis of the evolutionary significance of ultraviolet vision in vertebrates. *Proc. Natl. Acad. Sci. U. S. A.* 100:8308-8313.
- Sibley, C. G., and J. E. Ahlquist. 1990. *Phylogeny and classifications of birds: a study in molecular evolution*. Yale Univ. Press., New Haven.
- Siebeck, U. E., and N. J. Marshall. 2001. Ocular media transmission of coral reef fish — can coral reef fish see ultraviolet light? *Vision Res.* 41:133-149.
- 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.
- Thomas, R. J. *et al.*. 2002. Eye size in birds and the timing of song at dawn. *Proc. R. Soc. Lond. B Biol. Sci.* 269:831-837.
- Tucker, V. A., A. E. Tucker, K. Akers, and J. H. Enderson. 2000. Curved flight paths and sideways vision in peregrine falcons (*Falco peregrinus*). *J. Exp. Biol.* 203:3755-3763.
- Van Tuinen, M., D. B. Butvill, J. A. W. Kirsch, and S. B. Hedges. 2001. Conver-

- gence and divergence in the evolution of aquatic birds. *Proc. R. Soc. Lond. B Biol. Sci.* 268:1345-1350.
- Viitala, J., E. Korpimäki, P. Palokangas, and M. Koivula. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* 373:425-427.
- Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B Biol. Sci.* 265:351-358.
- Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. [A]* 183:621-633.
- Waldvogel, J. A. 1990. A bird's eye view. *American Scientist* 78:342-353.
- 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.
- 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. U. S. A.* 97:7366-7371.
- Zann, R. 1994. Effects of band color on survivorship, body condition and reproductive effort of free-living Australian Zebra Finches. *The Auk* 111:131-142.
- Zhang, J. 2003. Paleomolecular biology unravels the evolutionary mystery of vertebrate UV vision. *Proc. Natl. Acad. Sci. U. S. A.* 100:8045-8047.
- Ödeen, A., and O. Håstad. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* 20:855-861.

# Acta Universitatis Upsaliensis

*Comprehensive Summaries of Uppsala Dissertations  
from the Faculty of Science and Technology*

Editor: The Dean of the Faculty of Science and Technology

---

A doctoral dissertation from the Faculty of Science and Technology, Uppsala University, is usually a summary of a number of papers. A few copies of the complete dissertation are kept at major Swedish research libraries, while the summary alone is distributed internationally through the series *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology*. (Prior to October, 1993, the series was published under the title “Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science”.)

## Distribution:

Uppsala University Library  
Box 510, SE-751 20 Uppsala, Sweden  
[www.uu.se](http://www.uu.se), [acta@ub.uu.se](mailto:acta@ub.uu.se)

ISSN 1104-232X  
ISBN91-554-5824-6