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Ultraviolet sexual dimorphism and assortative mating in blue tits

Staffan Andersson*, Jonas Örnborg and Malte Andersson

Department of Zoology, University of Göteborg, Medicinaregatan 18, S-413 90 Göteborg, Sweden

In spite of strong evidence for viability-based sexual selection and sex ratio adjustments, the blue tit, *Parus caeruleus*, is regarded as nearly sexually monomorphic and no epigamic signals have been found. The plumage coloration has not, however, been studied in relation to bird vision, which extends to the UV-A waveband (320–400 nm). Using molecular sex determination and UV/VIS spectrometry, we report here that blue tits are sexually dichromatic in UV/blue spectral purity (chroma) of the brilliant crown patch. It is displayed in courtship by horizontal posturing and erected nape feathers. A previously undescribed sexual dimorphism in crown size (controlling for body size) further supports its role as an epigamic ornament. Against 'grey-brown' leaf litter and bark during pair formation in early spring, but also against green vegetation, UV contributes strongly to conspicuousness and sexual dimorphism. This should be further enhanced by the UV/bluish early morning skylight ('woodland shade') in which blue tits display. Among 18 breeding pairs, there was strong assortative mating with respect to UV chroma, but not size, of the crown ornament. We conclude that blue tits are markedly sex dimorphic in their own visual world, and that UV/violet coloration probably plays a role in blue tit mate acquisition.

Keywords: UV vision; spectral reflectance; colour signalling; sexual dichromatism; colour contrast; *Parus caeruleus*

1. INTRODUCTION

The blue tit, *Parus caeruleus*, is the only regularly polygynous parid (Kempenaers 1995). Females acquire extra-pair fertilizations from males with better survival than their social partner (Kempenaers *et al*. 1992), and even adjust offspring sex ratio towards sons when mated to such high-quality males (Svensson & Nilsson 1996). This suggests viability-based sexual selection (Andersson 1994), but a question left unanswered is how females judge the quality of their mate (Kempenaers *et al*. 1992).

Recently, a potential acoustic signal was suggested from longer song strophes of extra-pair fathers, but in visual traits their leg length differed from the within-pair fathers by only 0.4 mm (Kempenaers *et al*. 1997). This slight difference in tarsus length seems unlikely to be the basis for discrimination between prospective mates. The striking blue and yellow plumage suggests that visual ornamentation may be more likely. However, although male blue tits in the hand often appear 'brighter blue' than females (Perrins 1979), standard literature describes the plumage as closely similar between the sexes (Cramp & Perrins 1993) and considers it to be of only secondary epigamic value (Stokes 1960). The main problem with these conclusions is, however, that they are based on the UV-blind and yellow-biased human eye.

Perception of UV-A (320–400 nm) is a common feature of birds, including *Parus* species and other passerines (Bennett & Cuthill 1994), and is achieved through a UV cone mechanism absorbing maximally at 360–380 nm (Chen & Goldsmith 1986; Maier 1994; Bowmaker *et al*. 1997). This cone seems to be present also in the blue tit retina (N. Hart, unpublished observations). A lower spectral limit at 320 nm of the avian visual range is indicated by lens transmission that cuts off sharply in this region (Goldsmith 1990; Maier 1994). Although the adaptive function of avian UV vision has long-remained obscure (Bennett & Cuthill 1994; Goldsmith 1994), there is now accumulating evidence for colour-based mate choice in the UV (Bennett *et al*. 1996; Andersson & Amundsen 1997; Bennett *et al*. 1997).

By using UV/VIS spectrometry over the 320–700 nm spectral window, we explore the possible sexual dimorphism, signal quality and social function of the brilliant blue crown patch in blue tits. This plumage trait is displayed in agonistic and sexual interactions by horizontal 'head-forward' postures and erected nape feathers (Stokes 1960). Therefore, the blue tit crown might also be used for signalling in the UV part of the spectrum. In a breeding population of blue tits in south-western Sweden, we find strong evidence to support this.

2. METHODS

Fieldwork was done in April to June 1995 in a deciduous forest with nestboxes in Gunnebo, 5 km SE of Göteborg, Sweden. Birds were captured with song playback in mistnets or nestbox traps, and transported to a nearby (< 5 min) cottage for morphometric and spectrometric measurements and preliminary sexing and aging (1 or 2+ years old, see Svensson 1992). All birds were banded with unique colour combinations, excluding yellow and blue hues matching the plumage. To confirm initial assignments

*Author for correspondence (s.andersson@zool.gu.se).

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to pairs, nestboxes were visited repeatedly during incubation to identify the individuals.

(a) *Sex determination*

As morphological sexing criteria (mainly wing length; Svensson 1992) are not fully reliable, a small (50 µl) blood sample was also drawn from the carpal vein for molecular sex identification according to Ellegren (1996). DNA was extracted with Qiagen blood amp kit (Qiagen Inc., Hilden, Germany). With minor deviations from Ellegren's (1996) polymerase chain reaction protocol, we used his primers 2945F, cfR and 3224R to amplify a 630 b.p. fragment of the autosomal or Z-linked (i.e. both sexes) avian CHD gene, along with a 210 b.p. fragment from a W-linked copy of the same gene (i.e. only in females). The products were visualized and size-determined (Pharmacia 100 b.p. ladder) on agarose gels as one strong band for all individuals, and a weaker additional band in females.

(b) *Reflectance spectrometry*

Reflected radiance from the central crown (and other plumage regions; Andersson & Örnborg 1998) was measured with a S1000 diode-array spectrometer (Ocean Optics Inc., Dunedin, USA), and a trifurcated fibre optic probe with six 200 µm illuminating fibres surrounding a 200 µm measuring fibre that accepted light from a 28° solid angle. The probe was mounted inside a matt black plastic tube (inner diameter 7 mm) with the end cut to 45°. The tube end was held lightly against the crown plumage and rotated perpendicularly to the length axis of the head, providing 45°/45° illumination and recording from an oval 3 mm × 3.8 mm measuring spot. One illumination fibre was connected to an Ocean Optics LS-1 tungsten-halogen lamp, and the other to an UV-1A deuterium lamp (A.I.S. Inc., New Jersey, USA). Together these light sources provided light from 280 to 730 nm, sufficient for our target range of 320–700 nm. Using the C-spec software (Ancal Inc., Las Vegas, USA), spectral reflectance was measured in relation to a Spectralon (LabSphere Inc., North Sutton, USA) white standard, an almost perfect diffuser (98–99% reflectance from 300 to 750 nm) measured before each scan. The reflectance from each individual was averaged from five scans, removing the probe between each.

(c) *Objective colorimetrics*

Colour analyses, in terms of intensity (brightness) and spectral shape (hue, chroma), were restricted to the 320–700 nm spectral window, as suggested by the lens transmission cut-off at 320 nm in a congener, *Parus bicolor* (Goldsmith 1990), and another passerine *Leiothrix lutea* (Maier 1994). Lacking information on blue tit colour psychophysics, we objectively computed brightness as total reflectance (R_T), and 'chroma' (spectral purity) by dividing the reflectance of narrower spectral segments with R_T (see Endler 1990). We focus here on UV chroma, R_{UV}/R_T ($=R_{320–400}/R_{320–700}$), not because this is a particularly likely representation of a blue tit colour channel, but because the previous neglect of UV in avian colour communication (Bennett *et al*. 1994) makes the specific contribution of this waveband interesting to assess. Judging from cone absorbances from a variety of birds (Bowmaker *et al*. 1997), a 320–420 nm UV/violet colour channel might appear more likely. We calculated also a UV/violet chroma based on this segment, which changed numerical values slightly but not any conclusions. As an estimate of 'hue' (spectral location) we avoided colour channel assumptions altogether by computing the spectral positions of maximum reflectance ($\lambda(R_{max})$), and the maximum negative slope (λ_S). Variations in these measures were found to correlate strongly ($r_s > 0.9$) with the human CIELAB hue colorimetric (S. Andersson, unpublished data), and should be a reasonable predictors of hue variation in any colour opponency system.

The conspicuousness of a colour signal depends critically on the adapting background against which it is seen. We estimated contrast objectively by a signal (R_s) versus background (R_b) reflectance ratio ($(R_s - R_b)/R_b$)) (see Endler & Thery 1996). For background spectra we measured the reflectances from various natural surfaces in the blue tit habitat, but we simplify here to two general surface reflectance types in terrestrial, vegetated habitats (Osorio & Bossomaier 1992). The first general background type, 'grey-brown', includes soil, bark and dead plants. These are characterized by low UV and then rather uniformly increasing reflectance from 400 to 700 nm, gently for grey and dark brown and steeper for browns and reddish browns (figure 1*a*; see also Wyszecki & Stiles (1982), pp. 60–63). Because blue tit pair formation occurs before leaf emergence in Scandinavia (Cramp & Perrins 1993), and as the crown is displayed upwards (Stokes 1960), it is viewed against the forest floor which at this time of year consists mainly of dead leaf litter, grass and herbs. Bark and bare soil further contribute to the 'grey-brown' background, whereas 'leaf-green' colours (see below) are less common (except in habitats with much mosses or other evergreen plants). We use here the reflectance from dead, dry oak leaves (figure 1*a*) to estimate the contrast against 'grey-brown' backgrounds.

From growing herbs and emerging leaves (early May on the west coast of Swedish) the 'grey-browns' gradually give way to the 'leaf-green' spectrum common to most land plants (Osorio & Bossomaier 1992). This has a typical peak (caused by chlorophyll) at about 550 nm, decreasing below 500 nm and into the UV (figure 1*a*). Spectral shape variation is small and mainly in the long wavelength end of the spectrum (Lythgoe 1979; Osorio & Bossomaier 1992). For the 'leaf-green' background type, we use here the average leaf reflectance from three common tree species in the blue tit habitat: maple (*Acer platanifolius*), birch (*Betula pubescens*) and hazel (*Corylus avellana*) (figure 1*a*).

3. RESULTS

(a) *Sexual dimorphism*

Forty-one blue tits (14 subadult and nine adult females, 12 subadult and six adult males) were measured (in total, 18 breeding pairs and five additional females). Molecular sexing confirmed our morphometric sexing in all but one of the breeding pairs. In addition to reflectance variation within individuals (i.e. measuring error), there was highly significant variation between individuals, also within age/sex classes (e.g. adult females, reflectance at 50 nm intervals from 350 to 700 nm; nested two-factor ANOVAs: between, $F_{8,27}=5.1–9.9$, $p<0.0001$; within, $F_{9,27}=2.2–5.7$, $p=0.001–0.05$). The following results are based on the individual mean reflectances.

Significant sexual dimorphism, but no age effects, was found in crown reflectance shape (colour), showing a steeper and more short-wave peak in males (figure 1*a*). Expressed in the objective colorimetrics (see §2), males had stronger chroma (computed for UV as well as UV/violet) and a more short-wave spectral location or 'hue' (table 1). Conversely, in overall brightness, R_T, there was no significant sexual dimorphism but there was a significant age effect (table 1), adults being 21% brighter than

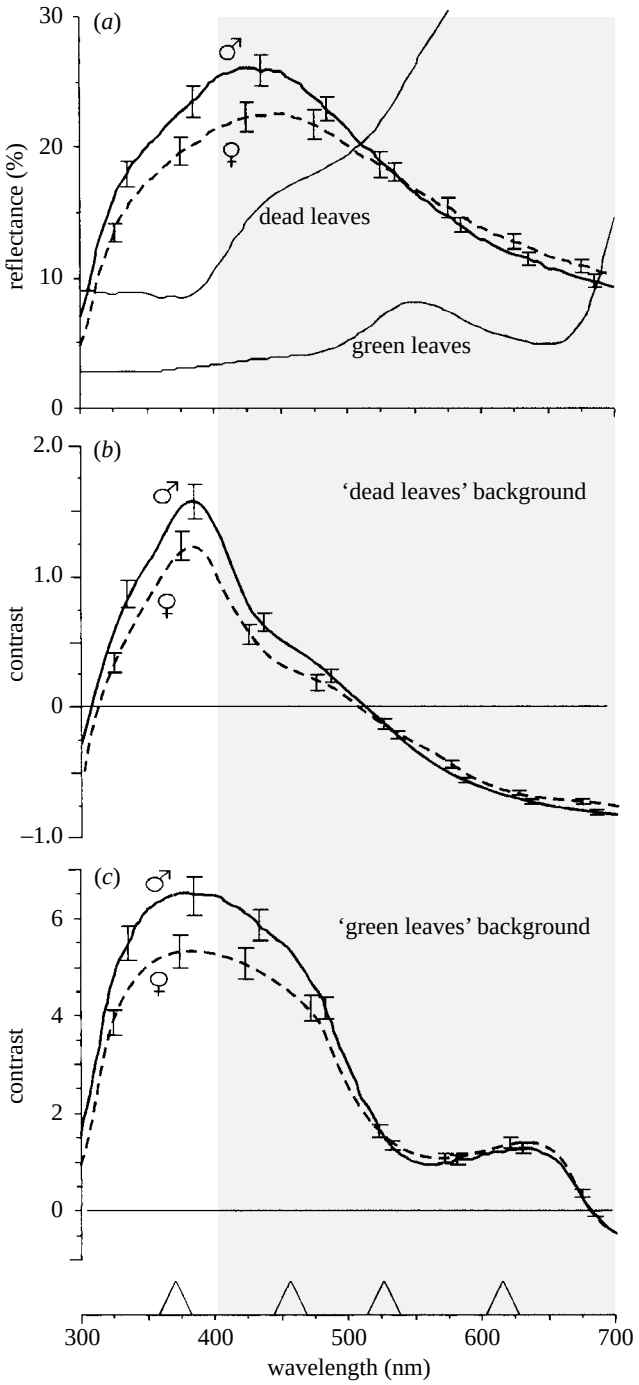

Figure 1. The blue tit crown signal spectra (±s.e.) in males ($n=18$, solid lines) and females ($n=23$, dashed lines). (*a*) Spectral reflectance of the crown plumage, together with natural surface reflectances representing the two major background colours: 'grey-brown' (dead, dry oak leaf) and 'leaf-green' (green leaves from three tree species; see text). Dead leaf reflectance above 550 nm (not shown) continues uniformly to about 50% reflectance at 700 nm. (*b*) Spectral contrast (signal versus background reflectance ratio; see text) of male and female crown colour against a 'dead leaves' background, typical of early spring habitat (before leaf emergence). (*c*) Spectral contrast against a 'green leaves' background. Cone symbols on bottom axis indicate the absorbance maxima of passerine cone receptor mechanisms; see text. Shaded area denotes the human-visible 400–700 nm spectral range.

subadults (R_T, 1 year old, mean±s.d.=62.5±12.4, $n=26$; 2+ years old, 75.7±13.0, $n=15$).

Figure 1 also shows the male and female spectral contrast functions against a 'grey-brown' background of dead leaves (figure 1*b*) and a 'leaf-green' background (figure 1*c*). Against both, but especially against the 'dead leaves' background typical of early spring, contrast and sexual dimorphism are maximized around 370 nm. Interestingly, this coincides with the receptor λ_{max} at 360–380 nm found by various methods in several passerines, including *Parus atricapillus* (Chen & Goldsmith 1986; Maier 1994; Bowmaker *et al*. 1997). The position of this receptor, and of the three other effective (cone + oil droplet) receptor λ_{max} that have been investigated in the passerine *Leiothrix lutea* (Maier 1994), is indicated in figure 1. According to Bowmaker *et al*. (1997), this tetrachromatic set of cone mechanisms seems consistent for Passeriformes (whereas some other taxa have a UV/violet cone just above 400 nm as their fourth and most shortwave receptor).

To sum up, the crown signal spectrum, its contrast against natural background surfaces and current knowledge of passerine vision, suggest that blue tits are sexually dimorphic in their own cognition, and primarily so in the UV-A waveband. Nearly invisible to the human observer (except in the hand for experienced ringers; Perrins 1979), this is to our knowledge the first (but probably not the last) example of 'hidden' sexual dimorphism in birds.

Moreover, a sexual size dimorphism of the crown further suggests a signalling, perhaps epigamic, function. The crown plumage, measured from the bill base to the tip of the erectible nape feathers, was 1.5 mm (8%) longer in males (table 1). This sex dimorphism was significant also when controlling for the allometric relation with body size (in table 1, effects were tested on the residuals from a significant linear regression of crown size on tarsus length).

(b) *Assortative mating based on UV chroma*

Among the 18 breeding pairs, there was significant assortative mating with respect to UV chroma (C_{UV}) of the crown (figure 2, $r_s=0.70$, $n=18$, $p=0.0041$), but not for any other colorimetric or morphometric trait. As discussed above (§2), UV/violet chroma (i.e. relative reflectance in the 320–420 nm segment) might be more relevant to blue tit colour perception. The assortative mating correlation was similar for this measure ($r_s=0.70$, $n=18$, $p=0.0038$). As neither spectral location ('hue', $\lambda(R_{max})$ or λ_S), nor brightness (R_T) was correlated between the sexes, spectral purity (chroma), appears to be the important signal dimension. To explore a chroma measure less confounded by hue, we also computed the ratio of maximum to minimum reflectance ($\lambda(R_{max})/\lambda(R_{min})$), for which the assortative mating correlation became still stronger ($r_s=0.77$, $n=18$, $p=0.0013$).

Age-assortative mating was not a confounding effect in this result, as evident from the non-significant age effect on chroma (table 1) and from the age composition of the pairs (in figure 2, filled top triangles indicate old males, and filled bottom triangles old females).

Table 1. *Colour and size of the crown ornament in male and female blue tits*

(Male and female mean estimates and degree of sexual dimorphism. Sex and age effects tested with two-factor ANOVA. All interaction terms (sex*age) non-significant ($p > 0.20$), and residuals checked for homoscedastic variance.)

		females (n=23) mean ± s.d.	males (n=18) mean ± s.d.	sexual dimorphism	two-factor ANOVA sex $F_{1,37}$	sex p	age $F_{1,37}$	age p
'brightness' (spectral intensity)								
total	$R_T[R_{320–700}]$	65.5 ± 15.2	69.7 ± 12.4	6%	0.6	0.44	9.6	0.004
UV	R_{UV} $[R_{320–400}]$	14.0 ± 3.5	16.4 ± 3.6	17%	4.5	0.041	10.1	0.003
'hue' (spectral location)								
peak	$\lambda(R_{max})$	443 ± 11	430 ± 13	−13 nm	14.0	0.001	1.8	0.19
slope	λ_s	540 ± 42	500 ± 22	−40 nm	12.1	0.001	3.3	0.077
'chroma' (spectral purity)								
UV	$C_{UV}[R_{320–400}/R_{320–700}]$	0.214 ± 0.016	0.234 ± 0.021	9%	11.4	0.002	2.3	0.14
UV/violet	$C_{UV/V}[R_{320–420}/R_{320–700}]$	0.288 ± 0.02	0.315 ± 0.025	9%	15.0	0.0004	2.3	0.14
size[a]								
length of erectible nape feathers (mm)		18.8 ± 1.0	20.3 ± 1.0	8%	11.2	0.0019	1.0	0.33

[a] Effects on crown size were tested on residuals from a linear regression of crown size versus tarsus length; $F_{1,39}$=11.4, p=0.002.

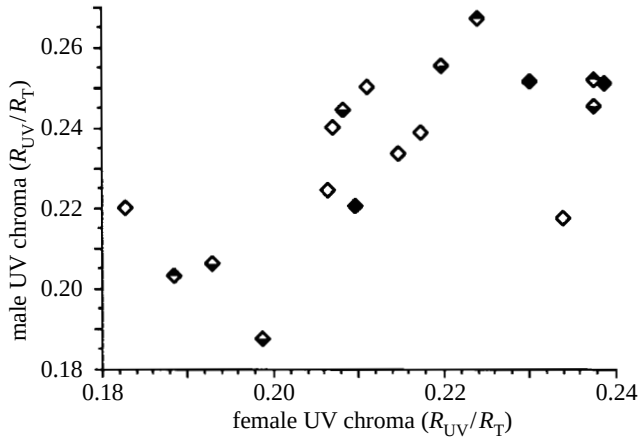

Figure 2. Male UV chroma ($R_{320–400}/R_{320–700}$) plotted against female UV chroma for 18 breeding blue tit pairs, showing assortative mating with respect to UV coloration (r_s=0.70, n=18, p=0.0041). Within symbols (i.e. pairs), filled upper triangle denote adult (2+ years) male, filled lower triangle adult female, and open triangles subadults (1 year).

4. DISCUSSION

(a) *UV vision and sexual dimorphism*

Although hardly perceivable in the field (except when directly compared in the hand) to the UV-blind and yellow-biased primates that write ornithological handbooks (see Cramp & Perrins 1993), blue tits appear to be markedly sex dimorphic in their own visual world. This applies also to other plumage regions (Hunt *et al.*, this issue; Andersson & Örnborg 1998). In principle, a UV-blind blue tit would perceive the crown dimorphism above 400 nm, like we do (barely) or better if they have a more shortwave-shifted sensitivity. However, all available evidence on avian UV vision, including UV sensitivity and lens transparency in other *Parus* species (Chen & Goldsmith 1986) as well as a UV cone in blue tits (N. Hart, unpublished data), suggests that UV is an integral part of the blue tit visual system. Indirectly, this is also supported by the strong contribution of UV to spectral contrast against the background (figure 1*b*,*c*), and by the strong assortative mating with respect to UV chroma (figure 2).

As regards colour vision, the significant dimorphism in 'UV brightness' but not in 'total brightness', and in the objective 'hue' and 'chroma' variables (table 1), suggest that spectral shape (i.e. colour) is an important dimension of the dimorphism. However, whether this involves true UV colour cognition (i.e. a hue sensation) or some other form of wavelength-specific perception, is beyond the scope of this study.

(b) *Assortative mating and sexual selection*

Based on better survival of polygynous males (compared to monogamous) and primary females (compared to secondary and monogamous), "strong assortative mating of high quality birds" has previously been suggested in blue tits (Kempenaers 1994). The assortative mating with respect to crown UV chroma implies that this ornament (or correlated aspects of plumage coloration not measured here) functions as a signal in contest competition over territories and mates, in mutual mate choice, or both (Andersson 1994). At this stage we cannot discriminate between these alternatives, but the conspicuous display of the crown patch in the male courtship dance (Stokes 1960) suggests that it plays some role in female choice. The sexual size dimorphism of the erectible crown feathers (controlling for body size) also suggests a role in sex-related signalling, with concerted signal amplification by size, colour and behaviour (Lorentz 1941; Hasson 1990).

These result are interesting in relation to earlier work on blue tit ecology and behaviour, a fascinating scenario of 'good genes' sexual selection (Kempenaers *et al.* 1992; Kempenaers 1994, 1995) where the remaining puzzle has been the signals used in mate assessment. The present objective colour quantification (Endler 1990), including UV, may thus reveal a previously overlooked cue that females use in seeking extra-pair copulations (Kempenaers *et al.* 1992) and in adjusting offspring sex ratios (Svensson

& Nilsson 1996). This possibility can be tested in future work on blue tit mate choice and sex ratio tactics, as well as in other species.

(c) *Signal production*

The mechanism responsible for the blue crown and dorsal coloration in blue tits is most likely the barb-borne 'spongy structure' that produce most non-iridescent shortwave feather hues (Dyck 1976), including UV (Finger 1995; Andersson 1998). Very little is known about the costs and constraints of such colours, and thus of their potential as for example honest signals of quality, but see Andersson (1998) for a discussion of this issue.

(d) *Blue tit light ecology*

The two generalized 'grey-brown' (leaf litter) and 'leaf-green' background spectra are much simplified representations of the three-dimensional forest mosaic in which blue tits display. However, because we are focusing on chromatic signalling (not pattern or movements) and on the relative spectral distribution of colour contrast, these main signalling backgrounds should capture much of the chromatic 'signal-to-noise ratio' (Endler 1992) and how it differs between the sexes. The strong contribution of UV to the computed contrast functions, especially against the 'dead leaves' background typical of early spring when most sexual and aggressive displays occur, suggests an important signal function of the UV reflectance. This contrast peak coincides with the 370 nm absorbance maximum of *Parus* and other passerine UV receptors (Chen & Goldsmith 1986; Maier 1994; Bowmaker *et al*. 1997).

In addition to signal and background reflectances and the receiver's visual system, variation in ambient light is an essential third factor in colour communication (Endler 1990). Blue tits display in deciduous forest subcanopy, mainly before leaf emergence and with an early morning activity peak (Cramp & Perrins 1993). Low sun angle, shade from topography, trunks and branches, but exposure to skylight, implies (if the sky is clear) a UV/shortwave-biased light ('woodland shade'; Endler 1993). Crown signal matching to this ambient spectrum should maximize conspicuousness (Endler & Thery 1996). Conversely, later in the day, yellowish sunlight from above ('small gaps' or 'large gaps'; Endler 1993) might decrease contrast by a poorer match with the UV/violet dorsal colours, and relatively more long wavelengths that match the 'dead leaves' background.

The light environment that might reduce the crown signal is 'forest shade' (Endler 1993) where most light is filtered through leaves, producing a greenish, UV-poor light similar to the 'leaf-green' reflectance spectrum (figure 1*a*). After leaf emergence (and after the main signalling period), this is probably a common light regime for the foraging and chick-feeding blue tits, which thereby might be less conspicuous to visually hunting predators such as sparrowhawks. Further studies of blue tit light ecology will address these possibilities.

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APPENDIX 1

When receiving our proofs, we were given the opportunity to read a paper by Hunt *et al*. (this issue) on a study of British blue tits that reaches similar conclusions. As in our analyses of other parts of blue tit plumage (Andersson & Örnborg 1998), Hunt *et al*. also find reflectance dimorphisms in other dorsal plumage regions than the blue crown ('crest') plumage. Although Hunt *et al*. do not take into account age (which has significant effects in our data), the described sex dimorphisms in spectral shape seem similar to our results when we also pool ages.

However, whereas a UV peak in the yellow chest spectra coincides well between the studies (except for an age effect not investigated by Hunt *et al*.), the crest (i.e. crown) spectra in Hunt *et al*. peak at 352 nm, 80 nm below the location at 430–443 nm in our population (table 1). This is a considerable peak ('hue') shift between the studies. As Hunt *et al*. discuss, this might indicate a real geographical difference in crown coloration, or a difference in measuring angles. Both studies measured reflectance at 45° against the feather plane, but in Hunt *et al*. this was 90° to illumination, with both parallel to the feather direction (rachis), in contrast to the unidirectional illumination/recording rotated perpendicularly against the feather direction in our study.

The optical mechanism responsible for 'non-iridescent structural' feather colours is not fully understood (Dyck 1976; Finger 1995), but it is conceivable that both spectral composition and intensity vary somewhat with illumination and viewing angles (although of course not nearly as dramatically as in classic thin-film interference in, for instance, hummingbirds). This is also suggested by the stronger peak intensity in our crown spectra (*ca*. 25% compared to 10% in Hunt *et al*., using the same white standard), whereas the chest reflectance spectra are of similar intensity in both studies.

Finally, it should be noted that in our estimates of spectral contrast against natural backgrounds (figure 1), the relative contribution of UV to conspicuousness would greatly increase with any shifts of the signal reflectance spectrum towards those reported by Hunt *et al*. Clearly, colour communication in blue tits deserves further study.

REFERENCES

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Andersson, S. 1998 Morphology of UV and violet reflectance in a whistling-thrush: implications for the study of structural colour signaling in birds. *J. Avian Biol.* (In the press.)

Andersson, S. & Amundsen, T. 1997 Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond.* B **264**, 1587–1591.

Andersson, S. & Örnborg, J. 1998 Blue tit or UV tit? Age and sex dimorphism in the ultraviolet.

Bennett, A., Cuthill, I., Partridge, J. & Lunau, K. 1997 Ultraviolet plumage colors predict mate preferences in starlings. *Proc. Natn. Acad. Sci. USA* **94**, 8618–8621.

Bennett, A. T. D. & Cuthill, I. C. 1994 Ultraviolet vision in birds: what is its function? *Vision Res.* **34**, 1471–1478.

Bennett, A. T. D., Cuthill, I. C. & Norris, K. J. 1994 Sexual selection and the mismeasure of color. *Am. Nat.* **144**, 848–860.

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. & Maier, E. J. 1996 Ultraviolet vision and mate choice in zebra finches. *Nature* **380**, 433–435.

Bowmaker, J., Heath, L., Wilkie, S. & Hunt, D. 1997 Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vision Res.* **37**, 2183–2194.

Chen, D. & Goldsmith, T. M. 1986 Four spectral classes of cone in the retinas of birds. *J. Comp. Phys.* A **159**, 473–479.

Cramp, S. & Perrins, C. M. 1993 *The birds of the western Palearctic*, vol. VIII. Oxford University Press.

Dyck, J. 1976 Structural colours. *Proc. Int. Orn. Congr.* **16**, 426–437.

Ellegren, H. 1996 First gene on the avian W chromosome (CHD) provides a tag for universal sexing of non-ratite birds. *Proc. R. Soc. Lond.* B **263**, 1635–1641.

Endler, J. A. 1990 On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315–352.

Endler, J. A. 1992 Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125–S153.

Endler, J. A. 1993 The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27.

Endler, J. A. & Thery, M. 1996 Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. Nat.* **148**, 421–452.

Finger, E. 1995 Visible and UV coloration in birds: Mie scattering as the basis of color in many bird feathers. *Naturwiss.* **82**, 570–573.

Goldsmith, T. H. 1990 Optimization, constraint, and history in the evolution of eyes. *Q. Rev. Biol.* **65**, 281–322.

Goldsmith, T. H. 1994 Ultraviolet receptors and color vision—evolutionary implications and a dissonance of paradigms. *Vision Res.* **34**, 1479–1487.

Hasson, O. 1990 The role of amplifiers in sexual selection: an integration of the amplifying and the fisherian mechanisms. *Evol. Ecol.* **4**, 277–289.

Hunt, S., Bennett, A. T. D., Cuthill, I. C. & Griffiths, R. 1998 Blue tits are ultraviolet tits. *Proc. R. Soc. Lond.* B **265**, 451–455. (This issue.)

Kempenaers, B. 1994 Polygyny in the blue tit—unbalanced sex ratio and female aggression restrict mate choice. *Anim. Behav.* **47**, 943–957.

Kempenaers, B. 1995 Polygyny in the blue tit—intra- and intersexual conflicts. *Anim. Behav.* **49**, 1047–1064.

Kempenaers, B., Verheyen, G. R., Vandenbroeck, M., Burke, T., Vanbroeckhoven, C. & Dhondt, A. A. 1992 Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* **357**, 494–496.

Kempenaers, B., Verheyen, G. R. & Dhondt, A. A. 1997 Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**, 481–492.

Lorentz, K. Z. 1941 Vergleichende bewegungsstudien an Anatinen. *J. F. Ornithol.* **89**, 194–294.

Lythgoe, J. N. 1979 *The ecology of vision*. Oxford: Clarendon Presss.

Maier, E. J. 1994 Ultraviolet vision in a Passeriform bird—from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. *Vision Res.* **34**, 1415–1418.

Osorio, D. & Bossomaier, T. R. J. 1992 Human cone-pigment spectral sensitivities and the reflectances of natural surfaces. *Biol. Cybern.* **67**, 217–222.

Perrins, C. M. 1979 *British tits*. London: Collins.

Stokes, A. W. 1960 Nest-site selection and courtship behaviour of the blue tit *Parus caeruleus*. *Ibis* **102**, 507–519.

Svensson, E. & Nilsson, J. A. 1996 Mate quality affects offspring sex ratio in blue tits. *Proc. R. Soc. Lond.* B **263**, 357–361.

Svensson, L. 1992 *Identification guide to European passerines*. Stockholm: Märstatryck.

Wyszecki, G. & Stiles, W. S. 1982 *Color science*. New York: Wiley.