IS THE ULTRAVIOLET WAVEBAND A SPECIAL COMMUNICATION CHANNEL IN AVIAN MATE CHOICE?

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Summary

There is growing evidence that ultraviolet (UV) wavelengths play an important role in avian mate choice. One of the first experiments to support this idea showed that female zebra finches (*Taeniopygia guttata*) prefer UV-reflecting males to males whose ultraviolet reflection has been removed. The effect was very strong despite little or no UV reflection from several plumage areas. However, it is not clear how the importance of the UV waveband compares to other regions of the bird-visible spectrum. We tested whether the response of female zebra finches to the removal of male UV reflection is greater than to the removal of other wavebands. We presented females with a choice of males whose appearance was manipulated using coloured filters. The filters removed single blocks of the avian visible spectrum corresponding closely to the spectral sensitivities of each of the zebra finch's single cone classes. This resulted in males that effectively had no UV (UV−), no short-wave (SW−), no medium-wave (MW−) or no long-wave (LW−) plumage reflection. Females preferred UV− and SW− males. LW− and MW− males were least preferred, suggesting that female zebra finches show the greatest response to the removal of longer wavelengths. Quantal catches of the single cone types viewing body areas of the male zebra finch are presented for each treatment. Our study suggests it is important to consider the role of the UV waveband in avian mate choice in conjunction with the rest of the avian visible spectrum.

Key words: ultraviolet, mate choice, zebra finch, colour vision, plumage colour.

Introduction

There has been considerable recent interest in both how and why birds have ultraviolet (UV) vision. It is now clear that most, if not all, diurnal birds are able to detect wavelengths down to approximately 320 nm in the near-UV (e.g. Bowmaker et al., 1997; Hart et al., 1998). Furthermore, a growing number of experiments suggest that birds use UV cues in important visual tasks such as mate choice and foraging (Cuthill et al., 2000a; Cuthill et al., 2000b, and references therein).

Avian UV vision is mediated via a dedicated UV-sensitive (UVS) or violet-sensitive (VS) retinal cone. UVS cones containing a visual pigment with maximum sensitivity below 400 nm have been found in all passerines investigated to date and the budgerigar *Melopsittacus undulatus* [wavelengths of maximum sensitivity (λ_{max}) range from 355 to 380 nm; see Table 1 in Cuthill et al., 2000b]. In contrast, non-passerines such as the pigeon and chicken have a visual pigment with peak sensitivity in the violet region of the spectrum (λ_{max} 402–426 nm). The reason for this dichotomy in the distribution of λ_{max} values is unknown at present (Bowmaker et al., 1997; Cuthill et al., 2000b; Yokoyama et al., 2000). All species studied so far also possess a short-wave-sensitive (SWS; λ_{max} 430–463 nm), medium-wave-sensitive (MWS; λ_{max} 497–510 nm) and long-wave-sensitive visual pigment (LWS; λ_{max} 543–571 nm), giving them a total of four single cone types. Although birds also have numerous long-wave-sensitive double cones, current evidence suggests that these are not used in colour vision (Campenhausen and Kirschfeld, 1998; Vorobyev and Osorio, 1998; Vorobyev et al., 1998). The UVS/VS cone is thus one component in a potentially tetrachromatic colour vision system based on the four single cones (Burkhardt, 1989; Goldsmith, 1990; Jacobs, 1992; Thompson et al., 1992; Bennett et al., 1994; Cuthill et al., 2000b). This raises the important question of how special UV cues are in avian signalling systems compared to other wavebands such as medium ('green') or long ('red') wavelengths.

Much of the interest in avian UV vision has focused on its possible role in mate choice (Bennett et al., 1994; Cuthill et al., 2000a). Colour-based signalling is common among birds. For example, plumage colour may be used as an indicator of the sex, phenotypic condition or genotypic quality of potential mates (Andersson, 1994). To measure plumage 'colour' objectively requires techniques such as reflectance spectroradiometry (Endler, 1990; Bennett et al., 1994; Cuthill

et al., 1999). Reflectance spectra from bird plumages have revealed that UV reflectance can be associated with most human-visible feather colours, including blues, greens, yellows and reds (Burkhardt, 1989; Burkhardt, 1996). Therefore, the extent to which feathers are UV-reflecting cannot necessarily be predicted from their human-visible appearance. Nor is UV plumage reflectance alone sufficient evidence that the UV component of the coloration has a signalling role, since feathers might reflect UV merely as a by-product of their structure or pigmentation (Andersson, 1996). Purely UV-reflecting feathers, as in the Asian whistling thrushes (*Myiophonus* spp; Andersson, 1996), and sexual dimorphism in UV coloration, such as that exhibited by bluetits (*Parus caeruleus*; Andersson et al., 1998; Hunt et al., 1998) and starlings (*Sturnus vulgaris*; Cuthill et al., 1999), are more suggestive of a signalling role. Nevertheless, convincing evidence that the UV is an adaptive part of signal design requires experimental manipulation of the UV component of the plumage coloration and measurement of a behavioural response.

To date, manipulative experiments have been published for relatively few species: Pekin robins (*Leiothrix lutea*; Maier, 1993), zebra finches (*Taeniopygia guttata*; Bennett et al., 1996; Hunt et al., 1997), starlings (Bennett et al., 1997), bluethroats (*Luscinia s. svecica*; Andersson and Amundsen, 1997; Johnsen et al., 1998) and bluetits (Hunt et al., 1999; Sheldon et al., 1999). Zebra finches and Pekin robins have predominantly long-wave-reflecting carotenoid- and melanin-pigmented plumage, while bluetits, starlings and the throat patch of the bluethroat are structurally coloured with much greater short-wave (including UV) plumage reflection. Despite these differences, females of all species prefer males with a full-spectrum appearance over males whose UV reflection has been removed. Furthermore, in the laboratory, rankings of male starlings by females were altered by the presence or absence of UV cues (Bennett et al., 1997). In the field, Johnsen et al. (Johnsen et al., 1998) showed that UV cues can influence extra-pair mating success as well as social mate choice in bluethroats. And most recently, Sheldon et al. (Sheldon et al., 1999) found that female bluetits adjust the sex ratio of their offspring according to the saturation (chroma) of the UV/blue crest of their male partners. Females mated to males with a high-chroma crest produced more sons; those mated to males with low-chroma crests produced more daughters. The relationship between offspring sex ratio and crest colour reversed when UV reflection was removed, showing that it is the UV component of the signal that provides females with the relevant information on male quality.

It is now clear, given the evidence cited above, that UV cues play an important part in the colour communication systems of birds. What is less clear, is whether the UV waveband is in any way a 'special' channel for avian signalling (Andersson, 1999; Bennett and Cuthill, 1994). Given the wavelength-dependent properties of light, there are plausible reasons for and against the UV playing some 'special' role in avian mate choice (Bennett and Cuthill, 1994; Bennett et al., 1996). Firstly, UV wavelengths are more highly scattered in air than longer wavelengths (Lythgoe, 1979), so might be advantageous in short-range communication such as mate choice, with less risk of attracting more distant predators (Burkhardt, 1989; Bennett and Cuthill, 1994). Secondly, as light is back-scattered by a surface, it is plane-polarized, an effect that increases towards shorter wavelengths (Lythgoe, 1979); the resulting polarization pattern can reveal details of underlying structure which could be useful in a mate-choice context, perhaps revealing quality. However, whether birds have polarization vision remains controversial (Kreithen and Eisner, 1978; Coemans et al., 1990; Coemans et al., 1994; Phillips and Moore, 1992; Able and Able, 1993; Able and Able, 1995; Munro and Wiltschko, 1995; Vos Hzn et al., 1995). Lastly, it has been suggested that the UV waveband might provide a 'private' communication channel for birds (e.g. Guilford and Harvey, 1998), perhaps enabling them to signal to conspecifics without being conspicuous to their predominantly UV-blind, mammalian predators (Jacobs, 1981). As far as we are aware, there are no explicit tests of these hypotheses.

In the present study, we experimentally investigate how important UV cues are in zebra finch mate choice, compared to other regions of the bird-visible spectrum. Zebra finches are a model species in studies of mate choice and sexual selection, and colour appears to be an important factor in choosing a mate (Zann, 1996). For example, female zebra finches may prefer males with redder beaks (Burley and Coopersmith, 1987; De Kogel and Prijs, 1996), and will choose males wearing red leg bands over those with orange, light green or no leg rings (Burley et al., 1982; Hunt et al., 1997). Interestingly, although neither the beak, nor the red, orange or green leg bands reflect greatly in the UV, both Bennett et al. (Bennett et al., 1996) and Hunt et al. (Hunt et al., 1997) found a large effect of removing ultraviolet reflectance on female preference. This may be because this alters the UV-reflecting (e.g. white) portions of the plumage, and hence changes the overall appearance of the bird or the contrast between plumage areas. Here we test the responses of female zebra finches to the removal of other wavebands within the zebra finch's spectral range. We use four types of filter designed to remove the regions of the spectrum corresponding approximately to the sensitivities of the zebra finch's four single cone classes. We predict that if the ultraviolet is a 'special' waveband for mate choice compared to other wavebands, the removal of UV wavelengths will have the greatest effect on female preferences. Conversely, if another waveband is more important, then males without reflection in this waveband will be the least preferred. We also calculate the predicted effect of the filters on the signals elicited in each of the four cone types by the plumage and beak of the male zebra finch.

Materials and methods
Mate choice

We used eight adult female and eight adult male, captive-bred, wild-type zebra finches, *Taeniopygia guttata*, housed in
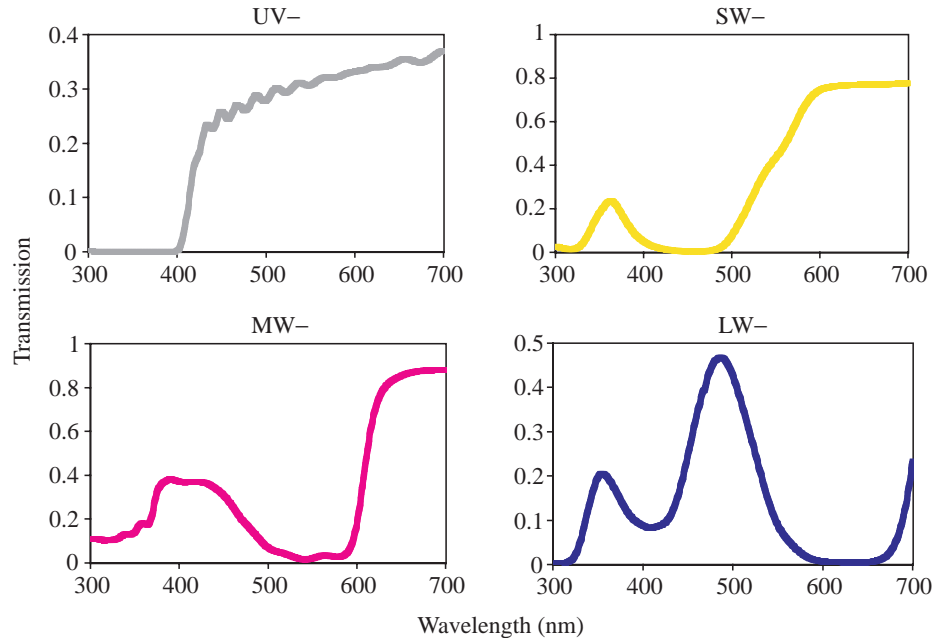
Fig. 1. The proportional transmission (300–700 nm) of the four filter-types: ultraviolet-blocking (UV−), short-wave-blocking (SW−), medium-wave-blocking (MW−) and long-wave-blocking (LW−). Each filter removes a portion of the bird visible spectrum, closely corresponding to the spectral sensitivity of one of the four zebra finch single cone types (see Bowmaker et al., 1997). Spectra are plotted in the colour that the filters appear to the human eye.

single-sex groups of four birds (cages 0.3×0.4×1.0 m). Males and females were visually, but not acoustically, isolated and therefore had not seen each other prior to the mate choice trials. Birds were maintained under a constant temperature (19±2 °C), humidity and photoperiod (16 h:8 h L:D) and had access to *ad libitum* seed and water. Both males and females were individually identified using a single numbered orange plastic leg band (A. C. Hughes, Middlesex UK), which closely matches the spectral reflection of the leg (Hunt et al., 1997). Lighting in the holding room consisted of standard fluorescent tubes, enhanced by the addition of six True-Lite[TM] tubes powered by high frequency ballasts. These provide greater emission of UV wavelengths than standard lighting, and are designed to approximate natural daylight (see Bennett et al., 1996; Hunt et al., 1999).

We carried out mate-choice trials in a wooden apparatus, cross-shaped in plan view, already used in a number of previous studies on mate choice in this species (e.g. Swaddle and Cuthill, 1994; Bennett et al., 1996; Hunt et al., 1997). We placed one choosing female in the centre of the apparatus, where she had access to a perch and *ad libitum* food and water. Males were placed in individual stimulus cages located at the end of each of four arms, again with access to a perch and *ad libitum* food and water. Females were separated from males by vertically mounted filters that transmitted all wavelengths across the bird-visible spectrum (UV+ filters; see Bennett et al., 1996). The placement of wooden baffles ensured that a female could see only one male at a time.

A bank of 12 equi-spaced True-Lite tubes, suspended 1 m above the apparatus, provided even full-spectrum illumination of the apparatus. In all central areas (in which the female moved), the apparatus was covered with 1 cm wire mesh only. Females therefore had a normal (i.e. full-spectrum) appearance to each male. However, the stimulus cages were covered with coloured filters. In each trial we used four filter types (see below), one resting horizontally above each stimulus cage. In this way, filters produced a different illumination (light environment) for each male and hence allowed us to manipulate the appearance of the males to the choosing female.

The transmission spectra of the four filter treatments are illustrated in Fig. 1. The filters were chosen such that they each removed a different waveband of the bird-visible spectrum. They are classified according to the main region of the spectrum that they removed and are hence termed UV-blocking (UV−), short-wave-blocking (SW−), medium-wave-blocking (MW−) and long-wave-blocking (LW−) (Lee Filter no. 229, Rosco Supergel[TM] filters 14, 339 and 73, respectively). The exact wavebands removed match as closely as possible the spectral sensitivity of the four zebra finch single cone types (see below). By removing a particular waveband, the filters each minimize the contribution of one of the four avian cones. Therefore, if the reflection from a given region of plumage usually stimulates all four cone types, then the same region of plumage below one of the filters should yield a similar relative stimulation in three of the four cone-types, but negligible signal in the fourth cone. The attenuation of the filters was adjusted by using multiple layers of filter material, such that they were approximately balanced for total quantal flux (the total amount of light transmitted between 300–700 nm). The exact ratios of quantal flux for the four treatments (UV−:SW−:MW−:LW−) were 1.23:1.09:1.12:1.00.

The eight female zebra finches were divided into two groups of four birds. Each group of four females was randomly allocated a group of four males. All females within each group were presented with the same four males during their mate-choice trials. However, males were allocated to the four filter treatments according to a Latin square design such that each male, viewed by four different females, was seen behind a different filter in each trial. In other words, all females saw a different male-filter combination.

As before (Bennett et al., 1996), mate-choice trials were 6 h long and divided into three consecutive 2 h phases: (1) control 1, the first 2 h of the trial, during which a female was placed in the apparatus but no males were present in stimulus cages, to test for general preferences for the four light environments created by the filter treatments, independent of mate choice; (2) mate assessment, the second 2 h of the trial, during which females viewed males placed into the stimulus cages; and (3) control 2, the second control phase, during which males were again removed. All trials began 2 h after dawn.

We recorded female preferences using electronically monitored perches located in each arm of the apparatus. A computer attached to the perches recorded the number of hops females made in front of each male. We analysed these data using a repeated-measures analysis of variance (ANOVA) in Minitab. The data were first log-transformed so that residuals were normally distributed.

Plumage colour

To relate any effects on mate choice to the likely influence of filters on colour perception, we calculated the quantal catch of each cone class when viewing zebra finch plumage, under each filter type. A 'colour space' is a geometric representation of the pattern of stimulation of the photoreceptors involved in colour vision (Burkhardt, 1989; Goldsmith, 1990; Neumeyer, 1992). Birds, whose colour vision seems to depend on the neural comparison of the four single cones (Osorio et al., 1999a; Osorio et al., 1999b), have a (potentially) four-dimensional colour space. This can be decomposed into a brightness component, related to the sum of cone outputs, and three hue dimensions (Thompson et al., 1992). Hue relates to the relative output of the cones, so the hues seen by a tetrachromat are usually modelled as the positions in a tetrahedron whose four axes represent the proportional stimulation of the UVS, SWS, MWS and LWS cones (Burkhardt, 1989; Goldsmith, 1990; Neumeyer, 1992; Thompson et al., 1992; Vorobyev et al., 1998). In our analysis we concentrated on hue differences, related to relative cone output, and disregarded any luminance signals (see Vorobyev and Osorio, 1998; Vorobyev et al., 1998; Fleishman and Endler, 2000). We return to this issue in the Discussion.

To calculate the position in zebra finch colour space of the principal areas of plumage coloration and the cage background, we first calculated the quantal catches of the four receptor types, by multiplying the irradiance spectrum of the True-Lite tubes (Fig. 3C) by the reflectance spectrum of each object (see Fig. 3A) and the effective spectral sensitivity of the cones (for specific formulae and further explanation, see Maddocks et al., 2001). We calculated cone spectral sensitivities from data on visual pigments and oil droplets reported elsewhere (Bowmaker et al., 1997), assuming that zebra finch optical media have a transmission similar to that of other estrildid finches measured by our group (wavelengths of 0.5 transmission, 316–318 nm; Hart et al., 2000). The resulting quantal catches define the position of each object in zebra finch colour space. In these calculations, we have to make an

assumption about colour constancy and the adapted state of the eye when viewing an object (Vorobyev and Osorio, 1998). We assumed that the birds' cones were adapted to the stimulus cage background (see Fig. 3A) illuminated by an unfiltered True-Lite tube, as experienced at the centre of the choice chamber. As this adapting background was aluminium covered in frosted UV-transmitting Perspex (as used in Bennett et al., 1996), this is equivalent to assuming that 'bird grey' is located at the centre of the colour space (equal stimulation of all cones; Vorobyev and Osorio, 1998; Vorobyev et al., 1998). We acknowledge that the actual perceived colours may not correspond directly to the relative quantal catches we have calculated, but these provide a first approximation in the absence of psychophysical data (Thompson et al., 1992).

Results

Mate choice

The effect of filter treatment on female preference varied significantly with phase (filter×phase interaction: $F_{6,42}=4.39$, $P=0.009$). We therefore carried out a separate ANOVA on the data from each phase of the trial. In control 1, there was no significant difference in the number of hops females made in each arm ($F_{3,21}=2.23$, $P=0.115$). In the mate assessment phase, females showed significant discrimination between the four filter treatments ($F_{3,21}=6.77$, $P=0.002$; Fig. 2). We examined the treatment differences with a series of orthogonal contrasts (Rosenthal et al., 2000), and found three simple linear models that gave a similar fit to the data and left no significant between-treatment variation. The best-fitting model was a linearly declining order of preference UV− >SW− >MW− >LW− ($F_{1,21}=18.43$, $P<0.001$, residual treatment effects
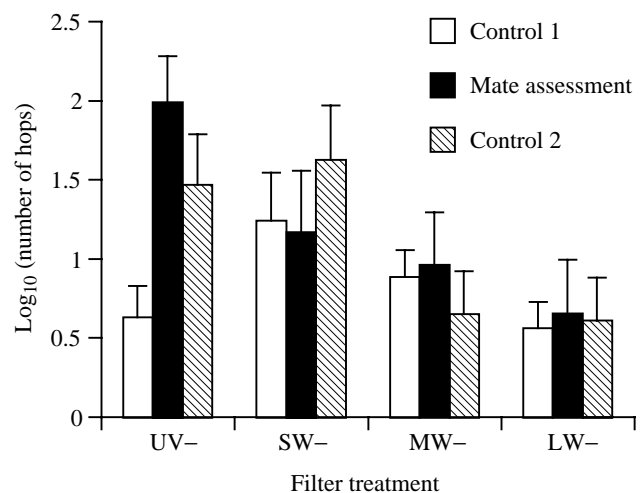

Fig. 2. Mean (+ s.e.m.) number of hops performed by females ($N=8$) in front of males under the ultraviolet-blocking (UV−), short-wave-blocking (SW−), medium-wave-blocking (MW−) and long-wave-blocking (LW−) filter treatments, during the three phases of the experiment. In control 1, females viewed empty stimulus cages; during mate assessment, a male was present in each cage; in control 2, males were once more removed.

$F_{2,21}$=0.94, P=0.406), but the preference ranking UV− >SW− >MW−=LW− was also a good fit to the data ($F_{1,21}$=17.57, P<0.001, residual treatment effects $F_{2,21}$=1.35, P=0.281). A preference ranking UV− >SW− >LW− >MW− also fitted the data well, but the between-treatment variation left unexplained was close to significant ($F_{1,21}$=13.39, P=0.001, residual treatment effects $F_{2,21}$=3.46, P=0.050). Note that because the data were log-transformed, a linear pattern of contrasts implies a constant ratio of differences between treatments, not a constant absolute difference. Other statistical models, which might be considered relevant in the light of the analysis of plumage reflectance spectra, are presented in the Discussion.

A slightly weaker but still significant effect was seen in control 2 ($F_{3,21}$=6.04, P=0.004). Four simple linear models fitted the data equally well and left no significant between-treatment variation. The best-fitting model was UV−=SW− >MW−=LW− ($F_{1,21}$=17.83, P<0.001, residual treatment effects $F_{2,21}$=1.79, P=0.192), with almost as good a fit being provided by UV− >SW− >MW−=LW− ($F_{1,21}$=14.52, P=0.001, residual treatment effects $F_{2,21}$=0.14, P=0.870). However, neither were significantly better than SW− >UV− >MW− >LW− ($F_{1,21}$=15.84, P=0.001, residual treatment effects $F_{2,21}$= 2.67, P=0.093) and UV− >SW− >MW− >LW− ($F_{1,21}$=13.37, P=0.001, residual treatment effects $F_{2,21}$=1.46, P=0.225), the best-fitting model from the mate-assessment phase. Overall, the consistent pattern is that removal of long- and medium-wavelength reflectance had the most detrimental effect on a male's attractiveness, and removal of UV and short-wavelength the least, with a carry-over effect on preferences for those stimulus cages in the second control phase.

Plumage colour

Fig. 3A shows reflectance spectra from the white cheek patch, red beak and brown cheek patch of the male zebra finch (see also Fig. 4). Fig. 3B gives the calculated quantal catches by each of the four single cones elicited by these areas of plumage, both under unfiltered True-Lite illumination and beneath the four filter types. A similar plot is shown for the frosted aluminium cage background against which the male birds are viewed. Note that, in the case of the cage background, cone catch values are fixed such that cones are fully and equally stimulated under unfiltered (natural) illumination, due to the assumption that the bird is adapted to this background under these conditions (see Materials and Methods). Photon catches for the plumage regions are therefore relative to those for the cage background.

The data for the cage background and the white cheek (both reflective across the entire bird-visible spectrum, Fig. 3Ai,ii) illustrate nicely the general effect of the filters: under 'natural' True-Lite illumination, all four cones are stimulated in equal or roughly equal proportions respectively, while under the filtered irradiances one cone signal is knocked out in each case (Fig. 3Bi,ii). The red beak and brown cheek both show greatest reflection at long wavelengths and hence, under 'natural' illumination, the greatest quantal catch is in the LWS cone (Fig. 3iii,iv). The relative effect of the four filter treatments is also similar for both beak and brown cheek. The SW− filter has high transmission across a broader range of long wavelengths than the other filter types (Fig. 1), therefore this treatment has the least effect on the quantal catch in the LWS cones (Fig. 3Biii,iv). By definition, blocking long wavelengths (LW−) has the greatest effect on the signal in the LWS cone, and therefore on the overall ratio of quantal catches in the four cones, which in turn is likely to determine perceived hue. In the case of the red beak, for example, the LW− treatment reduces almost exclusive stimulation of long-wave-sensitive cones (under 'natural' illumination) to virtually no cone stimulation.

Discussion

Earlier work showed that removal of UV cues from male zebra finches leads to a reduced preference for those males among choosing females, compared to normal full-spectrum (UV+) males (Bennett et al., 1996). Although this was a very strong effect, the experiment reported here, which involves simultaneously presenting males under UV−, SW−, MW− and LW− conditions, shows that removing other wavebands can have a similar or even greater influence. Female zebra finches showed the lowest preference for males under a filter removing the 'red' waveband; removal of UV wavelengths had the least effect. Under the experimental conditions used here, there is therefore no evidence that UV is a special waveband for sexual signalling in the zebra finch.

While the filters used in this experiment each produce a large change in the illumination in each stimulus cage, females showed no significant discrimination between the empty cages presented during control 1. It therefore seems likely that the preferences they exhibited during the mate-assessment phase are indeed related to the appearance of the males. These preferences can still be discerned in control 2. A probable explanation is that this is a carry-over effect from the mate-assessment phase, with females associating these stimulus cages with the males they have recently observed in them. Differences in the light environments produced by the filters might potentially have led to changes in the behaviour of the males. Unfortunately, the absorbency of the filters was too high to allow videotaping of male activity, and this will therefore require further investigation. However, the advantage of horizontal orientation of filters (cf. previous mate-choice experiments) is that the female appears very similar to each male; only reflectance of (filtered) light from the aluminium walls of the stimulus cages into the central area of the apparatus, could change the appearance of the female. And this would be largely swamped by the bright, unfiltered overhead illumination of the central part of the apparatus occupied by the female. This uniformity in female appearance should reduce any differences between male behaviour that might in turn influence the female's choice.

In the current experiment, we manipulated male colour by changing the illumination or light environment inside each of the stimulus cages. The fact that removal of the red waveband
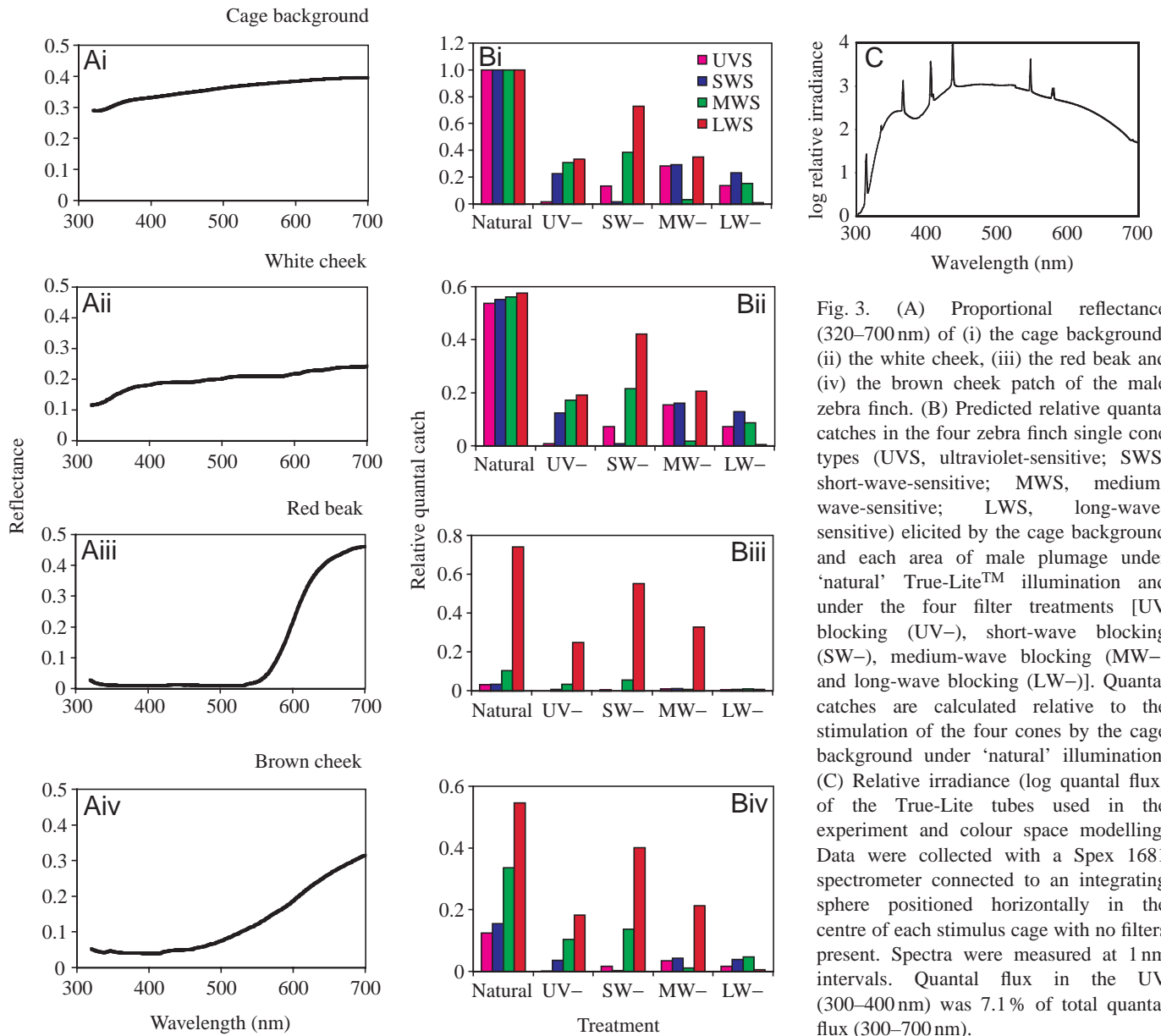
Fig. 3. (A) Proportional reflectance (320–700 nm) of (i) the cage background, (ii) the white cheek, (iii) the red beak and (iv) the brown cheek patch of the male zebra finch. (B) Predicted relative quantal catches in the four zebra finch single cone types (UVS, ultraviolet-sensitive; SWS, short-wave-sensitive; MWS, medium-wave-sensitive; LWS, long-wave-sensitive) elicited by the cage background and each area of male plumage under 'natural' True-Lite™ illumination and under the four filter treatments [UV blocking (UV−), short-wave blocking (SW−), medium-wave blocking (MW−) and long-wave blocking (LW−)]. Quantal catches are calculated relative to the stimulation of the four cones by the cage background under 'natural' illumination. (C) Relative irradiance (log quantal flux) of the True-Lite tubes used in the experiment and colour space modelling. Data were collected with a Spex 1681 spectrometer connected to an integrating sphere positioned horizontally in the centre of each stimulus cage with no filters present. Spectra were measured at 1 nm intervals. Quantal flux in the UV (300–400 nm) was 7.1 % of total quantal flux (300–700 nm).

had the greatest effect is consistent with the effect of the filters on the calculated quantal catches of the cones elicited by regions of the male's plumage. The beak (see Fig. 4), in particular, which is probably important in mate choice (Burley and Coopersmith, 1987; De Kogel and Prijs, 1996), has a predominantly long-wavelength reflection and very little reflection at short (including UV) or medium wavelengths (Fig. 3Aiii). The greatest change in its coloration will therefore be produced by the removal of these long wavelengths, as illustrated in Fig. 3Biii.

In this analysis, we focus on the question of colour signals mediated via the avian single cones, but the filters will also influence achromatic luminance cues. Although not presented here, modelling the responses of the avian double cones which, according to some theories at least (e.g. Campenhausen and Kirschfeld, 1998), are probably the primary contributors to the

avian luminance channel, yields a similar pattern to the analysis for single cones. The predicted spectral sensitivity of the double cones is broad-band, but highest in the medium and long wavelengths (Bowmaker et al., 1997; Hart et al., 2000). In other words, the medium- and long-wave-blocking filters have the greatest predicted effect on the brightness of the plumage as well as its hue. This is also partly due to the fact that the long wavelength treatments had slightly lower total quantal flux (see Materials and methods), but is principally because much of the plumage is long wavelength reflecting. For example, the bright red beak under the LW− filter is likely to appear black. Having said this, we feel it unlikely that the change in preferences can be explained by something as simple as the effect of the filters on the brightness or 'redness' of the beak alone. Indeed, the quantal catch of the LWS cone viewing the red beak (Fig. 3Biii) would predict a preference ranking

Fig. 4. A typical male wild-type zebra finch, showing the three regions for which reflectance was measured in Fig. 3A: the red beak (approximately 8 mm from base to tip), brown cheek patch and white region of the cheek.

SW− >MW− >UV− >LW−, which leaves significant residual treatment variation unexplained (model $F_{1,21}$=6.88, P=0.016, residual treatment effects $F_{2,21}$=6.72, P=0.006). The effects of the filters are therefore more likely to lie in the combined effects on all plumage areas, and the contrasts between areas. Given the dual effect of the filters on brightness and colour cues, an important aim of future experiments will be to separate chromatic from achromatic effects.

In the natural world, light environments vary continuously across space and time, causing changes in the appearance and conspicuousness of colour patterns. Animals may exploit these changes, for example, to balance the conflicting needs of advertising to conspecifics while avoiding predators. Endler and Théry (Endler and Théry, 1996) found that, in three species of tropical lekking birds (*Rupicola rupicola*, *Corapipo gutturalis* and *Lepidothrix serena*), males chose particular light environments such as sun flecks in which to display to females. These microhabitats exhibited a spectral irradiance that maximized both the within-body contrast between plumage patches and the contrast between the male and the background against which it was viewed during display. When not displaying, males avoided those light environments, even if they remained on the lek. Similarly, Endler (Endler, 1991) calculated the conspicuousness of guppies (*Poecilia reticulata*) in the light environments associated with courtship. In these locations, at the times of highest courtship activity, guppies were relatively conspicuous. However, they were relatively less conspicuous in locations and at times of day during which they experience maximum predation risk. The variability of the natural light environment of the zebra finch (mainly open grassland and arid areas of Australia; Zann, 1996) has not been investigated. One implication of the results we present here is that zebra finches might prefer certain light environments over others in which to perform courtship and mate choice.

The recent focus on the effects of UV wavelengths on avian mate choice has highlighted the need to consider the previously neglected contribution of these wavelengths to colour perception and visually based decision-making in birds. We now know that manipulation of UV cues can produce changes in foraging behaviour (Viitala et al., 1995; Church et al., 1998; Koivula and Viitala, 1999; Siitari et al., 1999), social mate choice (Maier, 1993; Bennett et al., 1996; Bennett et al., 1997; Andersson and Amundsen, 1997; Hunt et al., 1999), extra-pair mate selection (Johnsen et al., 1998) and even offspring sex-ratios (Sheldon et al., 1999). Here we provide the first experimental test of whether the UV is, in some way, a 'special' waveband for avian mate choice, and find no evidence for this. This is perhaps not surprising. While the benefits of sexual signalling in the UV are clear where a species has predominantly mammalian predators (but see Jacobs et al., 1991), many small passerines are also preyed on by birds of prey. Behavioural studies on kestrels (Viitala et al., 1995) and buzzards (Koivula and Viitala, 1999) imply that diurnal raptors are as likely to have UV vision as their smaller avian prey. More importantly perhaps, the avian UV-sensitive cone is merely one cone type among four single cone classes, and birds are sensitive across a range of wavelengths from approximately 320 nm in the UV up to 700 nm or so at long wavelengths (Bowmaker et al., 1997). Evidence to date suggests that all cones are likely to contribute to a tetrachromatic colour vision system. Reducing the input of any of these cones is therefore likely to have a pronounced effect on the colour signals perceived by the bird; the full range of bird-visible wavelengths, including the UV, is therefore likely to be essential for normal colour perception and normal visually based behaviours. For these reasons, it is necessary to consider the full spectrum to which birds (and other animals) are sensitive when testing colour-based predictions, as previously suggested (Endler, 1990; Bennett et al., 1994; Bennett et al., 1996; Bennett et al., 1997; Cuthill et al., 2000b).

Having said this, the relative importance of particular wavelengths is likely to vary from species to species and with the specific visual task required. We have addressed the question of waveband preferences in the context of zebra finch mate choice. Our experiment suggests that short-distance mate choice in zebra finches is a long-wavelength-dominated task. In other species, we may find the opposite result. For example, UV wavelengths may be more important in mate choice in species with short-wavelength-rich plumage such as bluetits, with predominantly UV/blue coloration. The relative importance of different wavebands might also change with the ambient light environment, for example, at dawn or dusk, when the proportion of UV light is higher. Particularly interesting is that even what appear to be relatively small changes in the visual task, can produce large shifts in the relative effect of different wavebands. For example, for zebra finches presented with mixtures of red and white millet seeds in foraging tasks, long wavelengths had the greatest effect on simple preferences (Maddocks et al., 2001), but UV wavelengths had the greatest influence on the direction of frequency-dependent selection (Church et al., 2001). UV vision may still have an as-yet-undiscovered 'special' function, as discussed earlier, for example in the detection of polarization patterns. Clearly one

should consider all wavelengths to which birds are sensitive, and use detailed measurements of the reflectance of stimuli, the light environments in which behaviours take place and the likely retinal and neural responses to assess the role of colour in avian signalling systems.

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