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Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*

SARAH HUNT, INNES C. CUTHILL, JOHN P. SWADDLE & ANDREW T. D. BENNETT
Centre for Behavioural Biology, School of Biological Sciences, University of Bristol

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Abstract. Zebra finches have previously been found to have preferences for particular colours of both natural and artificial traits among opposite sex conspecifics. For example, in some studies female zebra finches preferred males wearing red leg bands to orange-banded and unbanded birds and rejected light green-banded males. In other studies, females also preferred males with red beaks to orange-beaked males. However, several authors have failed to replicate these results. We show that females may fail to show a colour preference because of the absence or removal of ultraviolet light under experimental conditions. In mate-choice trials, females observing males through filters that transmitted ultraviolet preferred red-banded males but where females viewed males through ultraviolet-blocking filters, no such preference was observed. Further investigation revealed that the lack of a colour preference when ultraviolet was absent was probably due to the change in overall appearance of the bird, rather than the change in appearance of the rings themselves. This work highlights the importance of proper consideration of the sensory capabilities of animals in experimental design, particularly with regard to the role of ultraviolet light in avian colour perception.

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There is much conflicting evidence concerning the influence of the colour of both natural and artificial traits on female sexual preferences in zebra finches (Collins & ten Cate 1996). As zebra finches are a model species in studies of both sexual selection and the development of sexual preferences (references in Collins & ten Cate 1996; Zann 1996), a resolution of this conflict would have significant implications for both proximate and ultimate investigations of sexual preference. There may also be implications for the design of experiments investigating avian colour-based decision making (Cuthill & Bennett 1993; Bennett et al. 1994).

Zebra finches are monogamous, sexually dimorphic birds, in which the male's plumage is more ornate than that of the female (Zann 1996). Beak colour ranges from orange to red. Certain studies have shown that female zebra finches prefer males with red beaks to those with orange beaks (Burley & Coopersmith 1987; De Kogel & Prijs 1996). In contrast, Sullivan (1994) found a preference for males with orange-painted beaks, while others have demonstrated beak colour to be unimportant in female mate choice compared with factors such as song rate (Houtman 1992; Collins et al. 1994; Weisman et al. 1994; reviewed by Collins & ten Cate 1996). Similarly, in experimental mate-choice trials, Burley et al. (1982) found that females preferred males wearing red plastic leg bands to orange-banded or unbanded birds, and disliked males with light green leg bands. Furthermore, by artificially manipulating attractiveness in this way, Burley and her colleagues were able to show effects of band colour on individuals' life history traits, including the quality of mate obtained, reproductive success, the sex ratio of offspring, the level of parental care and mortality (Burley 1985, 1986a, b, 1988; Zann 1994). Others, however, have failed to replicate these results (e.g. Ratcliffe & Boag 1987).

The extent to which female zebra finches show colour preferences during mate choice is therefore

Correspondence: S. Hunt, Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K. (email: sarah.hunt@bristol.ac.uk). J. P. Swaddle is now at the Division of Environmental & Evolutionary Biology, Institute of Biomedical & Life Sciences, University of Glasgow, Glasgow G12 8QQ, U.K.

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unresolved. One possible cause of the conflicting results among previous studies is a failure to consider the colour vision of the zebra finch, in the design of experimental protocols (Bennett et al. 1994). Zebra finches, like other passeriforms studied, can see ultraviolet light (Bennett & Cuthill 1994; Bennett et al. 1996), with one of their visual pigments absorbing maximally at a wavelength of 360–380 nm (Bowmaker et al. 1997). The fact that the UV (ultraviolet) retinal cone cells are one of four spectrally distinct cone types (Bowmaker et al. 1997) implies not only that they can see light to which humans are blind, but that they have the potential for tetrachromatic colour vision. If this is the case, UV cones are likely to contribute to colour perception of objects that reflect in the human visible spectrum, as well as in the ultraviolet region of the spectrum. In addition, measurement of the reflectance of zebra finch plumage shows that near-ultraviolet wavelengths (300–400 nm) are reflected from several regions of the bird (Bennett et al. 1996). Finally, experiments where UV reflectance is selectively removed show that females prefer to view potential mates under full (avian) spectrum conditions (Bennett et al. 1996). This strongly implies that UV reflectance, presumably in conjunction with human-visible wavelengths, plays a role in intra- or inter-sexual signalling (Bennett & Cuthill 1994; Bennett et al. 1996, 1997).

There are several reasons why the UV vision and plumage of zebra finches are relevant to the question of whether females exhibit colour preferences. First, in many of the above studies, paints and nail varnishes have been used to manipulate male beak colour (e.g. Collins et al. 1994; Sullivan 1994; Vos 1995), without consideration of how these may affect the UV reflectance of the beak, or how these manipulated colours might be perceived by birds (Bennett et al. 1994; Collins & ten Cate 1996). Second, choice trials sometimes involve the use of mirrored or one-way glass (e.g. Houtman 1992; Swaddle & Cuthill 1994a, b), which often absorbs UV light. Removing UV wavelengths in this way might be analogous to removing blue or red wavelengths in experiments on colour perception in humans. Third, standard laboratory lighting is weak in emission of UV wavelengths compared with natural daylight (Wysecki & Stiles 1967), a factor that may also affect the appearance and colour perception of the animals.

In this paper we investigate the effect of the presence or absence of UV light on leg-band colour preferences in female zebra finches. We present the results of mate-choice trials, following the protocol of Burley et al. (1982), where females were given a choice of males either unbanded or banded with red, orange or light green leg rings. Experiment 1 is a replication of the main experiment in Burley et al. (1982), using identical apparatus and procedures to experiments in which we have previously demonstrated preferences for symmetry of natural and artificial ornamental traits (Swaddle & Cuthill 1994a, b). In experiments 2 and 3, we test the hypothesis that female zebra finches show a Burley-type band-colour preference (a preference for red-banded males and a dislike of light green-banded males) when male birds are viewed under illumination similar to natural daylight, but no such band-colour preference when UV wavelengths are removed.

EXPERIMENT 1

Methods

We used 14 adult female and 24 adult male, captive-bred, wild-type zebra finches, obtained from two different suppliers so that the sexes were not familiar with each other. All birds were approximately 2 years old and were unmated. They were housed in single-sex cages (1.0 × 0.4 × 0.3 m) and ringed with a single numbered orange leg band. The cages were maintained in visual, but not acoustic, isolation on an 18:6 h light:dark photoperiod, at a constant temperature of 18°C. Commercial bird seed and water were available ad libitum.

The test apparatus was identical to that used by Swaddle & Cuthill (1994a, b; see Figure 1 in either paper). The chamber consisted of a central area, where food and water were available ad libitum, and four stimulus arms. The stimulus arms had baffles such that the female was in visual contact with only one male at any one time, and in the central compartment the test bird was not able to see any of the males. Unlike in Burley et al. (1982), one-way glass was placed at the end of the stimulus arms, so that the test female could see a stimulus male, but not vice versa. This controlled for any effect that female display characteristics may have on male behaviour. Room illumination was by two 80 W fluorescent tubes 1.5 m above the apparatus. In addition, an 8 W fluorescent tube was placed at the back of each stimulus cage to ensure a gradient of increasing light intensity towards the stimulus cage and hence ensure correct functioning of the one-way glass.

All female birds were familiarized with the choice chamber apparatus for 6 h, so they became acclimatized to their novel surroundings. From the initial pool of 14 females, we chose the eight individuals that moved most actively between stimulus compartments for the experimental trials. All of these eight individuals visited every stimulus compartment during their familiarization trials. For the purpose of familiarization trials, unbanded non-experimental males were placed in the stimulus compartments.

Following the protocol of Burley et al. (1982), we placed a cage of males wearing the colour bands to be used in the experiment (see below) in view of the females' home cage prior to actual mate-choice trials. This pre-exposure may enable females to establish preferences for particular ring colours (Burley et al. 1982) and reduces the potential for neophobic responses to novel colour bands during choice trials. Pre-exposure began 5 days before the first experimental trials and involved different males (but from the same supplier) from those the females would see in the choice chamber. Band colours were rotated between males every day, so that particular colours could not be associated with particular males (Burley et al. 1982).

We began each experimental trial by placing four (experimental) males in the peripheral stimulus cages. Each male was randomly assigned to one of four leg-band treatments: red, light green, orange or unbanded (bands supplied by A. C. Hughes, Middlesex, U.K., as in Burley et al. 1982). Banded males wore one ring of the given colour on each leg. A (test) female was released in the central section of the apparatus and was allowed to move freely between all stimulus compartments during a 2-h acclimatization period. During this period the female visited all stimulus compartments, and so was exposed to all four males. The trial then lasted for 5 h, and the total amount of time spent, and the number of ritualized display jumps performed, by females in front of each manipulated male (see Burley et al. 1982), were recorded by means of microswitch perches placed in every stimulus compartment, each linked to a micro-computer (Swaddle & Cuthill 1994a, b). Females were tested three times each, with 6–15 days (mode 7) between trials, using different males each time. Subject to the latter criterion, the four experimental males for each trial were selected at random from the pool of 24. Food and water were provided for all birds during each trial.

On inspection of normal probability plots, we square-root transformed the hop data to conform with the assumptions of repeated measures ANOVA; the time data did not require transformation. Two-tailed tests of probability are used throughout. All statistical analyses were performed on SPSS (SPSS Inc. 1988).

Results and Discussion

Females showed no preference for any particular band colour in terms of time ($F_{3,21}=1.00$, NS) or numbers of hops ($F_{3,21}=1.28$, NS). Nor were the trends consistent with those observed by Burley et al. (1982): the mean times spent in front of red, orange, unbanded and light green males were 1055, 1624, 1628 and 1788 s, respectively. This did not seem to be a result of the females being unmotivated to view males, as on average females spent 34% of the 5-h trial in front of males, even though the central compartment contained their food and water. This figure is similar to that for experiments where strong preferences were exhibited (for symmetry; 37% of time viewing males; Swaddle & Cuthill 1994a). We specifically used identical apparatus, the same general protocols and birds from the same breeders, as used in previous experiments (Swaddle & Cuthill 1994a, b) in order to maximize the chances of detecting colour-band preferences. Obviously there could be a large number of reasons why the null hypothesis was not rejected, but a few are particularly plausible in the light of a review of all similar experiments (Collins & ten Cate 1996). One-way glass, used so that males cannot see the female that is choosing them, may reduce or abolish male display (males can still hear the female). Since male display seems to be important in sex recognition (Vos 1995) and female choice (Houtman 1992; Collins et al. 1994), females may have expressed social rather than sexual preferences in experiment 1 (Collins & ten Cate 1996). In experiments 2 and 3 we focus on another possibility, also discussed by Collins & ten Cate (1996), that the full spectrum of light to which zebra finches are sensitive is necessary for correct colour identification.

EXPERIMENT 2

Methods

We used 16 adult female and 32 adult male, captive-bred, wild-type zebra finches, maintained in single-sex groups so that males and females had no prior experience of each other. We randomly assigned females to one of two groups (UV+ and UV−; see below), each containing eight birds. All females wore one numbered orange leg ring allowing individual identification. We randomly divided males into two groups of 16 birds (also UV+ and UV−). Within each group males were assigned either red, orange, light green or no leg bands, at random, such that four birds within each group received the same leg-band treatments. Males wore one band of the given colour on each leg.

The experimental birds were housed in single-sex cages (0.5 × 0.5 × 0.5 m), each holding four females or eight males (two red-banded, two orange-banded, two light green-banded and two unbanded birds). Birds had access to ad libitum food and water and were maintained under a constant 12:12 h light:dark photoperiod, at a constant temperature of 18°C. Lighting included two daylight-mimicking fluorescent tubes, with greater emission of UV wavelengths than standard artificial lighting (Bennett et al. 1996).

As in experiment 1 and Burley et al. (1982), we pre-exposed females to banded males for 5 days prior to actual mate-choice trials. Again, the individual males viewed by a female in pre-exposure were not those used during her subsequent mate-choice trials and band colours were regularly rotated between males so that particular colours could not be associated with particular males. During pre-exposure (and for periods between mate-choice trials), males and females viewed each other through filters held vertically between each pair of cages. Filters were either transparent to all wavelengths down to 300 nm (UV+ filters) or were transparent only down to 400 nm and therefore opaque to wavelengths in the ultraviolet (UV− filters) (Fig. 1). These filters were balanced for total quantal flux (Fig. 1) such that although they differed in the wavelengths transmitted, the total amount of light transmitted (300–700 nm) was similar (see Bennett et al. 1997). Of the 16 test females, eight were pre-exposed to males through UV+ filters (UV+ females) and eight through UV− filters (UV− females). As a consequence, males were also pre-exposed to females under UV+ or UV− conditions and are referred to as UV+ males or UV− males as appropriate.

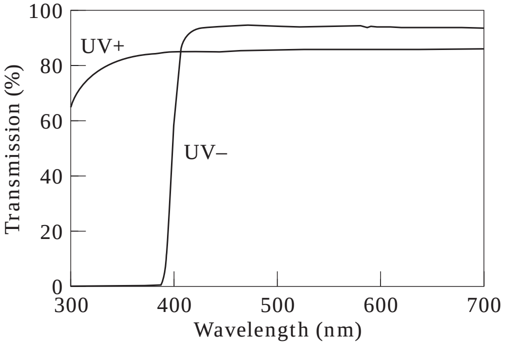

Figure 1. Transmission spectra of UV-transmitting (UV+) and UV-blocking (UV−) filters used in experiment 2. Identical UV+ filters were used in experiment 3. Spectra are the mean of five randomly located measurements on each filter, taken with a Unicam Prism spectrophotometer.

We conducted mate-choice trials using the apparatus described in Bennett et al. (1996; Fig. 1 in that paper), identical to that used in experiment 1 and by Swaddle & Cuthill (1994a, b), but modified to house filters between the stimulus arms and the stimulus males. Females were separated from males by two-way transmitting filters of the same type as those used during pre-exposure. The eight females pre-exposed to males through UV+ filters (UV+ females) always viewed males in the mate-choice apparatus through UV+ filters. Similarly, UV− females always observed males through filters that removed UV wavelengths. Even overhead illumination was provided by 12 equispaced (at 10-cm intervals) 1.8 m, 100 W fluorescent tubes suspended 0.6 m above the test apparatus and powered by 240 V, 71 W, 35–40 kHz ballasts. Unlike normal fluorescent tubes these produce significant UV and have a spectral emission similar to natural skylight. Downward irradiance inside the stimulus cages gave a ratio of ultraviolet quantal flux to total quantal flux (Endler 1990) $Q_{t300\text{–}400\ \mathrm{nm}}/Q_{t300\text{–}700\ \mathrm{nm}}=9.2\%$ (measurements with a Spex 1681 spectrophotometer connected to an integrating sphere mounted horizontally at the centre of stimulus cages). Cages were lined with aluminium foil overlaid with frosted ultraviolet-transmitting acrylic sheet. Further details of the apparatus and optical conditions within the chamber can be found in Bennett et al. (1996).

A single trial lasted 3 h, with two trials carried out per day. Experience indicated that this shorter trial length was sufficient to detect preference changes as a result of blocking UV light (Bennett et al. 1996). One UV+ female and one UV− female were tested each day, in a random order. Each female underwent two trials, one on each of 2 consecutive days, giving a total of 32 trials over 16 days. The two trials (both carried out using the same filter type, either UV+ or UV− as appropriate) consisted of (1) a choice of males pre-exposed under the same UV conditions as the female and (2) a choice of males from the opposite UV pre-exposure. A UV+ female was therefore tested once with four UV+ males and again with four UV− males, in a random order. The aim was to test for an effect of male behaviour on female choice. We hypothesized that the motivation of males to attract the female would be higher in (1) than in (2) since males would be familiar with viewing females under the former conditions, and have no experience of females' appearance under the opposite UV conditions. This might be reflected in differences in the intensity or pattern of female choice between the two trials.

For a given trial, we picked at random one male from each band treatment, within a particular male UV pre-exposure group. We used each male four times but in different combinations of four males. As stated above, females were naive to the quartet of males they encountered in the mate-choice apparatus, ensuring that female choice was not influenced by previously established male–female bonds. Other factors that may influence female choice, such as size, condition, beak colour or song rate of males, were assumed to be random with respect to colour of leg band. As further insurance, we rotated bands among sets of males between trials as well as during pre-exposure. In addition, we allocated males to particular stimulus cages, particular filters and arms of the mate-choice apparatus at random, so that female band-colour preference should not be confounded by any unknown bias.

As before, we analysed the time spent by the female, and the number of hops, in front of each of the four males, including data only after she had visited each male at least once. We performed repeated measures ANOVA to test for an effect of band colour, and variation in band-colour preference with both female UV treatment and male pre-exposure. This was followed by a separate analysis of variance within each female UV treatment. Square root transformation normalized the residuals from the hop analysis; the time data did not require transformation. Analysis was performed using the routine MANOVA in SPSS (SPSS Inc. 1988) with simple contrasts used to compare all band treatments with the unbanded condition.

Results

The time spent viewing males with different colour bands differed between those females who viewed males through UV-transmitting filters (UV+ females) and those for whom any UV reflectance from male plumage and leg bands was removed (UV− females) (ring colour*female UV treatment interaction: $F_{3,21}=6.10$, $P<0.01$). Separate analysis of the preferences of UV+ and UV− females showed that only UV+ females showed an effect of band colour (band colour $F_{3,21}=6.13$, $P<0.01$) whereas UV− females showed no preference ($F_{3,21}=1.03$, NS). In the case of the UV+ females, the colour preference was in the same direction as that found by Burley et al. (1982). On average, females spent most time in front of red-banded males and least in front of light green-banded males (Fig. 2). Orange and unbanded males appeared to be of intermediate attractiveness (red versus unbanded: $t_{21}=2.66$, $P<0.05$; orange versus unbanded: $t_{21}=1.05$, NS; green versus unbanded: $t_{21}=-1.49$, NS). Analysis of the number of hops made in front of each of the males yielded an identical pattern of results and significance as the time analysis described above.

An apparent lack of band-colour preference among UV− females may arise if females spend roughly equal amounts of time in front of the four stimulus males, or if individual females show strong preferences for different band colours so that the mean preferences across females are equal. We carried out a two-sample *t*-test on the standard deviation of the time females spent in front of each of the four males. Standard deviations were significantly higher for UV+ females than UV− females ($t_{13}=2.25$, $P<0.05$), implying

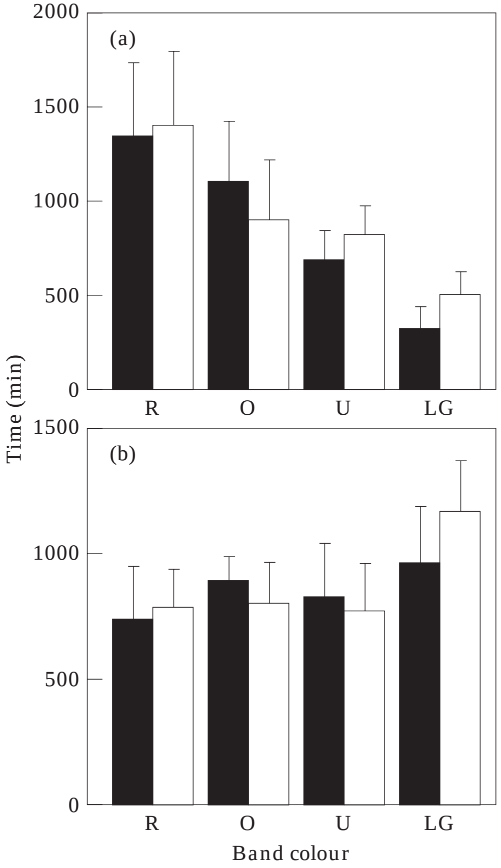

Figure 2. Mean time (+SE) spent by females in front of red- (R), orange- (O), light green-banded (LG), or unbanded (U) males in experiment 2. In (a) females viewed males through UV+ filters, in (b) females viewed males through UV− filters. ■: Females viewing UV+ pre-exposed males; □: females viewing UV− pre-exposed males.

that UV+ females showed strong preferences for particular males (usually red-banded males) whereas UV− females visited males more equally.

We found no effect of male pre-exposure on female choice. There was no difference in the preference of females in trials where males were pre-exposed under the same UV conditions as the female compared with trials where males were pre-exposed under the opposite UV conditions (female UV∗male pre-exposure interaction: $F_{1,14}=0.02$, NS). Similarly, the colour preference of females did not vary between trials with males of the same or opposite pre-exposure treatment (ring colour∗female UV∗male pre-exposure interaction: $F_{3,42}=0.08$, NS).

EXPERIMENT 3

Methods

In experiment 3 we tried to determine whether the absence of a female band-colour preference under UV− conditions resulted from (1) the change in appearance of the leg bands or (2) the change in the overall appearance of the birds. We used 16 female and 32 male zebra finches, bought from separate suppliers 2 weeks before the experiment began. The procedure was very similar to that followed in experiment 2. However, for this experiment we used two types of leg band: UV+ leg bands (red, orange and light green) and UV− bands (again red, orange or light green to human eyes, but with ultraviolet reflectance removed). These were standard coloured plastic leg bands coated by either UV-transmitting or UV-blocking filters (as in Bennett et al. 1996, experiment 3).

We divided males into two groups and assigned them either UV+ or UV− colour bands. Eight females were pre-exposed to males wearing UV+ bands (Band: UV+) and eight to males wearing UV− bands (Band: UV−). All were pre-exposed through UV+ filters so that the difference between the two groups lay only in the UV nature of the rings and not in the appearance of male plumage, beaks or legs.

Pre-exposure lasted 5 days after which mate-choice trials began. Again, trials were 3 h long with two trials per day. Each female was tested only once, with males of the same treatment to which she had been pre-exposed (either Band: UV+ or Band: UV− males), but with individuals she had not previously encountered. During mate-choice trials, males and females always viewed each other through UV-transmitting filters. All other details are as described for experiment 2.

Results

There was a significant overall effect of band colour on the time females spent in front of each of the four males ($F_{3,42}=10.35$, $P<0.001$). But there was no difference between the colour preference of Band: UV+ females and Band:

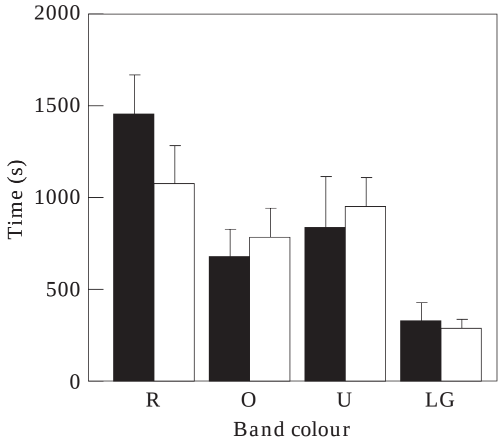

Figure 3. Mean time (+SE) spent by females in front of males of red- (R), orange- (O), light green-banded (LG), or unbanded (U) males in experiment 3. ■: Bands were overlain with UV-transmitting filters; □: bands were overlain with UV-blocking filters.

UV− females (band colour∗treatment interaction; hops: $F_{3,42}=0.32$, NS, time: $F_{3,42}=0.88$, NS). As in the UV+ treatment of experiment 2, females showed a Burley-type preference for red-banded males over orange and unbanded birds, and a dislike of light green-banded males (Fig. 3; time: red versus unbanded $t_{42}=2.17$, $P<0.05$; orange versus unbanded $t_{42}=-0.92$, NS; green versus unbanded $t_{42}=-3.33$, $P<0.01$). Analysis of the number of hops revealed an identical pattern of results.

GENERAL DISCUSSION

Under conditions where UV wavelengths were available to the birds, female zebra finches preferred males with red leg bands to unbanded or orange-banded males and avoided light green-banded males. This supports the original findings of Burley and her colleagues (e.g. Burley et al. 1982). In contrast, we found that when females viewed males through one-way glass (experiment 1) or UV-blocking filters (experiment 2), no band-colour preferences were observed. This accords with the previous finding that the UV waveband is involved in female mate choice in zebra finches (Bennett et al. 1996).

The absence of a female band-colour preference under UV− conditions in experiment 2 might be explained by (1) a change in the appearance of the bands (including possible changes in the perceived hue, luminance, saturation or an associated change in the relative conspicuousness of bands), or (2) a change in the males' overall appearance or the appearance of traits other than the leg bands. However, in experiment 3, females chose between sets of males wearing either UV+ or UV− colour bands, but both viewed through UV-transmitting filters, and showed a Burley-type colour preference regardless of the UV character of the bands. This indicates that females can discriminate and rank different coloured bands according to preference without the UV component (perhaps not surprising given the variation in spectral reflectance of the bands in the human visible spectrum, 400–700 nm; Fig. 4). Therefore it is probably the overall appearance of the birds or the appearance of traits other than the leg bands that is the key to the lack of female band-colour preference under UV− conditions in experiment 2.

There appear to be several potential explanations for the disappearance of a band-colour preference when the UV reflectance of males' plumage is removed. Owing to the unusual appearance of males under UV− conditions, females may no longer express sexual preferences or may use different choice criteria (e.g. male song). The mean time spent viewing males did not differ significantly between UV+ and UV− females ($F_{1,13}=0.04$, NS); however, UV− females spent more equal amounts of time in front of the four males than their UV+ counterparts. This suggests that females may take longer to assess males under UV− conditions and that our trials were perhaps not sufficiently long for a band-colour preference to emerge. A further possibility is that differences in male behaviour are responsible for the differences in the pattern of choice between UV+ and UV− females. Male behavioural patterns (e.g. posture, song, display) play an important role in sex recognition in female zebra finches (Vos 1995) and female choice is strongly influenced by the behaviour of males towards females (ten Cate & Mug 1984; ten Cate 1985; Houtman 1992; Collins et al. 1994). A lack of band-colour preference under UV− conditions might therefore be due to reduced male motivation to attract a male, as well as reduced female motivation to select one. Without using one-way filters (we tried, but failed, to manufacture one-way UV-transmitting filters),

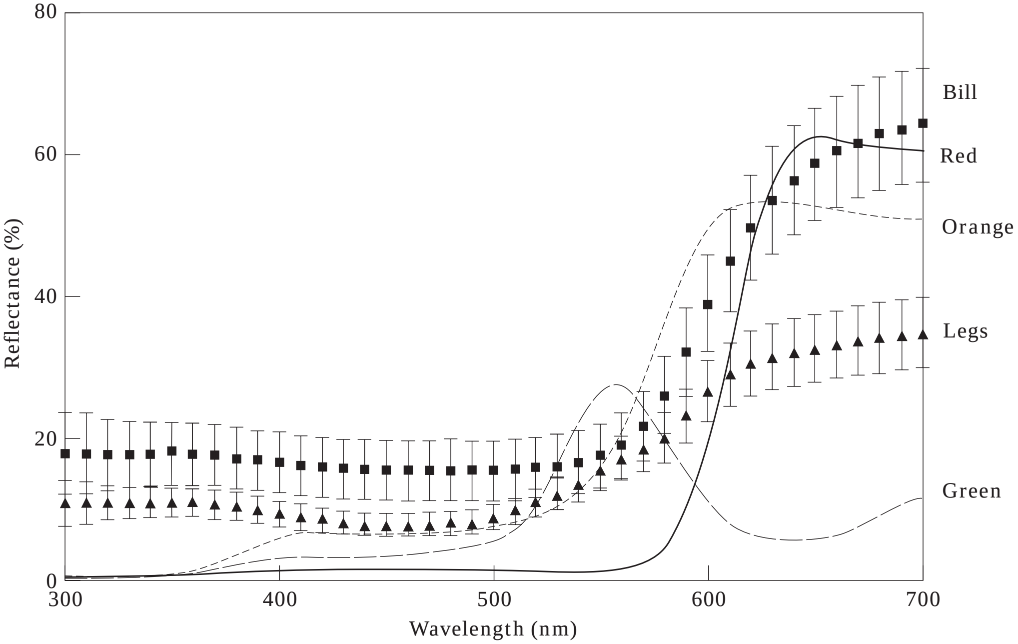

Figure 4. Spectral reflectance of upper mandibles (‘bill’) and legs of male zebra finches, and of red, orange and green colour bands. All values are the mean of five replicates from different individuals/bands selected at random; birds were sexually active but unpaired at the time of measurement. Spectra are the radiance of the sample relative to that of a 99% reflection Spectralon white standard. Illumination was by Xenon lamp and the reflected radiance was measured with an S1000 spectroradiometer using approximately parallel radiance beams. Illumination and reflection were taken at 45° to the sample’s surface. Bill and leg means (± SE) are plotted at 10-nm intervals for clarity only; measurements were actually taken at 0.35-nm intervals. Standard errors for band measures are too small to plot.

it was impossible to isolate one effect from the other.

Male behaviour may have had an effect on female choice but male UV treatment during pre-exposure had no detectable influence. Males viewing females under the opposite UV conditions to those they experienced during pre-exposure did not elicit a different pattern or intensity of female response from males that were pre-exposed through the same filter type as encountered in their mate-choice trials. This implies that treatment during pre-exposure had no effect on males’ behaviour towards females and their willingness to engage in courtship under different UV conditions. Alternatively, reduced male motivation to attract females may not interfere with the mate-choosing behaviour of the female, as measured by the time spent viewing, or the number of hops in front of, potential partners. This seems unlikely given the importance of male behaviour already outlined above.

Our data support the idea that female zebra finches have a preference for red leg bands, although the possibility that females are responding to properties other than hue, such as the intensity or saturation of the rings, cannot be ruled out (Burley et al. 1982). A potential explanation for such a colour preference is the transfer or extension of a preference for red beaks. Figure 4 shows the similarity in spectral reflectance of red bands and bills, although red bands have a steeper rise in reflectance at long wavelengths than the range of bills we measured, and thus are liable to appear more saturated in colour to human or avian eyes (see e.g. Endler 1990). Of course, how similar these colours appear to zebra finches will depend on their, as yet unknown, hue discrimination ability. A preference for red may be acquired during sexual imprinting. Weisman et al. (1994) found that female zebra finches prefer males with the same bill colour as their father, to males with the same bill colour as their mother.

Since males generally have redder beaks than females (Burley & Coopersmith 1987), such a mechanism would normally lead to a preference for red-beaked males. It is thus possible that a preference for a red beak is a mechanism for sex recognition, although why females should choose to respond to beak colour in the presence of far less ambiguous indicators such as the red cheek patches, or black and white chest stripes, is unclear.

The redness of the beak may also be used as a criterion for assessing the phenotypic quality of males since beak colour is correlated with male fitness, brood size and offspring weight at fledging (Houtman 1992; De Kogel & Prijs 1996). Beak colour is also highly correlated with song rate (Houtman 1992; De Kogel & Prijs 1996) and several authors have found that beak colour is unimportant (Weisman et al. 1994; Vos 1995) or that song rate is the more important cue for female choice (Burley 1981; Houtman 1992; Collins et al. 1994). However, given the influence of ultraviolet cues demonstrated above, observation of a preference among females for red beaks may simply depend on appropriate laboratory lighting conditions. The effect may not be straightforward, as a key factor may be the lighting of the test apparatus in relation to that in the familiar home cage, or when sexual imprinting occurred. However, we note that in cases where a preference for red beaks has been demonstrated, males with naturally red beaks were presented (Burley & Coopersmith 1987; De Kogel & Prijs 1996), whereas in almost all cases where beak colour proved unimportant, the colour of the beaks was manipulated by painting with nail varnishes. The spectral reflection of these paints, including the UV, has not been investigated.

There is a possibility that leg-band colour influenced other male characters, such as display rate, and that the latter were the primary cue for female choice. Collins et al. (1994) found no effect of manipulation of beak colour on song rate but whether leg-band colour could affect such traits requires further investigation. There is evidence that band colour can influence interactions between males, with red-banded males dominant over light green-banded males (Cuthill et al. 1997). Such interactions could be observed by females during pre-exposure and might influence their subsequent mate preferences. It is, nevertheless, unlikely that the cue(s) responsible for the band-colour preference can explain mate-choice preferences without consideration of the overall appearance of the birds, as shown by the masking of the colour-band preference when UV plumage reflections are removed.

This study suggests that failure to detect colour preferences among female zebra finches may be due to the absence or removal of UV wavelengths under experimental conditions, as can occur with the use of standard artificial illumination or one-way mirrors. Our findings support the conclusions of Bennett et al. (1996, 1997; Andersson & Amundsen, in press) that UV plumage reflections have an important influence on mate-choice decisions and therefore highlight the extreme importance of considering the nature of the avian visual system in investigations of the evolution and role of colour in avian behaviour. These considerations extend to the choice of lighting and use of materials transparent to humans, in laboratory experiments on non-human subjects.

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