

## THE EFFECTS OF THE LIGHT ENVIRONMENT ON PREY CHOICE BY ZEBRA FINCHES

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### Summary

Recent research has highlighted the extent to which birds utilise ultraviolet vision in mate choice and foraging. However, neither the importance of the ultraviolet compared with other regions of the visual spectrum nor the use of wavelength cues in other visual tasks have been explored. We assessed the individual choices of zebra finches (*Taeniopygia guttata*) for different-coloured seeds (red and white millet) under lighting conditions in which filters selectively removed blocks of the avian-visible spectrum corresponding to the spectral sensitivity of the four retinal cone types that subserve colour vision in this species. The effects corresponded to those predicted from the calculated distances between seed types, and between

each seed type and the background, in a simple model of tetrachromatic colour space. As predicted for this foraging task, the removal of long-wavelength information had a greater influence than the removal of shorter wavelengths, including ultraviolet wavelengths. These results have important implications for predator–prey interactions and suggest that future studies of natural foraging should consider variations in the light environment.

Key words: foraging, behaviour, light environment, colour vision, ultraviolet vision, zebra finch, *Taeniopygia guttata*.

### Introduction

Recent research has highlighted the extent of the differences between human and avian colour vision (for a review, see Cuthill et al., 2000). Avian retinæ typically possess four spectrally distinct single-cone types (compared with three in humans; Walls, 1963). One has maximum sensitivity ( $\lambda_{\max}$ ) in either the ultraviolet or violet region of the spectrum (see e.g. Bowmaker et al., 1997; Cuthill et al., 2000). This means birds are visually sensitive to ultraviolet light, broadening the avian visual spectrum (approximately 320–700 nm) compared with humans (approximately 400–700 nm). This additional cone type also means that birds are potentially tetrachromatic and may perceive many more hues than humans (Burkhardt, 1989; Cuthill et al., 2000; Goldsmith, 1990; Jacobs, 1992; Vorobyev et al., 1998). These findings have major implications for all visually orientated tasks within the behavioural repertoire of birds. The majority of recent work into avian colour vision has focused primarily on the use of conspecific ultraviolet plumage cues in mate-choice decisions (for a review, see Cuthill et al., 1999). However, since the diets of many birds potentially contain some ultraviolet-reflective prey items, such as fruits, seeds and invertebrates (Burkhardt, 1989; Church et al., 1998a; Silberglied, 1979; Willson and Whelan, 1989), the use of ultraviolet wavelengths for prey detection, discrimination and

recognition is not surprising. Indeed, recent research has suggested that ultraviolet wavelengths may provide important cues in avian foraging behaviour (Church et al., 1998b; Koivula and Viitala, 1999; Siitari et al., 1999; Viitala et al., 1995).

Avian ultraviolet vision is of particular interest since humans are blind to these wavelengths, and research indicates that ultraviolet vision is extensively utilised in birds (see references above). However, there are no strong reasons for assuming that it is an especially important region of the avian visual spectrum, and other regions of the visual spectrum may be equally or more important depending on the visual task in question (but see Andersson, 1999; Bennett and Cuthill, 1994). Hence, this study investigates the effects of blocking different regions of the avian visual spectrum on foraging choice in the zebra finch. In one experiment, we examine the effects of removing ultraviolet wavelengths on preferences for different seed types and test the effect of decreasing conspicuousness through the use of non-edible distracters. In a second experiment, we manipulate the light environment across the entire spectrum, including the ultraviolet wavelengths, to determine how blocking different spectral regions affects the foraging choices of zebra finches.

### Materials and Methods

#### Experiment 1: the effect of ultraviolet cues and distracters on prey choice

We used a total of 12 captive-bred, wild-type, male zebra finches, eight test birds (housed individually) and four companion birds (housed together), obtained from commercial suppliers. The birds were housed under a photoperiod of 16h:8h L:D, at a temperature of  $19 \pm 2^\circ\text{C}$ . Birds were also ringed with a single orange leg band. Commercial bird seed and water were available *ad libitum* during non-experimental periods. Room illumination consisted of one high-frequency fluorescent tube and one Truelite tube (described below).

'Prey' items in the foraging trials consisted of red and white millet seeds, with or without similarly sized stone distracters (termed D+ and D-, respectively). The distracters were also red and white. Prior to the trials, the reflectance spectra of both seed and stone types were measured. Measurements were made, normal to the plane of the sample, using a Zeiss MCS 500 spectrophotometer, with samples illuminated at  $45^\circ$  to normal by a Zeiss CLX xenon light source. Five measurements were taken from random locations within each sample, and each area measured was a circle of 2 mm diameter. Spectra were measured against a 99% Spectralon™ reflectance standard, at intervals of 0.81 nm from 300 to 700 nm (Church et al., 1998a).

The apparatus consisted of a central area and four arms, each leading to a foraging arena within a moveable cage (Fig. 1). The cages were lined with aluminium foil overlaid with frosted ultraviolet-transmitting acrylic sheet to maximise the quantal flux within each cage and ensure that the birds were photopically adapted (as in Bennett et al., 1996).

Overhead illumination was provided by 12 equally spaced

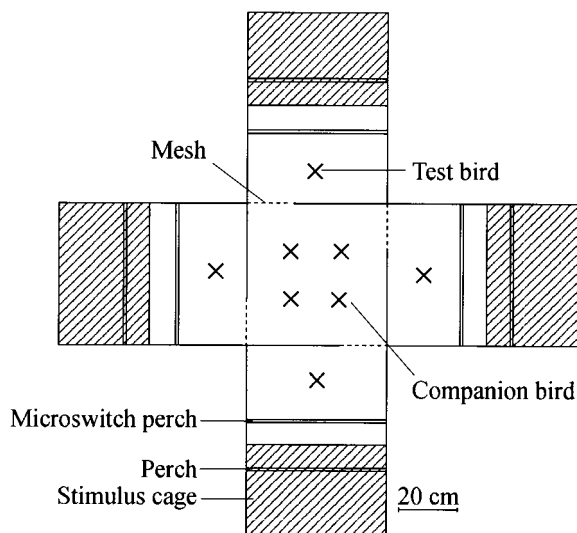


Fig. 1. Plan view of the apparatus used in experiments 1 and 2, consisting of a central chamber with four arms, ending in detachable cages. Filters are placed horizontally over the cages in each arm of the apparatus. During each trial, there is one test bird in each arm and four companion birds in the central chamber (indicated by x).

(at 10 cm intervals) 1.8 m long, 100 W, Truelite fluorescent tubes suspended 1.5 m above the apparatus. There are no specific data for zebra finches' natural light environment, and there is huge variation in those natural light environments that have been measured (see, for example, Endler, 1993). The key point was not to reproduce the irradiance spectrum of a particular light environment, but to use lighting that has a spectral emission incorporating wavelengths across the entire avian-visible spectrum. These tubes have a spectral emission designed to reproduce the ultraviolet component of natural daylight, with more ultraviolet emission than standard fluorescent tubes (Fig. 2A). The percentage of the total quantal flux ( $Q_{t\ 300-700\text{ nm}}$ ) that was in the ultraviolet ( $Q_{t\ 300-400\text{ nm}}$ ) was 7.1%. Measurements were taken using a Spex 1681 spectrophotometer connected to an integrating sphere positioned horizontally at the centre of the cages.

Prior to the experiment, all birds were acclimated to the apparatus (including the filters) and the foraging task for approximately 9 h. On experimental days, transparent filters were mounted over the cages to control the wavelengths transmitted into each cage such that ultraviolet wavelengths were either transmitted (UV+) or blocked (UV-). Any difference in the total amount of light transmitted through these filters was minimised by balancing the total quantal flux to reduce any potentially confounding effects due to variations in brightness (Bennett et al., 1996). This was achieved by using

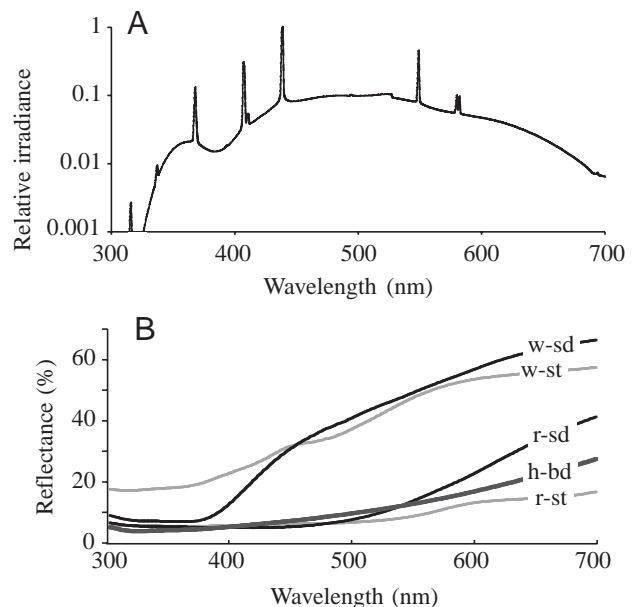


Fig. 2. (A) The relative irradiance of the Truelite tubes used in the experiment (quantal flux scaled to a maximum of 1). A logarithmic y-axis is used because of the large spikes in emission at certain wavelengths; this is typical of fluorescent lighting. (B) Mean reflectance spectra for each seed type and corresponding stone distracter used in experiment 1 (w-st, white stone; w-sd, white seed; r-st, red stone; r-sd, red seed), plus the brown hardboard background (h-bd) used in experiment 2. Reflectance is relative to a 99% white reflectance standard.

a thicker UV+ filter to compensate for the reduction in total quantal flux under the UV- filter resulting from the blocking of ultraviolet wavelengths.

On experimental days, food was removed from all birds before the lights came on (08:00 h; approximately 3 or 4 h of food deprivation for the early and the late trial, respectively). During trials, four companion birds were placed in the central area (with *ad libitum* commercial seed and water), and one test bird was placed in each of the four arms. The companion birds were introduced since zebra finches are gregarious (Zann, 1996) and were relatively inactive in isolation during habituation trials. The mesh section in each arm was offset; the test birds could view the companion birds but not the other test birds. The experiment had a repeated-measures design. Test birds, stimulus cages, filters and the presence or absence of stone distracters were arranged according to a hyper-Graeco-Latin square design (Fisher and Yates, 1963), with four treatments (UV+ or UV-, and D+ or D-). All test birds had one trial on each of four experimental days (two early and two late trials).

Each trial lasted 40 min; for the first 10 min, test birds were prevented from entering the foraging arena by a vertically mounted UV+ filter to allow habituation to the light environment; the filter was then removed, and the birds were allowed to forage for 30 min because, during habituation trials, this was enough time for them to eat a significant proportion of the seeds without eating all the seeds (which would prevent any determination of preference). The foraging arenas were hardboard trays containing a random mixture of 80 seeds (40 red millet seeds and 40 white millet seeds) either with or without 80 similarly sized stone distracters (again 40 red and 40 white).

At the end of each trial, birds were returned to their home cages, and the number of each type of seed eaten was recorded. As these data were not normally distributed, they were Box-Cox-transformed (Aitken et al., 1989) prior to analysis of variance (ANOVA). Where significant univariate results are reported, multivariate analysis of variance (MANOVA) on the number of white and red seeds, as joint dependent variables, was also significant (based on Wilk's  $\lambda$ ; see Chatfield and Collins, 1995).

#### *Experiment 2: the effect of blocking different regions of the avian-visible spectrum*

The protocol was similar to experiment 1, using the same birds. However, there were four filter types (Fig. 4A), each specifically chosen to block regions of the spectrum corresponding approximately to the regions of sensitivity of each single cone type in the zebra finch (Bowmaker et al., 1997). The filters, henceforth referred to as ultraviolet-blocking (UV-), short-wavelength-blocking (SW-), medium-wavelength-blocking (MW-) and long-wavelength-blocking (LW-), consisted of Lee Filter 226 and Rosco Supergel™ filters 14, 339 and 73, respectively. These filters were balanced as closely as possible for total quantal flux, again to control for potential effects due to variation in brightness (ratio

1.00:0.91:0.89:0.81 for UV-, SW-, MW- and LW- filters, respectively). As in experiment 1, birds were acclimated to the different light environments by manipulating the lights in their holding room using the filters described above (for a minimum of 6 h per filter) and habituated to the experimental apparatus (for approximately 9 h). Trials differed in two important aspects from those in experiment 1. First, distracters were not used because they had no significant effect in the first experiment. Second, the duration of trials was increased to 1 h and the number of each seed type was doubled to 80 (160 seeds in total). As before, the number of each seed type eaten (Box-Cox-transformed) was the dependent variable in MANOVA and ANOVA.

To relate any effects on foraging performance to the likely influence of filters on colour perception, we calculated the distance in zebra finch colour space between seed types and between each seed type and the background, 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 output from the four single cones (Osorio et al., 1999a; Osorio et al., 1999b), are assumed to have a four-dimensional colour space. This can be decomposed into a brightness component, related to the sum of cone outputs, and three hue dimensions (see extensive discussion in 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 UV-, SW-, MW- and LW- sensitive cones (Burkhardt, 1989; Goldsmith, 1990; Neumeyer, 1992; Thompson et al., 1992; Vorobyev et al., 1998). The general approach follows that of Vorobyev and Osorio (Vorobyev and Osorio, 1998) and Hart (Hart, 1998) but somewhat simplified because, unlike these authors, our aim was simply to represent objects in avian colour space rather than to calculate threshold spectral sensitivities. The final model parallels that of Fleishman and Endler (Fleishman and Endler, 2000), which was based on data from Hart et al. (Hart et al., 1998) for the starling (*Sturnus vulgaris*).

To calculate the position in zebra finch colour space of the two seed types and the background, we first calculated the photon catches of the four receptor types by multiplying the irradiance spectrum of the Truelite tubes by the reflectance spectrum of each object and the effective spectral sensitivity of the cones. Following the notation of Vorobyev et al. (Vorobyev et al., 1998), the quantal catch of the  $i^{\text{th}}$  cone,  $Q_i$ , is given by Equation 1:

$$Q_i = \int_{\lambda=300}^{750} R_i(\lambda)S(\lambda)I(\lambda)d\lambda, \quad (1)$$

where  $R_i(\lambda)$  is the spectral sensitivity of cone  $i$ ,  $S(\lambda)$  is the reflectance spectrum of the object being viewed, and  $I(\lambda)$  is the irradiance spectrum of the illuminant. Integration was over

the avian-visible spectrum (wavelengths,  $\lambda$ , from 300 to 750 nm; this is a conservative estimate, as effective spectral sensitivity drops rapidly below 320 nm and above 700 nm). The reflectance spectra of the seeds and background (Fig. 2B) and the irradiance spectrum of the Truelite tubes (Fig. 2A) were measured as described previously. The spectral sensitivity, at a given wavelength, of each cone type was calculated as

$$R_i = P_i(\lambda)D_i(\lambda)M(\lambda), \quad (2)$$

where  $P_i(\lambda)$  is the normalised absorptance of the visual pigment in the  $i^{\text{th}}$  cone,  $D_i(\lambda)$  the transmission of the oil droplet in that cone, and  $M(\lambda)$  the transmission of the other optical media (cornea, aqueous humour, lens, vitreous humour) in the light path. Data on the absorbance of zebra finch visual pigments were taken from Bowmaker et al. (Bowmaker et al., 1997), using the visual pigment templates provided rather than the raw data. Following Hart (Hart, 1998), oil droplets were modelled as perfect cut-off filters (see also Bowmaker et al., 1997), based on the cut-off wavelengths ( $\lambda_{\text{cut}}$ ) provided (Bowmaker et al., 1997). The oil droplet  $\lambda_{\text{cut}}$  values correspond well to the equivalent data for four closely related Estrildid species measured by Hart et al. (Hart et al., 2000). We used the mean transmittance of these species' optical media in our model (wavelengths of 50% transmission of 316–318 nm; Hart et al., 2000), as these data were not available for the zebra finch.

The photon catches,  $Q_i$ , define the position of each object in zebra finch colour space. We used the Euclidean distance between any two objects in this colour space as our measure of 'colour' difference. 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). With perfect colour constancy, the colour would not change with the illuminant, which can be modelled by assuming that, whatever the illuminating spectrum, a grey object is located at the centre of the colour space (equal stimulation of all cones; Vorobyev and Osorio, 1998; Vorobyev et al., 1998; Fleishman and Endler, 2000). Our filters were chosen to remove the entire waveband to which each cone is sensitive, so we assume that colour constancy will fail in the conditions of our experiment (indeed, previous experiments indicated that this is true for the ultraviolet filter; Bennett et al., 1996; Hunt et al., 1997). To model this, we assume that the finch cones are always adapted to a grey background illuminated by an unfiltered Truelite tube, rather than adapting independently to the illumination in each filter treatment. This assumption is tested indirectly, because if zebra finches have perfect colour constancy in our experiment, then we expect to see no effect of treatment. We acknowledge that the actual perceived colour difference may not correspond directly to the metric we have used, but the latter provides a first approximation in the absence of psychophysical data (Thompson et al., 1992). We note here that we present our results in terms of a colour space centred on the achromatic locus (grey/white), as this is conventional for such representations (e.g. Burkhardt, 1989; Goldsmith, 1990;

Fleishman and Endler, 2000). Analysis with the brown hardboard experimental background as the adapting background produces directly equivalent results in terms of distances between objects in colour space.

As blocking light of a particular waveband may affect both perceived brightness and hue, we calculated two further metrics. The first, which we call 'single cone brightness', is the summed output of the four single cones. The weighted sum of cone outputs would correlate with perceived brightness in humans (Endler, 1990) and, in the absence of information on the relative weightings in zebra finches, we take the simple sum to approximate the avian equivalent. However, birds have another retinal cell type, the 'double cones', which are thought by some, on account of their abundance and broad spectral sensitivity, to constitute a secondary, or even the primary, achromatic ('brightness') channel in birds (see Cuthill et al., 2000; Vorobyev and Osorio, 1998). Thus, we calculated a further metric, 'double cone brightness', based on the calculated quantal catch of the double cones (again based on data in Hart et al., 2000; Bowmaker et al., 1997). Vorobyev et al. (Vorobyev et al., 1998) based their double-cone sensitivity calculations on that of the primary member of the cone-pair, thus ignoring the partial short-wavelength-sensitivity of the secondary member. We calculated double-cone photon catch assuming either that only the primary member contributes (as in Vorobyev et al., 1998), or that both members contribute in proportion to their cross-sectional area. In practice, for the objects and backgrounds in our experiment, this made a trivial difference, so we present only the data based on primary-member-only calculations here. All colour metrics are scaled such that the maximum possible distance between two points (e.g. black and white, or two saturated primary colours) is 1.

## Results

### Experiment 1

#### Reflectance spectra

The spectra of each colour seed and stone type were relatively well matched across all wavelengths (Fig. 2B). The greatest differences in reflectance between red and white millet seeds occurs in between the short- and long-wavelength regions of the spectrum (450–700 nm). The differences between the spectra of red seeds and red stones are greatest at long wavelengths. However, the white seed and white stone spectra differ marginally in both the long-wavelength and ultraviolet (300–400 nm) regions.

#### Foraging behaviour

Removing the ultraviolet component of the light environment had no significant effect on the numbers of each seed type eaten (red seeds:  $F_{1,7}=1.01$ ,  $P=0.348$ ; white seeds:  $F_{1,7}=4.52$ ,  $P=0.071$ ), despite a non-significant trend to eat more white seeds under UV+ (Fig. 3). There was also no effect of stone distracters (red seeds:  $F_{1,7}=0.02$ ,  $P=0.893$ ; white seeds:  $F_{1,7}=0.02$ ,  $P=0.884$ ) and no interaction between filter



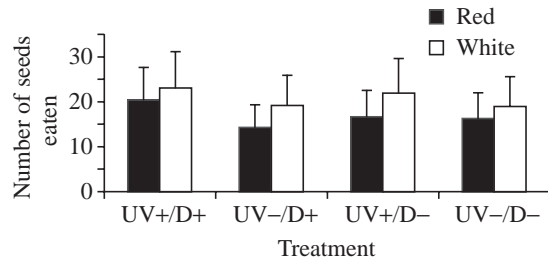


Fig. 3. Histogram indicating the numbers of each seed type (red or white) eaten under 'cryptic' and 'conspicuous' treatments (the presence or absence of stone distracters; D+ or D-), with or without ultraviolet (UV+ or UV-) wavelengths. Values are means + S.E.M. ( $N=8$  birds).

type and distracter type (red seeds:  $F_{1,7}=2.48$ ,  $P=0.159$ ; white seeds:  $F_{1,7}=0.27$ ,  $P=0.621$ ).

### Experiment 2

#### Colour space modelling

Fig. 4B–D indicates that, as must be the case, the maximum distances in colour space between seed types and each seed type *versus* background occur under natural light (incorporating all wavelengths). In addition, red seeds are always more similar to the hardboard background than the white seeds. Removal of particular wavebands has qualitatively similar effects for all discriminations: red *versus* white seeds or either seed type *versus* the background. Whether considering colour space, or only the brightness dimension encoded by the single cones, the removal of long wavelengths is predicted to have the greatest effect, with almost no difference between red seeds and background when long wavelengths (600–700 nm) are removed (Fig. 4B,C). The effect of removing other wavebands is qualitatively the same for both colour space and a single-cone-mediated brightness dimension. However, we would predict the double-cone mechanism to be most affected by the removal of medium wavelengths (500–600 nm; Fig. 4D).

#### Foraging behaviour

The number of each type of seed eaten varies significantly when different regions of the spectrum are blocked (MANOVA;  $F_{6,40}=2.36$ ,  $P=0.048$ ; Fig. 5). Although the number of red seeds eaten does not vary significantly between filters (red seeds;  $F_{3,21}=0.75$ ,  $P=0.565$ ), the data follow a similar pattern to the distances between seeds and background in colour space (Fig. 4B) or single-cone brightness (Fig. 4C), although the removal of ultraviolet wavelengths has somewhat less effect than predicted. The number of white seeds eaten varies significantly across the light environments (white seeds;  $F_{3,21}=4.63$ ,  $P=0.012$ ), increasing as red seeds become more difficult to distinguish (i.e. as the distance in colour space between the seeds and the background decreases). This is particularly apparent when long wavelengths are blocked (LW-). It should also be noted that these variations do not match the predicted effect of waveband removal on a putative

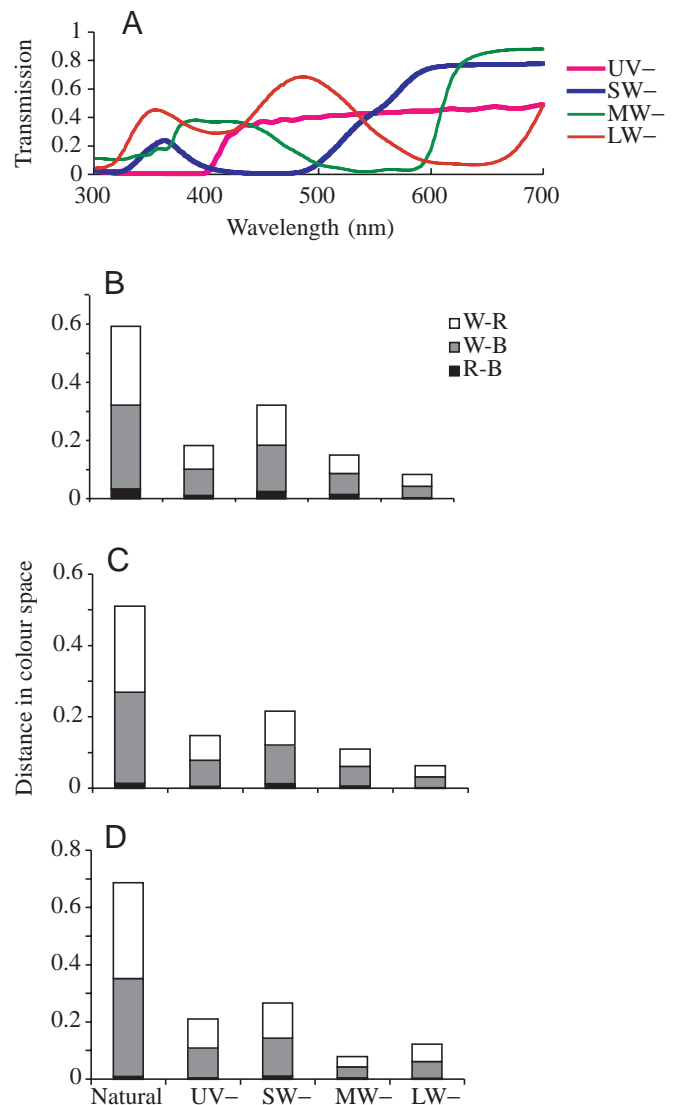


Fig. 4. (A) Mean transmission spectra for the four filter types used in experiment 2; ultraviolet-blocking (UV-), short-wavelength-blocking (SW-), medium-wavelength-blocking (MW-) and long-wavelength-blocking (LW-). (B–D) The relative distance in tetrahromatic colour space between the white and red seeds (W-R), the white seeds and the hardboard background (W-B), and the red seeds and the background (R-B) under natural light and the four filter types (B). (C) Equivalent distances calculated for a single-cone-mediated achromatic (brightness) mechanism. (D) Equivalent distances for a putative double-cone-mediated achromatic (brightness) mechanism.

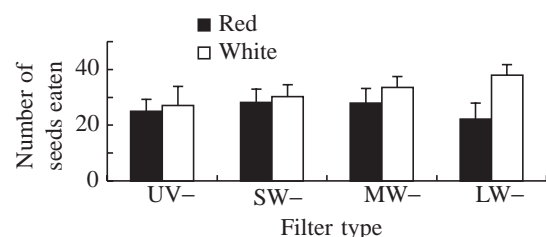


Fig. 5. Numbers of each seed type eaten under each of the four filter types (see Fig. 4A). Values are mean + S.E.M. ( $N=8$  birds).

double-cone brightness mechanism, where MW– should be most deleterious.

### Discussion

Our experiments provide new insights into the effects that modification of ambient light spectra can have on avian foraging behaviour. Contrary to most recently published studies (Church et al., 1998b; Koivula and Viitala, 1999; Siitari et al., 1999; Viitala et al., 1995), our first experiment revealed no significant effect of the removal of ultraviolet wavelengths on foraging behaviour. This experiment also failed to demonstrate any effect of the presence or absence of stone distracters. However, our second experiment demonstrated that blocking other regions of the spectrum has a significant effect on the seed choices of zebra finches.

In experiment 1, distracters did not affect foraging choices, suggesting that the birds did not find the foraging task more difficult when presented with additional similarly coloured, but non-edible, items. This raises the question of whether the distracters actually affected the crypticity of the seeds as perceived by the birds. Hence, it would be interesting to assess the effects on foraging behaviour of backgrounds that would have a greater effect on textural cues, for example those made entirely of distracters. These results also showed no effect of the absence of ultraviolet wavelengths on foraging choice. This is consistent with the low level of ultraviolet reflectance from the seeds and background (and the corresponding distances in colour space; Fig. 2B, Fig. 4B). However, in these experiments, it was not possible to determine the exact time the first seed was eaten nor its type. Such data would have been useful since previous research into foraging rates suggests that ultraviolet cues may be important in initiating searches, especially for cryptic prey (Browman et al., 1994; Church et al., 1998b).

In experiment 2, the nature of the ambient light spectra affects prey choice. The removal of long wavelengths had the greatest effect on choice, increasing the number of white seeds eaten (Fig. 5) whilst tending to reduce the number of red seeds eaten (though not significantly). This is consistent with the predicted differences in perceived colour between the seeds and the background because the distance in colour space between the red seeds and the background under this filter is negligible (Fig. 4B). The result is also consistent with an analogous experiment on female mating preferences in zebra finches, in which blocking the long-wavelength component of male plumage reflectance produced the greatest reduction in attractiveness (Hunt et al., 2001). The data presented here and elsewhere (Hunt et al., 2001) do not allow us to say whether the effect of blocking long wavelengths is through alterations in perceived hue or brightness, or both, because the predicted effect of treatments is similar (Fig. 4B,C). Likewise, effects on hue perception are not necessarily the result of changes in tetrachromatic colour space, but from altered two- or three-way comparison of cone types. The tetrachromatic goldfish *Carassius auratus* becomes trichromatic under some lighting

conditions (Neumeyer and Arnold, 1989). However, the fact that blocking the long waveband has a greater effect than blocking the medium waveband suggests that the single cones are more important than the double cones for the foraging task in this experiment. Double cones, whilst possessing the same visual pigment as the long-wavelength single cones, have a less densely pigmented oil droplet, so have a shorter wavelength of effective peak sensitivity than the long-wavelength single cones (Bowmaker et al., 1997; Hart et al., 2000). This is why removal of the medium (500–600 nm) waveband would affect double-cone function more than that of the long-wavelength single cones.

These results also indicate a lack of perfect colour constancy since, if this were the case, there should not have been variations in seed choice under the different light environments. When explicitly modelling separate adaptation to each filtered light environment (results not shown), there were no shifts in the separation of objects in colour space between treatments. This was expected as the model assumes perfect independent adaptation of each photoreceptor to the background, even when there is minimal light (see Vorobyev and Osorio, 1998; Vorobeyev et al., 1998). Despite research into avian spectral sensitivity (Emmerton and Delius, 1980; Prescott and Wathes, 1999), there is little research into the extent of avian colour constancy because of the difficulties associated with its determination. However, it has been suggested that avian colour constancy should be good, as a result of the small overlap in spectral sensitivity between the single cone types (Vorobyev et al., 1998). The goldfish, another tetrachromat, exhibits colour constancy (Neumeyer et al., 1997), so it would be surprising if birds did not. The key question that requires exploration if visually directed behaviours are to be fully understood is, under which condition is constancy expected to break down? It seems to under the large manipulations of the light environment in this experiment, but future research should also examine the extent of these effects under a range of natural light environments. This should be investigated under ambient light spectra and with natural backgrounds, particularly those with a relatively high ultraviolet reflectance (such as sand or snow) *versus* those without (such as clay soil).

Since the appearance of objects can alter significantly in different light environments, there are obvious implications for visually orientated behaviours (Endler, 1993; Endler and Théry, 1996). We speculate that if prey choice also varies between more natural light environments, selection pressure on prey and plant species that rely on animal dispersal could also vary in different environments. Since zebra finch vision is also similar to that of other passerines (Bowmaker et al., 1997; Cuthill et al., 2000), variations in the light environment will potentially affect many bird species. Zebra finches tend to inhabit drier areas with seeding grasses (Zann, 1996), which will experience a fairly limited range of light environments compared with some habitats (although there will obviously still be large fluctuations as a result of climate changes and time of day; Endler, 1993). There could be even stronger

implications for prey of other avian species, particularly of tree-foraging guilds, since woodlands possess a far greater range of light environments (Endler, 1993).

Changes in the spectral quality of light also have the potential to affect the behaviour of visually guided predators in ways that have direct consequences for prey population dynamics. Our results only reflect simple choices between equally available seed types; however, it may be fruitful in future to consider the effects of frequency-dependent availability on seed choice (see Church et al., 2001), since these will have greater implications for plant population stability and dynamics (Greenwood, 1985; Pacala and Crawley, 1992). Overall our results suggest that future work incorporating visually orientated behaviours needs to take into account the potential effects of any variation in the light environment.

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