

AVIAN ULTRAVIOLET VISION AND FREQUENCY-DEPENDENT SEED PREFERENCES

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Summary

It is well established that ultraviolet sensitivity plays an important role in the visually guided behaviour of birds. From a foraging perspective, evidence now exists that ultraviolet wavelengths are used by birds when foraging for insects, berries, seeds and mammals. Here, we present the results of two laboratory experiments that test the effect of removing (i) ultraviolet wavelengths and (ii) wavebands in the human-visible region on the frequency-dependent seed preferences of zebra finches (*Taeniopygia guttata*). Although the seeds and backgrounds used in our experiments reflected mainly at long wavelengths, we found that removal of ultraviolet wavelengths significantly changed the strength and direction of frequency dependence compared with full-spectrum illumination. We also found that the removal of ultraviolet wavelengths (300–400 nm) did not affect the strength of frequency

dependence compared with the removal of short wavelengths (approximately 400–500 nm), medium wavelengths (approximately 500–600 nm) or long wavelengths (approximately 600–700 nm). Since frequency-dependent selection has direct consequences for the stability of prey populations and the spectral quality of ambient light is known to vary considerably with climate, time of day and local habitat geometry, our results suggest that ultraviolet wavelengths might play an important role in the dynamics of plant populations. However, we urge caution about overestimating the importance of ultraviolet wavelengths compared with wavelengths in the human-visible spectrum.

Key words: zebra finch, *Taeniopygia guttata*, ultraviolet, colour vision, seed preference, foraging, frequency-dependent selection.

Introduction

Birds, like many other vertebrate and invertebrate taxa (Jacobs, 1992; Tovée, 1995), are visually sensitive to ultraviolet wavelengths. Avian 'ultraviolet vision' has important implications for our understanding of colour patterns in the natural world because experimental studies involving birds have been instrumental in developing our conceptual understanding of sexual and defensive coloration (Bennett et al., 1994). However, with some notable exceptions (Burkhardt, 1982; Burkhardt, 1989), the role of ultraviolet information in avian behaviour was largely overlooked until the 1990s. Most studies of coloration that involved birds as selective agents did not consider a true 'bird's-eye' perspective (Bennett and Cuthill, 1994; Cuthill and Bennett, 1993; Cuthill et al., 2000), but instead relied on potentially flawed approaches based on human colour perception. Recent experimental evidence has revealed that ultraviolet information has a widespread impact on avian behaviour (Cuthill et al., 2000), most notably in the areas of mate choice (e.g. Bennett et al., 1996; Bennett et al., 1997; Hunt et al., 1997; Hunt et al., 1998; Hunt et al., 1999; Andersson and Amundsen, 1997; Andersson et al., 1998) and, of particular relevance here, foraging behaviour (Viitala et

al., 1995; Koivula and Viitala, 1999; Siitari et al., 1999; Church et al., 1998b; Church et al., 2001).

Avian colour vision

Human colour perception is derived from differential stimulation of three types of single cone cell in the retina. These cones have peak sensitivities (λ_{\max}) at wavelengths of approximately 560 nm ('red'), 530 nm ('green') and 420 nm ('blue') (Dartnall et al., 1983), and human spectral sensitivity ranges from approximately 400 to 700 nm. In contrast, physiological and behavioural studies suggest that diurnal birds almost always possess four spectrally distinct single-cone types (reviewed by Cuthill et al., 2000), with spectral sensitivity extending into the near-ultraviolet (320–400 nm). Microspectrophotometry of the avian retina (e.g. Bowmaker et al., 1997; Hart et al., 1998; Hart et al., 1999; Hart et al., 2000) has shown the presence of long-wave-sensitive (LWS; λ_{\max} 543–571 nm), medium-wave-sensitive (MWS; λ_{\max} 497–509 nm), short-wave-sensitive (SWS; λ_{\max} 430–463 nm), and either violet-sensitive (VS; λ_{\max} 402–426 nm) or ultraviolet-sensitive (UVS; λ_{\max} 355–376 nm) cone types. Birds are therefore sensitive to ultraviolet wavelengths that

humans cannot detect, and are also likely to possess 'four-dimensional' or tetrachromatic colour vision (Thompson et al., 1992). While the mere possession of four cone types does not guarantee that colour vision is tetrachromatic (Neumeyer, 1992), all four cones have been shown to be involved in opponent channels in birds (Osorio et al., 1999a; Osorio et al., 1999b). Each type of avian single cone cell is also associated with a characteristic pigmented oil droplet (not found in humans), through which light is filtered prior to reaching the photopigment-containing cone outer segments (Partridge, 1989; Bowmaker, 1991). These droplets act as short-wavelength cut-off filters and narrow the range of sensitivity of each cone type, possibly increasing the discriminability of certain classes of spectra (Govardovskii, 1983; Goldsmith, 1990; Vorobyev et al., 1998) and enhancing colour constancy (Osorio et al., 1997; Vorobyev et al., 1998).

Avian ultraviolet vision and foraging behaviour

The role that ultraviolet wavelengths play in the foraging behaviour of birds is only just beginning to be understood. As an integral part of the avian visual system, it is reasonable to suppose that ultraviolet wavelengths provide some visual information which birds are able to utilize for prey detection and assessment. This assertion is strengthened when one considers that many of the invertebrates, fruits, seeds and flowers on which birds feed reflect in the ultraviolet to some extent (Silberglied, 1979; Burkhardt, 1982; Willson and Whelan, 1989; Church et al., 1998a). However, the importance of ultraviolet wavelengths in a foraging task will depend upon the ultraviolet reflectance characteristics not only of the prey but also of the background against which the prey item is viewed (Church et al., 2001). While it is true that many natural backgrounds of insects (e.g. soil, bark, leaves) do not usually reflect strongly in the ultraviolet (Kevan et al., 1996; Church et al., 1998a), other natural backgrounds, such as the sky (Silberglied, 1979), clouds (Mazokhin-Porshnyakov, 1957) and some fruits (Burkhardt, 1982; Willson and Whelan, 1989), flowers (Silberglied, 1979; Chittka et al., 1994; Dyer, 1996) and sands (Pope and Hinton, 1977) may have a strong ultraviolet component.

The handful of studies which have been carried out have provided evidence that ultraviolet wavelengths can be used by birds when foraging for seeds, berries, insects and mammals. There is also evidence that ultraviolet wavelengths enhance the conspicuousness of planktonic prey to foraging fish (Browman et al., 1994). One of the earliest demonstrations that ultraviolet wavelengths could be used by birds in a basic seed detection task was performed by Emmerton and Remy (Emmerton and Remy, 1983). They demonstrated that pigeons (*Columbia livia*) could forage successfully (although not very efficiently) for corn seeds presented on a diffusing plate illuminated by ultraviolet light, even though their peak foraging rate for the task was at much longer wavelengths (approximately 580 nm). However, the first experiments to demonstrate the importance of ultraviolet cues in a natural setting were carried out by Viitala et al. (Viitala et al., 1995), who demonstrated that

kestrels (*Falco tinnunculus*) used the ultraviolet-reflecting scent marks of voles to locate areas of high vole abundance; the kestrels spent more time hunting in areas containing artificial scent marks rather than in areas containing water-treated trails or no trails at all. Similar results were obtained for rough-legged buzzards (*Buteo lagopus*) by Koivula and Viitala (Koivula and Viitala, 1999). In contrast, laboratory experiments on adults and juveniles of another major predator of voles, Tengmalm's owl (*Aegolius funereus*), revealed no preference for arenas containing vole scent marks under ultraviolet illumination (Koivula et al., 1997). However, *A. funereus* is a nocturnal predator, and owls may lack ultraviolet cones (Bowmaker and Martin, 1978).

Ultraviolet wavelengths may also be used by birds foraging for fruits and berries. Some fruits, particularly those with waxy layers or 'blooms', reflect ultraviolet wavelengths, and it had long been postulated (Burkhardt, 1982) that these wax layers served to attract birds. Siitari et al. (1999) showed that adult redwings (*Turdus iliacus*) exhibited a significant preference for bilberries (*Vaccinium myrtillus*) in which the waxy, ultraviolet-reflecting layer was intact over berries with the wax rubbed off. This preference disappeared when ultraviolet cues were experimentally removed. This preference for ultraviolet-reflecting berries was probably learned, since juveniles failed to show similar preferences (Siitari et al., 1999).

Insects are important prey items for birds and many species, particularly among adult Lepidoptera, reflect ultraviolet strongly (Silberglied, 1979). However, avian ultraviolet vision may also have a role to play when searching for cryptic prey species. Church et al. (Church et al., 1998b) looked at the behaviour of blue tits (*Parus caeruleus*) searching for cabbage moth (*Mamestra brassicae*) or winter moth (*Operophtera brumata*) caterpillars on natural leafy backgrounds in a laboratory arena. They found that the blue tits took longer to find the first prey item in trials where ultraviolet wavelengths were removed from the illuminating light. This effect was greatest when the ultraviolet contrast between prey and background was largest, namely *M. brassicae* against a cabbage leaf. However, this reduction in foraging performance was temporary, presumably because the birds were subsequently able to learn to attend other salient visual cues (Church et al., 1998b). Since these experiments were carried out on cryptic prey, they are likely to represent conservative tests of the effects of ultraviolet wavelengths on foraging because most natural visual backgrounds (e.g. leaves, bark, soil) reflect relatively little ultraviolet light.

Evolutionary and ecological implications of avian ultraviolet sensitivity

While the use of ultraviolet wavelengths by foraging birds is now becoming well established, the evolutionary and ecological consequences of this fact have barely been explored. One major consequence is that our understanding of animal protective colour patterns (e.g. crypsis, warning coloration, mimicry) that have evolved in response to selection by birds is incomplete unless we consider the wavelengths to which

birds are sensitive (Church et al., 1998a; Majerus et al., 2000; Church et al., 2001). Consideration of the ultraviolet information available to birds could radically change our interpretation of the function of a given colour pattern. For example, in the grey shoulder knot (*Lithophane ornitopus*) caterpillar, which appears moderately cryptic against a leafy background to the human eye, maximum reflectance is in the ultraviolet. As a result, it is feasible (although not yet tested) that the grey shoulder knot is aposematic rather than cryptic, and is advertising distastefulness to birds via an ultraviolet communication channel (Church et al., 1998a).

Variation in the amount of ultraviolet present in ambient light spectra might also have important ecological consequences (Endler, 1993; Endler, 1997) via its impact on avian foraging behaviour. The spectral quality of light in terrestrial ecosystems is very diverse, varying with weather, time of day and local habitat geometry (Endler, 1993). For example, short wavelengths tend to dominate at dawn and dusk, and in certain shaded areas of woodland (Endler, 1993). This spectral variation has important consequences for the evolution and diversity of animal colour patterns and for visual perception by animals living in spectrally diverse environments (Endler and Théry, 1996; Fleishman et al., 1997). Crucially, the perception of the colours of prey by birds can change with the spectral quality of the illuminating light (Endler, 1990), although the magnitude of this effect will depend on how effective neural mechanisms of colour constancy are. If light spectra are sufficiently variable, it is likely that some fundamental processes that underpin population and community dynamics (e.g. visually mediated prey preferences) will be affected. Indeed, Endler (Endler, 1997) states that “Any factor that alters the function, reception and perception of colour can have dire consequences at the population, species or subspecies level”. While this general argument is not restricted to ultraviolet wavelengths, it is clear that variation in the ultraviolet component of irradiance spectra has the potential to affect the visually guided foraging behaviour of birds.

Avian colour vision and frequency-dependent seed preferences

Experimental studies which have addressed the effect of ultraviolet wavelengths on foraging behaviour have generally focussed either on whether the bird is simply able to detect ultraviolet or whether the bird's foraging performance (in terms of foraging rate or simple prey preferences) is affected by the addition or subtraction of ultraviolet wavelengths. However, since foraging behaviour is inextricably linked with population dynamics (Fryxell and Lundberg, 1994), it is possible that changes in foraging behaviour due to the amount of ultraviolet present in the environment could have ecological implications. Here, we examine the effect of varying the ultraviolet component of ambient light on frequency-dependent selective predation ('switching') by avian seed predators (Allen, 1988; Greenwood, 1984). Frequency-dependent selection is an important ecological process because

'apostatic' frequency-dependent selection (the over-predation of common prey types) tends to promote stability and diversity in prey populations by virtue of favouring the survival of relatively rare prey (Clarke, 1962; Murdoch and Oaten, 1975; Hassell, 1978), while 'anti-apostatic' selection (the overpredation of rare prey) tends to be highly destabilizing (Chesson, 1984). Thus, if the strength and/or direction of frequency-dependent seed selection depends upon the nature of the light environment, it could have important consequences for the local dynamics and diversity of plant populations.

In addition to considering the effects of ultraviolet wavelengths on frequency-dependent selection, we also examine the effect of wavebands in the human-visible spectrum on selectivity. It is arguable that previous research in this field has focussed on ultraviolet wavelengths at the expense of other wavelengths to which birds are sensitive. This could help to perpetuate the notion that ultraviolet wavelengths are somehow 'special' compared to other wavelengths. Only by comparing the effects of different wavebands on behaviour can we identify which wavelengths are most important for a given behavioural task (see also Maddocks et al., 2001; Hunt et al., 2001).

Materials and methods

Experimental subjects

Subjects were male zebra finches (*Taeniopygia guttata*), housed individually under a natural photoperiod. The birds holding room was illuminated by an ultraviolet-emitting fluorescent tube, as outlined in the experimental methodology below, and a conventional fluorescent tube. Subjects were maintained on a diet of commercial seed mix, and water was available *ad libitum*.

Experiment 1: the effect of ultraviolet wavelengths on frequency-dependent seed preferences

In this experiment, we examined the frequency-dependent seed preferences of eight male zebra finches foraging for red and white millet seeds on a sand background in the presence or absence of ultraviolet wavelengths. In each trial, 200 red and white seeds were presented in a ratio of either 9:1 or 1:9 (i.e. 180:20 or 20:180). Foraging trials were carried out in a purpose-built indoor arena (1 m×0.8 m×0.6 m) adapted from one used in previous studies (Church et al., 1998b). The inner surfaces of the arena were painted with a black vinyl matt emulsion, which had very low reflectance in the wavelength range 300–700 nm. A window (0.55 m×0.75 m) on the top surface of the arena was fitted with either an ultraviolet-blocking (UV-) or ultraviolet-transmitting (UV+) filter (Fig. 1A). The arena was illuminated by eight 100 W ultraviolet-emitting fluorescent tubes, powered by 240 V, 71 W, 35–40 kHz ballasts mounted above the filters (as used by Church et al., 1998b). A cage containing four 'companion' male zebra finches was attached to one end of the arena so that test individuals could forage in the normal context of a flock. These companion birds were not experimental subjects.

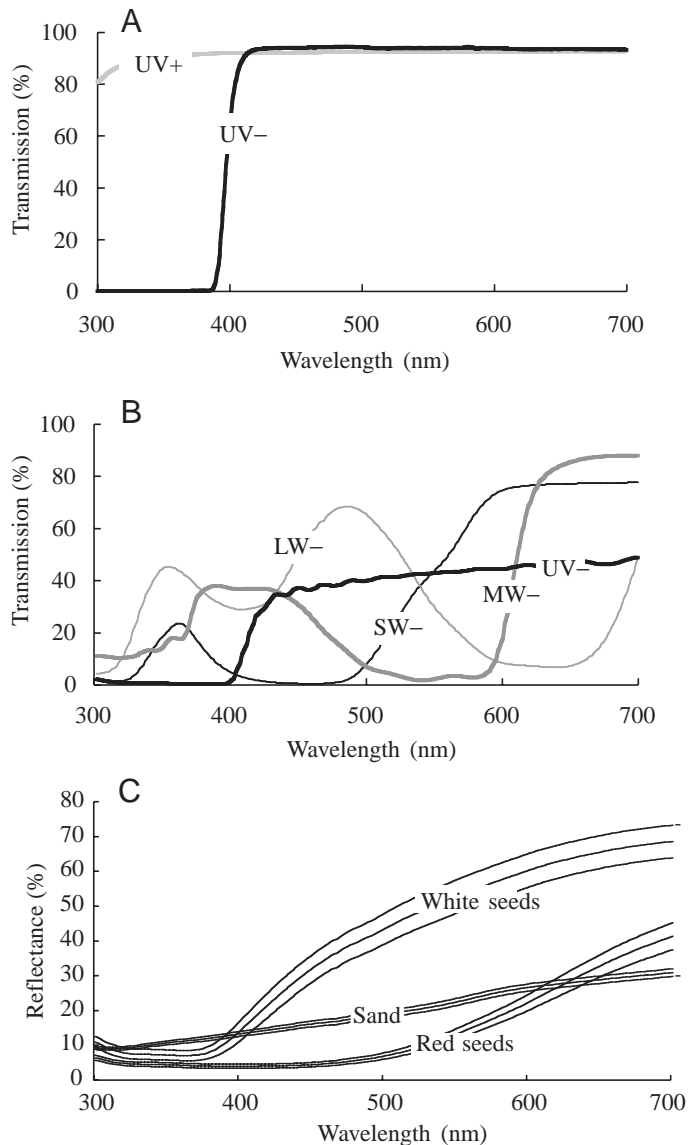


Fig. 1. (A) Mean transmission spectra of ultraviolet-transmitting (UV+) and ultraviolet-blocking (UV-) filters used in experiment 1. (B) Mean transmission spectra of ultraviolet-blocking (UV-), short-wavelength blocking (SW-), medium-wavelength blocking (MW-) and long-wavelength blocking (LW-) filters used in experiment 2. (C) Reflectance spectra of red millet seeds, white millet seeds and their sand background used in experiments 1 and 2. Values are means \pm S.E.M. ($N=8$ for all three means).

Subjects were allowed to forage for the seeds on a plywood tray (0.15 m \times 0.15 m) positioned in the centre of the arena floor. The foraging plot was covered in a thin layer of sand. In each trial, 200 randomly mixed seeds were distributed haphazardly throughout the plot. The density of prey was calculated as 8889 seeds m $^{-2}$. This density was comparable to the high prey densities used in previous experimental studies of frequency-dependent selective predation (e.g. Allen and Anderson, 1984; Allen, 1988; Allen et al., 1998).

Seed selection was measured under four experimental treatments: (i) UV+ filter, 90% red seeds; (ii) UV+ filter, 10%

red seeds; (iii) UV- filter, 90% red seeds; (iv) UV- filter, 10% red seeds. A balanced, randomised repeated-measures design was used, with all treatments presented to the subjects in a random order and all four treatments being carried out once each day. Individuals received each treatment once, with each of the four trials being carried out on alternate days of the experiment. The birds were deprived of food for 3 h prior to the start of a trial. Trials were conducted between 12:00 h and 17:00 h each day and lasted for 1 h. At the end of each trial, birds were removed from the arena and the number of each seed type remaining was counted.

Initial habituation to the foraging arena took place during the week prior to the experiment. Individuals were subject to one UV- and one UV+ habituation trial. Here, birds were given an equal number of red and white seeds (100 of each) and were again tested in a random order.

Experiment 2: the effect of different spectral regions on frequency-dependent seed preferences

The protocol of experiment 2 was virtually identical to that of experiment one, with the exception that different filters were used to manipulate ambient light. As in experiment 1, the experimental subjects were eight male zebra finches. In this experiment, though, we used filters that were broadly designed to block out the input to each of the cone cells of the zebra finch. This was achieved by using four different colour filters (Rosco SupergelTM filters number 73 'peacock blue', 339 'broadway pink', 14 'straw yellow', and Lee filter number 299 'ultraviolet'; Fig. 1B), with each filter blocking out a different part of the light spectrum (long wavelengths, LW-, medium wavelengths, MW-, short wavelengths, SW- and ultraviolet wavelengths, ultraviolet-, respectively). The filters were also selected so that the total quantal flux transmitted was approximately equal over the wavelength range 300–700 nm.

The frequency-dependent seed selection of each subject was measured under all eight combinations of filter (four levels: ultraviolet-, SW-, MW- or LW-) and frequency (two levels: 10% or 90% red seeds). Subjects were habituated to each of the four filter types for a total of 16 h in their holding rooms, during the 2 weeks prior to the start of the experiment. They also underwent initial habituation to the filter in the foraging arena. As with experiment 1, this was a balanced, randomised, repeated-measures design.

Spectrophotometric measurements

We measured reflectance spectra from samples of the red and white millet seeds and their sand background. Measurements were made at 0° to normal using a Zeiss MCS 500 spectrophotometer with samples illuminated at 45° to normal by a Zeiss CLX 500 xenon light source. The numerical apertures of the receiving and illuminating optics were approximately 1.9 and 1.5, respectively. The diameter of the measuring spot was 2 mm. Eight spectra were recorded for the sand and each of the seed types at 0.81 nm intervals from 300 to 700 nm and measured relative to a SpectralonTM 99% reflectance standard.

Data analysis

The β index (Manly, 1974) was used as a measure of preference in each experimental trial. In our experiments, with prey not replaced during experimental trials, the preference for red millet seeds, β_{red} was estimated by Equation 1:

$$\beta_{\text{red}} = \frac{\log(r/R)}{\log(r/R) + \log(w/W)}, \quad (1)$$

where R and W are the numbers of red and white millet seeds present at the start of a trial and r and w are the numbers remaining at the end of a trial. β lies in the range 0–1, with $\beta_{\text{red}}=1$ representing exclusive preference for red seeds and $\beta_{\text{red}}=0$ representing total rejection of red seeds. β cannot be calculated when all of one type of prey are eaten. On the few occasions when this occurred, a β value was calculated by setting the number of remaining prey equal to 0.0001.

Since individual birds were subjected to more than one trial in each experiment, all statistical analyses consisted of repeated-measures analysis of variance (ANOVA).

Results

Reflectance spectra

The reflectance spectra of the red and white millet seeds were generally dominated by long wavelengths (Fig. 1C). The sand background had a relatively flat reflectance, but tended to be more reflective at long wavelengths. The greatest differences in reflectance between red and white millet seeds occurred in the medium and long wavelength regions of the spectrum (500–700 nm). Although there was a discrepancy between the reflectance of these seeds between 380 and 400 nm, the greatest source of contrast in the ultraviolet was between the red seeds and the background. Red seeds were more similar to the sand background than white seeds at long wavelengths (600–700 nm), but the white seeds matched the background better in the ultraviolet (300–400 nm). The largest reflectance differences between both seed types and the sand occurred in the blue–green region of the spectrum (approximately 500 nm).

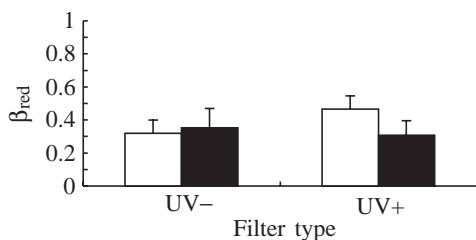


Fig. 2. Experiment 1: the effect of frequency and filter type (UV+ or UV-; see Fig. 1) on seed selectivity (β_{red}) by zebra finches. Open columns represent a 1:9 ratio (20:180) and filled columns a 9:1 ratio (180:20) of red:white millet seeds. Values are means + S.E.M. ($N=8$).

Experiment 1

We found no significant effect of either filter ($F_{1,7}=2.51$, $P=0.157$) or frequency ($F_{1,7}=1.04$, $P=0.341$) on the preferences of zebra finches for red seeds. However, there was a significant interaction between filter and frequency ($F_{1,7}=11.02$, $P=0.013$), with weak apostatic selection (i.e. an increased preference for red seeds when common) under UV- treatments and a stronger anti-apostatic effect in the UV+ treatments (Fig. 2). When analyzed independently, the anti-apostatic effect under the UV+ treatment was of borderline significance ($F_{1,7}=5.38$, $P=0.053$), while the apostatic effect under the UV- treatment was not significant ($F_{1,7}=0.25$, $P=0.633$). There tended to be an overall preference for white seeds over red seeds (i.e. mean β_{red} value for each treatment was less than 0.5), but this frequency-independent effect was not significant ($t=1.65$, d.f.=7, $P=0.14$).

β values can be subject to biases when less than 50% of available prey are eaten in experimental trials (Weale, 1992). We therefore examined whether our experimental manipulations affected the total number of seeds consumed (i.e. red seeds plus white seeds). In experimental trials subjects ate, on average, around 20% of the 200 seeds available (39.09 ± 17.58 seeds, mean \pm S.D., $N=32$). There was no effect of filter type on the total number of seeds eaten ($F_{1,7}=1.14$, $P=0.321$), but significantly more seeds were consumed in trials in which red seeds were rare than when they were common ($F_{1,7}=6.99$, $P=0.033$). There was no interaction between filter type and frequency ($F_{1,7}=0.38$, $P=0.558$).

Experiment 2

In this experiment, we found no evidence that seed preferences were frequency-dependent or that these preferences were modified by different light environments. Thus, there were no significant main effects of either filter ($F_{3,21}=0.18$, $P=0.911$) or frequency ($F_{1,21}=0.67$, $P=0.440$) and no significant interaction between filter and frequency ($F_{3,21}=0.65$, $P=0.590$; Fig. 3). Inevitably, all individual tests for frequency-dependent selection were non-significant (UV-: $F_{1,7}=0.00$, $P=0.997$; SW-: $F_{1,7}=2.35$, $P=0.169$; MW-:

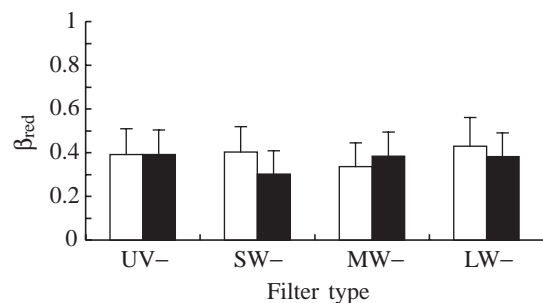


Fig. 3. Experiment 2: the effect of seed frequency and filter type (ultraviolet-blocking (UV-), short-wavelength blocking (SW-), medium-wavelength blocking (MW-) or long-wavelength blocking (LW-) on selectivity (β_{red}) by zebra finches. As in Fig. 2, open columns represent a 1:9 ratio (20:180) and filled columns a 9:1 ratio (180:20) of red:white millet seeds. Values are means + S.E.M. ($N=8$).

$F_{1,7}=1.08$, $P=0.333$; LW-: $F_{1,7}=0.67$, $P=0.439$). As with experiment 1, there was no overall frequency-independent preference ($t=1.3$, d.f.=7, $P=0.24$) even though the mean β_{red} value for each treatment was less than 0.5.

Zebra finches on average consumed approximately 25% of the 200 seeds available (49.20 ± 18.15 seeds, mean \pm S.D., $N=64$). There was no significant difference between the total number of seeds consumed at different frequencies or under different filters (frequency: $F_{1,21}=0.13$, $P=0.733$; filter: $F_{3,21}=2.35$, $P=0.101$; filter \times frequency: $F_{3,21}=0.83$, $P=0.495$).

Discussion

Our results are somewhat counterintuitive yet, if generally applicable, provide some interesting insights into the role that variation in spectral quality might play in ecological processes. We found that adding or removing ultraviolet wavelengths could significantly change the direction of frequency-dependent seed preferences, from weakly apostatic when ultraviolet was experimentally excluded to anti-apostatic when ultraviolet was present. However, frequency-dependence was unaffected by whether ultraviolet, SW, MW or LW wavebands were removed from the illuminating spectrum. The significant effect of ultraviolet was perhaps surprising considering that this is a visual task that is dominated by long-wavelength reflectance of the seeds and their sand background. Indeed, other long-wavelength-dominated behavioural experiments that have used similar filters have revealed that the LW-treatment has the greatest measurable effect (Hunt et al., 2001; Maddocks et al., 2001). However, previous behavioural studies have demonstrated that there need not be large amounts of ultraviolet reflectance or contrast to produce a significant effect. For example, removing ultraviolet wavelengths reduced the initial foraging success of blue tits foraging for cryptic green caterpillars, even though the caterpillars and their leaf backgrounds reflected relatively little ultraviolet (Church et al., 1998b), and ultraviolet cues could significantly affect the mate choice behaviour of zebra finches, even though no areas of plumage had peak reflectance in the ultraviolet (Bennett et al., 1996).

It would be unwise to suggest that ultraviolet wavelengths are somehow 'special' in these experiments. The only filter type that produced a near-significant frequency-dependent effect was UV+ (i.e. full-spectrum illumination). Thus, rather than ultraviolet being particularly important, it might be that the mechanisms underlying frequency-dependent selection in these experiments might only be expressed if the illuminant is essentially 'white' (i.e. all four of the single cone types of the zebra finch are highly stimulated; Cuthill et al., 2000). The removal of different wavebands (i.e. UV-, SW-, MW- or LW-) in experiment 2 would have meant that the seeds in these treatments might have been perceived by the zebra finches as more similar in colour to each other as a result of the inevitable loss of some visual information. If, as has been suggested, anti-apostatic selection at high density arises because of a 'confusion' effect, due to the contrast between the rare seed

type against a background of common seeds (Greenwood, 1984), then it is likely that the degree of confusion would be reduced if part of the illuminating spectrum was removed, resulting in the selection of the birds becoming closer to random, as observed. However, since this was a long wavelength-dominated task, we would not necessarily expect this effect to be identical for all wavebands.

It is not clear whether the results we obtained were due to the manipulations of the light environment affecting the hue of the seeds and background, their brightness or a combination of both. In experiment 1, the UV+ and UV- filters only differed in light transmitted at ultraviolet wavelengths, resulting in a higher total quantal flux in the UV+ treatment than the UV- treatment. In experiment 2, approximate matching of the quantal flux for the coloured filters necessitated a lowering of the mean transmission of filters compared to experiment 1. Such changes in brightness are consistent with our results, with the strongest frequency-dependent effect being observed under the brightest treatment (i.e. full-spectrum illumination in experiment 1). However, in a similar study that investigated the effect of different light environments on the 'simple' seed preferences of zebra finches, Maddocks et al. (Maddocks et al., 2001), contrary to the results presented here, found that long wavelengths had the greatest effect on relative seed consumption and that there was no difference between seed preferences under UV+ and UV- treatments. Thus, in these experiments, the finches were least selective in the brightest (UV+) treatments. Other behavioural studies that have explicitly manipulated brightness (e.g. Bennett et al., 1996), while testing for the effects of ultraviolet, have found no significant effect of brightness on behaviour. Recently, however, it has been demonstrated that achromatic cues may be more important than chromatic cues for chicks foraging for prey items around 2 mm in diameter (Osorio et al., 2001), similar to the size of the seeds in our experiments. While our experiments were not designed to elucidate the visual mechanisms underlying any frequency-dependent effects, it is clear that more work is needed in this area.

It is worth noting that Manly's β index (Manly, 1974) can be subject to apostatic biases when less than 50% of the total prey items available are consumed (Weale, 1992; Church et al., 1996; Church et al., 1997). Since the number of seeds consumed in our experiments was usually between 20% and 25%, such biases were likely to be present. One consequence of this is that the borderline anti-apostatic effect under the UV+ filter in experiment 1 is likely to be a slight underestimate of the true anti-apostatic effect. In experiment 1, we also found that significantly fewer seeds were consumed in trials in which red was common than when red was rare. This could be due to the general, albeit non-significant, trend towards an overall (frequency-independent) preference for white seeds. However, this difference would not have affected the qualitative interpretation of results with regards to the effects of ultraviolet wavelengths, since any biases would have had similar effects under each filter treatment.

These data are intriguing in that they suggest the possibility that changes in ambient light spectra could, whether mediated by changes in hue or brightness, change the strength and direction of frequency-dependent selective predation. This will have concomitant consequences for plant population dynamics on a local and global scale (Greenwood, 1985). Since the spectral composition and quantal flux of ambient light varies from habitat to habitat and even within the same habitat as weather and time of day vary (Endler, 1993), it raises the possibility that selection pressures imposed via frequency-dependent selective predation may change on a daily or seasonal basis. Thus, the evolutionary and ecological consequences of selection might change depending on such fine-grained events as the time of day of maximum predation. Despite these theoretical possibilities, it is not clear at present how important these effects are likely to be in natural ecosystems. Certainly, the experimental treatments described here represent quite extreme manipulations of ambient light spectra. Spectral variation in terrestrial systems, while clearly not insignificant, is by no means as high as that found in aquatic habitats (Chiao et al., 2000). One crucial factor that is likely to be important in determining the real-world implications of variation in ambient light spectra is how good avian colour constancy is. Colour constancy is the phenomenon whereby objects are perceived as the same colour despite changes in the illuminant (Hurlbert, 1996). It has been suggested that the narrowing of spectral sensitivity of the single cone cells of birds will increase their ability to be colour constant (Vorobyev et al., 1998). Indeed, recent models of avian tetrachromatic vision (Vorobyev and Osorio, 1998; Vorobyev et al., 1998) make the explicit assumption that birds are colour constant. However, it must also be true that avian colour constancy cannot be perfect when significant behavioural effects have resulted from modification of the ultraviolet component of ambient light (e.g. Bennett et al., 1996; Bennett et al., 1997; Hunt et al., 1997; Hunt et al., 1998; Hunt et al., 1999; Church et al., 1998b). It seems logical to conclude that there must be some point at which colour constancy breaks down. Since we currently lack experimental data regarding (i) the ability of birds to be colour constant, and (ii) the degree of natural variation in ambient light spectra that birds encounter when performing specific foraging tasks, we are unable to answer this question. In addition, what general information does exist on natural variation in terrestrial ambient light environments does not, unfortunately, extend to measurement of ultraviolet levels (Endler, 1993; Chiao et al., 2000).

In summary, our experiments do not necessarily demonstrate that ultraviolet wavelengths are in any way special in their effects on the frequency-dependent seed preferences of zebra finches. While it is important to determine the role of ultraviolet wavelengths in any behavioural task, it may prove more illuminating to consider the whole range of wavelengths to which birds are sensitive, rather than focusing explicitly on one waveband. Our data also highlight the fact that there are gaps in our knowledge concerning both the ecological consequences of visually mediated behaviours of birds

(including ultraviolet wavelengths) and the visual mechanisms underlying these behaviours.

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