Ultraviolet cues affect the foraging behaviour of blue tits

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The function of avian ultraviolet (UV) vision is only just beginning to be understood. One plausible hypothesis is that UV vision enhances the foraging ability of birds. To test this, we carried out behavioural experiments using wild-caught blue tits foraging for cabbage moth and winter moth caterpillars on natural and artificial backgrounds. The light environment in our experiments was manipulated using either UV-blocking or UV-transmitting filters. We found that the blue tits tended to find the first prey item (out of four) more quickly when UV cues were present. This suggests that UV vision offers benefits to birds when searching for cryptic prey, despite the prey and backgrounds reflecting relatively little UV. Although there was no direct effect of UV on the time taken to find all four prey items in a trial, search performance in the absence of UV wavelengths tended to increase over the course of an experiment. This may reflect changes in the search tactics of the birds. To our knowledge, these are the first data to suggest that birds use UV cues to detect cryptic insect prey, and have implications for our understanding of protective coloration.

Keywords: blue tit; crypsis; foraging; ultraviolet; Lepidoptera

1. INTRODUCTION

Ultraviolet (UV) vision is widespread throughout the animal kingdom (Jacobs 1992). Avian ultraviolet vision is of particular interest to evolutionary ecologists because birds have played a central role in our understanding of sexually selected colour patterns and protective coloration (Bennett *et al.* 1994). Although birds possess 'probably the most advanced visual system of any vertebrate' (Goldsmith 1990), the vast majority of studies of animal coloration involving birds as selective agents have not considered a 'birds-eye' perspective (Bennett & Cuthill 1994; Cuthill & Bennett 1993; Church *et al.* 1998). Instead, most studies have relied on approaches based on human colour perception. Although birds can detect wavelengths in the same wavelength range as humans (*ca.* 400–700 nm), most species can also detect UV wavelengths in the range 300–400 nm (Huth & Burkhardt 1972; Wright 1972; reviewed by Bennett & Cuthill (1994)). Furthermore, birds possess at least four (compared to three in humans) spectrally distinct single cone types (Chen & Goldsmith 1986; Bennett & Cuthill 1994; Bowmaker *et al.* 1997; Hart *et al.* 1998), associated with coloured oil droplets acting as cut-off filters (Partridge 1989; Bowmaker *et al.* 1997). As a result, birds have the potential for higher dimensions of colour space, modulated by wavelengths which humans cannot perceive (Thompson *et al.* 1992).

Bennett & Cuthill (1994) focused on three hypotheses regarding the functional significance of avian UV vision: (i) mate choice, (ii) foraging, and (iii) navigation. To date, behavioural studies have provided evidence that UV cues play an important role in conspecific signalling in several bird species (Maier 1993; Bennett *et al.* 1996, 1997;

Andersson & Amundsen 1997; Hunt *et al.* 1997, 1998; Andersson *et al.* 1998). Here, we focus on the hypothesis that UV vision enhances foraging. This hypothesis is highly plausible for three reasons. First, some of the invertebrates, fruits, seeds and flowers on which birds feed reflect in the UV (Burkhardt 1982; Silberglied 1979; Willson & Whelan 1989). Second, as UV sensitivity appears to be common among birds (Bennett & Cuthill 1994) and is used in mate choice, sexual selection theories involving sensory drive (Endler 1992, 1993a), sensory exploitation (Ryan 1990) or other aspects of receiver psychology (Guilford & Dawkins 1991) would predict that UV signalling has been 'co-opted' from an ancestral function such as foraging. Third, kestrels appear to use UV-visible scent marks to locate areas where voles are present (Viitala *et al.* 1995). However, there is currently no evidence that birds use UV cues when foraging for insects, or in detection or discrimination of cryptic prey.

In this paper, we investigate whether UV cues are used by foraging blue tits (*Parus caeruleus*). In particular, we focus on whether UV cues affect the rate of foraging on caterpillars of the winter moth (*Operophtera brumata*, Geometridae) and the cabbage moth (*Mamestra brassicae*, Noctuidae) on natural and artificial backgrounds. Foraging for cryptic lepidopteran larvae is likely to have significant fitness consequences for blue tits as they rely heavily on these prey items to provision their brood during the breeding season (Perrins 1991).

2. METHODS

(a) *Experimental subjects*

Blue tits were caught near Bristol, UK, during February and March 1997 and housed individually under a natural photoperiod. 'Daylight' fluorescent tubes, identical to those used in the

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Figure 1. Foraging apparatus used in experiments 1 and 2.

foraging trials (see below), were present in the holding room. The blue tits were maintained on a diet of mealworms, peanuts, sunflower seeds and commercial insect mix.

(b) *Experiment 1: cabbage moth larvae*

In this experiment, we examined the behaviour of seven male blue tits foraging for cabbage moth larvae on different backgrounds in the presence or absence of UV. Early instar larvae were reared from eggs on organically farmed white cabbage supplemented with an artificial, wheatgerm-based diet. Although this species shows colour polymorphism, it is not fully evident until the fourth or fifth instar (Goulson 1994).

Foraging trials were conducted in a purpose-built indoor arena (1 m × 0.8 m × 0.6 m; figure 1). 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 (figure 2a). A window (55 cm × 75 cm) on the top surface of the arena was fitted with either UV blocking (UV–) or UV transmitting (UV+) filters to modify the ambient light environment (figure 3). Illumination of the arena was provided by ten 100 W fluorescent tubes, powered by 240 V, 71 W, 35–40 kHz ballasts mounted above the filters and producing a spectral emission similar to natural skylight (downward irradiance at the base of the arena, measured using a Spex 1861 spectrophotometer connected to an integrating sphere, gave $Q_{300-400\text{ nm}}/Q_{300-700\text{ nm}} = 9.4\%$).

Blue tits were trained to forage for caterpillars in a 0.4 m × 0.4 m area containing the background substrate (cabbage leaves or black painted surface) in the centre of the arena floor. A plywood grid (8 cells × 8 cells) was placed on top of the flat substrate and provided a foothold for the birds without disturbing the prey items. Two perches (height 20 cm) were mounted on each side of the grid.

The foraging behaviour of the birds was measured under four experimental treatments: (i) UV+ filter and cabbage background, (ii) UV+ filter and black paint background, (iii) UV– filter and cabbage background, and (iv) UV– filter and black background. We used a randomized block design, with each subject having all four treatments in a random order within a block. The experiment consisted of two blocks. Individuals were

Figure 2. Mean reflectance spectra of (a) cabbage background, black painted background (and inner wall of foraging arena) and cabbage moths in experiment 1, and (b) winter moths and upper and lower surfaces of oak leaves in experiment 2.

Figure 3. Light transmission properties of UV-transmitting (UV+) and UV-blocking (UV–) filters.

tested once per day, and food-deprived for three hours before a trial. The seven birds were tested (in a random order) each day of the experiment, with trials carried out between 13.00 and 17.30. After initial habituation to the foraging arena, each bird was subjected to two UV– and two UV+ ‘practice’ trials in the week before the start of the experiment.

In each trial, four randomly chosen cabbage moth caterpillars (mean length $\pm$ s.d.: 6.13 ± 0.75 mm) were randomly distributed among the 64 cells of the foraging grid. Each prey item was placed with dorsal side uppermost in a roughly central position in the cell. Caterpillars were killed before the experiment by freezing at -84°C for 4–5 min in order to remove any confounding effects of movement. All specimens were used in a trial within 45 min of thawing.

To avoid direct handling, the birds were transferred from their home cages to the foraging arena in small, plastic ‘start boxes’, which they would readily enter from their home cages. A sliding door allowed the bird to exit the start box and enter the foraging arena. The bird was allowed a maximum of 10 min to consume all four prey items. Each trial was recorded on videotape.

Behaviours were transcribed from videotape, blind to the type of filter used in each trial. All analysis was carried out by one person, who had practised transcribing more than 40 trials beforehand. We recorded the search time required to find each of the four larvae in turn. Because the birds were highly motivated to feed, we recorded all time during which the bird was active and located on the perch or grid as 'searching', with the exception of time handling prey or in vigilance. Our analysis focused on two dependent variables: (i) search time required to find the first prey, and (ii) total search time required to find all four prey. Data were analysed using repeated-measures ANOVA on $\log_{10}$ -transformed data.

(c) *Experiment 2: winter moth larvae*

Experiment 2 was very similar in design to experiment 1. Subjects were the same six blue tits used in experiment 1. The prey were winter moth caterpillars, sampled from oak trees in Wytham Woods, Oxford, and Ashton Court Estate, Bristol. The background consisted of a bed of randomly mixed oak leaves (*Quercus robur*), obtained from at least two different trees on the morning of each trial. Because the winter moths were much larger than the cabbage moths (mean length $\pm$ s.d.: 12.23 ± 1.60 mm), the task for the birds was made more difficult by randomizing the placement of the caterpillars within a cell. Each larva was placed in a random cell and in one of four quarters of the cell, in a natural position and random orientation.

This experiment also followed a randomized block design, with each block consisting of one UV+ trial and one UV- trial, performed in a random order for each bird. A total of four blocks were performed over a 15-day period, with the two trials within a block always being performed on consecutive days.

(d) *Spectrophotometric measurements*

We measured reflectance spectra from 40 cabbage moth larvae, 40 winter moth larvae and from samples of the backgrounds. Caterpillars were freeze-killed and spectra obtained within 30 min of thawing. Reflectance measurements were taken normal to the dorsal surface of the caterpillars using a Zeiss MCS 500 spectrophotometer focused, via a fibre optic and lens, to a measuring spot approximately 2 mm in diameter. Specimens were illuminated at 45° to the normal by a Zeiss CLX 500 Xenon light source. Spectra were recorded at 0.81 nm intervals between 300 and 700 nm and measured relative to a SpectralonTM 99% reflectance standard. Between three and six measurements were taken per caterpillar. Measurements were also taken from the cabbage and oak leaf backgrounds over the course of the experiments. Reflectance spectra of live winter moths were collected concurrently (data used in Church *et al.* (1998)), which allowed us to determine if there was any effect of freezing and death on coloration. To compare living and dead specimens, we used principal components analysis (PCA) to reduce our spectral data to two or three orthogonal variables which summarized variation in spectral shape and mean reflectance (Endler 1990; Bennett *et al.* 1997; Cuthill *et al.* 1998). ANOVAs were then used to test for differences between principal component scores.

3. RESULTS

(a) *Experiment 1: cabbage moth larvae*

The search time required to find the first cabbage moth caterpillar (figure 4a) was significantly lower for the UV+ treatment than the UV- treatment ($F_{1,4}=63.14$, $p=0.001$). The first prey item was also found significantly

faster in the second block of the experiment ($F_{1,4}=132.22$, $p<0.001$). There was no effect of background type ($F_{1,4}=0.66$, $p=0.461$), and there were no significant two-way interactions (background $\times$ block, $F_{1,4}=0.03$, $p=0.865$; background $\times$ filter, $F_{1,4}=3.05$, $p=0.156$; block $\times$ filter, $F_{1,4}=0.01$, $p=0.914$). There was a significant three-way interaction between background, block and filter ($F_{1,4}=35.78$, $p=0.004$), the effect of filter being pronounced only for the cabbage background and only in the first block.

For the time required to find all four prey (figure 4b) there was no significant main effect of background ($F_{1,2}=5.30$, $p=0.148$), block ($F_{1,2}=0.19$, $p=0.707$) or filter ($F_{1,2}=1.39$, $p=0.360$). The effect of filter differed with block (block $\times$ filter, $F_{1,2}=22.84$, $p=0.041$), with search time under UV- decreasing in the second half of the experiment. There were no other significant two- or three-way interactions (background $\times$ block, $F_{1,2}=0.15$, $p=0.739$; background $\times$ filter, $F_{1,2}=0.56$, $p=0.533$; background $\times$ block $\times$ filter, $F_{1,2}=11.04$, $p=0.080$). Some tests have reduced degrees of freedom owing to missing values resulting from birds not consuming all prey during a trial.

(b) *Experiment 2: winter moth larvae*

In experiment 2, one bird was removed from the analysis as it failed to consume any prey during the second block of the experiment. The time taken for blue tits to find the first winter moth (figure 4c) differed between the blocks of the experiment ($F_{3,12}=4.426$, $p=0.026$), with the greatest difference between blocks one and four. Although there was a tendency for the first prey to be found more quickly under UV+ conditions, the effect was not significant ($F_{1,4}=6.795$, $p=0.060$). There was no interaction between block and filter ($F_{3,12}=1.063$, $p=0.401$).

For the time taken to find all four prey items (figure 4d), there were no main effects of either block ($F_{3,12}=1.038$, $p=0.411$) or filter ($F_{1,4}=0.148$, $p=0.720$). There was a significant block $\times$ filter interaction, with search times under UV+ faster than UV- in the first half of the experiment, but slower in the second ($F_{3,12}=3.617$, $p=0.046$).

(c) *Spectrophotometric data*

The mean spectra of the caterpillars and backgrounds used in experiments 1 and 2 are presented in figure 2a,b. On the basis of these spectra, winter moths appeared to be more closely matched to their oak leaf background than cabbage moths did to their cabbage leaf and black paint backgrounds.

For the winter moth, the first two principal components accounted for 93.8% (PC1 78.8%, PC2 15.0%) of the variation among the spectra of live and freeze-killed specimens. There were no significant differences between the principal component scores (PC1, $F_{1,78}=0.78$, $p=0.381$; PC2, $F_{1,78}=0.00$, $p=0.984$), indicating that freezing had no detectable effect on coloration in our experiments.

4. DISCUSSION

Our results demonstrate that UV contributes to the visual cues used by blue tits when foraging for certain caterpillar prey. In both experiments, the birds found the

Figure 4. Effect of block, background (cabbage or black; experiment 1 only) and filter (empty columns, UV+; filled columns, UV-) on (a) search time required to find first cabbage moth in a trial in experiment 1, (b) total time required to find all four cabbage moths in experiment 1, (c) search time required to find first winter moth in a trial in experiment 2, and (d) total time required to find all four winter moths in experiment 2. For clarity, between-bird variation has been removed from the data.

first prey item in a trial more quickly under UV+ conditions (although the effect was marginally non-significant, at $p=0.06$, in experiment 2, when foraging on winter moths). These results suggest that UV cues may be advantageous when initiating search for cryptic prey items. The effect was particularly strong with cabbage moth prey, possibly because there was a greater degree of mismatch in the UV between this caterpillar and its backgrounds compared with that of the winter moth. Browman *et al.* (1994) suggested a similar explanation to account for the effect of UV on fish foraging behaviour; removing the UV component of downwelling irradiance reduced the spectral contrast between the prey and background.

It might be argued that the search time to find the first prey was greater under UV- conditions because subjects were more wary when placed in a light environment that differed from their usual UV+ housing conditions. Although we cannot entirely rule out this possibility, we believe that it is unlikely for two reasons. First, the blue tits had experience of both UV+ and UV- trials before both experiments and were therefore familiar with the experimental apparatus and lighting conditions. Second, being food-deprived, they were highly motivated to forage for the caterpillars immediately.

The effect of filter type on the total search time required to find all four prey items was not clear-cut. However, foraging rate under UV- significantly increased relative to UV+ during the second half of both experiments. This is puzzling given that the birds consistently found the first prey item more quickly under UV+ throughout both experiments. One possibility is that there was a persistent 'start-of-trial' effect (when the birds were relatively 'naive' to the task ahead), but that they tended to modify their subsequent search tactics over the course of an experiment as they learned that cues based on hue or brightness were less reliable than non-spectral cues such as texture (Kiltie & Laine 1992) or shape. It is also possible that these data were influenced by subtle changes in the colour match between prey and background during the experiments, which subsequently affected the ability of the blue tits to locate prey.

Our experiments, like those of Maier (1993), Viitala *et al.* (1995) and Andersson & Amundsen (1997), were not designed to reveal whether blue tits were using the UV cues to discriminate between object and background using hue or brightness. Hue perception results from comparison of cone outputs, brightness from their summation (e.g. Thompson *et al.* 1992). Although it has

been demonstrated that birds show wavelength discrimination in the UV (Emmerton & Delius 1980), it is also plausible that the UV single cones of passerines contribute to perceived brightness. This could increase prey detectability when foraging under low light levels because a wider spectral range is used. Future experiments that manipulate brightness independent of UV levels are required to test this possibility.

None of the prey or backgrounds in our experiments reflected a large amount of UV, yet removing this part of the spectrum significantly affected foraging behaviour. This is consistent with the suggestion that avian spectral sensitivity is quite high in the UV (Kreithen & Eisner 1978; Burkhardt & Maier 1989). Nevertheless, at this stage it would be unwise to claim that UV is somehow 'special' compared to human-visible wavelengths. Rather, we aim to draw attention to the fact that the UV is used in avian foraging and has been overlooked in studies of prey coloration.

UV wavelengths are likely to play a role in various aspects of the visual ecology of blue tits. In addition to foraging, blue tits are dimorphic in the UV and seem to use these cues in mate choice (Andersson *et al.* 1998; Hunt *et al.* 1998). Furthermore, some of the light environments likely to be present in a blue tit's habitat—'woodland shade' (Endler 1993b) in particular—may be quite rich in short wavelength light. However, quantification of irradiance with higher spectral resolution would be needed to determine precisely the ambient light conditions where blue tits find their prey in the wild.

If general, our data also have implications for our understanding of protective coloration in species susceptible to bird predation. Although the need to explicitly consider predator visual systems has been repeatedly stated (Endler 1978, 1984), our present understanding of mimicry and crypsis is still based almost entirely on human perception (Cuthill & Bennett 1993; Church *et al.* 1998). If UV cues are used in foraging, then prey items that humans might class as cryptic or mimetic are not necessarily perceived in the same manner by avian predators. These results, in combination with studies of mate choice and social signalling, reinforce the view that it is unwise to ignore the UV in studies of visually guided behaviour in birds.

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