

Can ultraviolet cues function as aposematic signals?

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The fact that birds are sensitive to ultraviolet light (UV, 320–400 nm) has been largely ignored by previous studies of aposematism. Therefore, in the present article we investigated whether great tits preferred ultraviolet-reflecting colors compared to colors without UV reflection and whether UV cues alone could function as aposematic signals. We were able to manipulate prey visibility in UV light by changing the UV reflectance of prey items as well as altering the lighting conditions. In order to perform a preference experiment we used three pairs of colors (green+UV vs. green, gray+UV vs. gray, yellow+UV vs. yellow) on a black background. The birds ate both UV types equally for all three colors. Thus, there was no avoidance of the UV-reflecting prey. Next we tested the possibility that UV reflection may affect avoidance learning. We used either green or green+UV as a signal for unpalatability. In this set-up the difference in UV did not allow avoidance learning to occur. Our experiment with great tits does not support the hypothesis that UV cues alone might work effectively as aposematic signals. *Key words*: aposematism, ultraviolet, ultraviolet-reflecting, ultraviolet-absorbing, avoidance learning. [*Behav Ecol* 12:65–70 (2001)]

Already by the early 1970s the fact that birds are also able to see in near-ultraviolet light (UV, 320–400 nm) was established for the hummingbird, *Colibri serrirostris* (Huth and Burkhardt, 1972) and for the pigeon, *Columbia livia* (Wright, 1972). Since then the ability to see UV has been demonstrated for several other bird species (Bennett and Cuthill, 1994; Cuthill et al., 2000), perhaps excluding nocturnal birds (Bowmaker and Martin, 1978; Koivula et al., 1997). Most diurnal birds have at least four kinds of photopigments in the cones of their eyes (Bowmaker et al., 1997; Bowmaker and Hunt, 1999; Cuthill et al., 2000) including a spectral sensitivity peak in near-ultraviolet light at 360–380 nm (Burkhardt and Maier, 1989; Chen et al., 1984; Chen and Goldsmith, 1986). The vision of some bird species is even more sensitive to short wavelengths than to the visible spectrum (Burkhardt and Maier, 1989; Kreithen and Eisner, 1978; Maier, 1994) and birds are able to discriminate between differences in hues in the UV region (Emmerton and Remy, 1983). Among vertebrates the presence of UV sensitive cones is not a unique feature of the avian eye. It also occurs among amphibians, reptiles, fish, and mammals (reviews by Jacobs, 1992; Tovéé, 1995).

Four-dimensional color vision in birds has been ignored by many studies of color signals (Bennett et al., 1994). Recently, the function of UV vision in birds has received much attention. Several studies have shown UV vision to play a role in mate choice (Andersson and Amundsen, 1997; Andersson et al., 1998; Bennett et al., 1996, 1997; Hunt et al., 1998; Johnsen et al., 1998; Maier, 1993; Sheldon et al., 1999), but studies of the role of UV vision in foraging are far fewer. It has been suggested that kestrels (*Falco tinnunculus*) may use the UV-reflecting scent marks of voles to locate feeding areas (Viitala et al., 1995), and blue tits (*Parus caeruleus*) found cabbage moth larvae faster in the presence of UV light (Church et al., 1998a).

Church et al. (1998b) measured the reflectance spectra of

both lepidopteran larvae and their natural backgrounds. The data indicated that many caterpillars matched the leaf background in the UV region as well as visibly and thus they were cryptic over the entire range of wavelengths. On the other hand, caterpillars that seem to be cryptic in those wavelengths visible to the human eye may be conspicuous in UV. Larvae of the gray shoulder knot (*Lithophane ornitopus*) are cryptic on the leaves of oak tree (*Quercus robur*) only in the range 400–700 nm, but not in UV (Church et al., 1998b). The possibility thus arises that by being conspicuous in UV prey animals might advertise unpalatability to predators. The use of conspicuous colors (yellow, red, and orange) by prey in order to convey distastefulness, or other unpleasant properties, is called aposematism (Cott, 1940; Edmunds, 1974; Poulton, 1890). Predators are able to learn to avoid prey exhibiting warning colors but they may also have unlearned aversions towards certain colors or patterns (Schuler and Hesse, 1985; see review by Schuler and Roper, 1992).

There are no existing studies of aposematism that consider signals, which use the reflection of UV light. Therefore, we investigated whether predators exhibit a preference for (or avoidance of) UV-reflecting or UV-absorbing prey. A preference experiment was conducted with three pairs of colors (green, gray, and yellow) differing only in the UV region. Our second goal was to explore whether a difference in the visibility of UV reflectance might play a role in avoidance learning. In previous behavioral studies UV light has typically been blocked by a filter (Bennett et al., 1996, 1997; Church et al., 1998a; Maier, 1993) or with sunblock (Andersson and Amundsen, 1997). By contrast, Silberglied and Taylor (1978) used a method where they increased UV reflection with the use of chalk. We have combined these approaches by reducing the reflection of UV light by titanium dioxide and increasing UV reflection with the use of chalk.

MATERIAL AND METHODS

Predators and training

We conducted the experiments on adult great tits (*Parus major*) in May 1998 at Konnevesi Research Station, in Central Finland. We had permission (Central Finland Regional Environment Center, permission LS-12/98) to keep birds in cap-

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tivity. The birds captured by mist nets were maintained on a diet of sunflower seeds, peanuts, and water ad libitum on 18 h light/6 h dark conditions. They were held in individual, visually isolated cages (0.60 m × 0.60 m × 1.0 m). The birds were trained to consume almonds which were glued to pieces of white paper (see prey item section). The birds were accustomed to the experimental cage in order to ensure that they searched for food from the floor. To motivate the birds to forage they were deprived of food for at least 2 h before the trials. After the experiments we released the birds back into the wild.

Prey items

Slices of almond glued under pieces (1.0 × 1.5 cm) of colored paper (light green, gray, and pale yellow) were used as prey items. The paper coverings were designed to either reflect (green+UV, gray+UV, and yellow+UV) or absorb (green, gray, and yellow) UV light. Those which reflected UV light were covered with chalk, modifying the method used by Silberglieb and Taylor (1978; see also Derim-Oglu and Maximov, 1994). They used only one kind of chalk on each prey but we coated the ultraviolet reflecting items with either both white and colored chalk (green or yellow) or with white chalk only (gray). The chalk increased the brightness only in the UV waveband. We coated the UV-absorbing prey items with a mixture of titanium dioxide (TiO₂) and chalk powder (2.5 g green, white or yellow chalk/15 g TiO₂). Chalk was added to the titanium dioxide in order to make the UV-absorbing prey items exactly the same color as the UV-reflecting ones. The mixture was then spread evenly over the paper coverings. It reduced reflectance in the region of the light spectrum under 400 nm retaining almost the same spectral reflectance across the 400–720 nm range (Figure 1). This method allowed us to use only relatively pale colors. For us UV+ and UV- items appear perfectly alike and so were impossible to separate from each other. However, it was also necessary to exaggerate the sensation of UV colors by changing the lighting conditions as explained below. Admittedly also UV- items reflected some UV but they were less bright in UV than UV+ items. The difference was perceivable to the birds (see Control test of the UV manipulation).

The reflectance of the prey items in the range 320–720 nm was recorded at 2 nm intervals using a spectroradiometer (EG&G Gamma Scientific GS3100 Radiometer, Light Touch Software 1.04a) under the same light conditions as those used for the experimental cages (see below). Reflectances were measured as a proportion of the light reflected from a calibrated 98% white standard (LabSphere[®]).

To visualize the set-up of the experiment, photographs of the prey were taken with a Nikon camera in daylight through the UV transmission filter (Nikon UV filter) and again without the filter on an UV-sensitive black and white film (Kodak Tmax 400pro). The UV-reflecting areas appear pale while the UV-absorbing areas appear dark in the UV photographs (Figure 2).

Experimental cages and illumination

The experiments were performed in a matt black painted cage (0.50 m × 0.70 m × 0.96 m) inside a dark room to ensure that there was no daylight. Since the sensation of colors is dependent on the amount and spectral composition of the ambient light (Endler, 1990), we used a light regime that was much richer in UV than natural light. This was done by using an Osram Eversun L40W/79K rich in UV together with an Osram L18W/72 Biolum fluorescence tube, which provided light from 320 to 720 nm in the experimental cages (Figure

3). Under these lighting conditions UV reflection, that matched the ambient light peak, appeared brighter than under the light that would have contained low levels of UV region. Thus, the difference in the UV region between UV+ and UV- prey items was exaggerated. There was an opening of 12 cm × 33 cm in the floor of the cage, through which prey items could be placed onto the tray without disturbing the bird. A perch (at a height of 30 cm) was also available for the bird. We observed the behavior of the birds through a small net-covered window. During both the training and experimental periods water was available ad libitum.

Control test of the UV manipulation

Since both UV+ and UV- items appear similar to us, we tested whether we managed to create a sufficiently large difference between the two prey types (UV-absorbing vs. UV-reflecting). We tested these two prey types by placing one UV-absorbing (i.e., cryptic) and one UV-reflecting (i.e., conspicuous) palatable prey item side by side on a background with a color similar to that of the UV-absorbing prey (Figure 2). Thus, the same mixture of titanium dioxide and chalk was used for the background as for the UV-absorbing prey items. If the difference in the UV spectrum is adequate between two prey types, then birds are able to see simultaneously presented UV-reflecting items better than UV-absorbing ones in the presence of UV, if presented on UV-absorbing background. Therefore, they are expected to eat more UV-reflecting prey items in UV-present conditions (both UV light and visible light sources switched on) than in UV-absent conditions (only visible light source switched on). Due to the fact that even Biolum fluorescence tubes emit small amounts of UV light and that birds are excellent at color discrimination, we used plexiglass (thickness 1 cm) to completely block the UV wavelengths in the UV-absent treatment (see Figure 3). We conducted two separate treatments for each bird ($n = 10$), one with UV present and one with UV absent, in green, gray, and yellow, in random order. To each bird we presented, in sequence, a choice session of five pairs (UV+ and UV-) of each color (green+UV vs. green, gray+UV vs. gray, and yellow+UV vs. yellow). We only allowed the birds to eat the first prey item attacked.

Preference experiment

If UV colors play an important role in aposematism it could be expected that wild birds would exhibit an innate or learned avoidance of these colors. We designed the experiment to compare the preferences between UV-reflecting and UV-absorbing prey types (green+UV vs. green, gray+UV vs. gray, and yellow+UV vs. yellow). Similar palatable prey items were used as explained above but this time they all were clearly contrasted with the background. We presented one UV-absorbing and one UV-reflecting item simultaneously to the bird, on the black tray (9.0 cm × 10.0 cm) and then we recorded the order of prey choice. We allowed the birds ($n = 36$) to eat both prey items. For each of the three colors there were five consecutive replicate pairs (UV+/UV-). The colors were tested in random order.

Learning experiment

We tested whether great tits could learn to discriminate the unpalatable prey items from the palatable ones if their reflection of the light differed only in the UV region. We chose the color green since the birds had not exhibited any preference between the green and the green+UV items. Furthermore, in nature green is usually an indicator that something is edi-

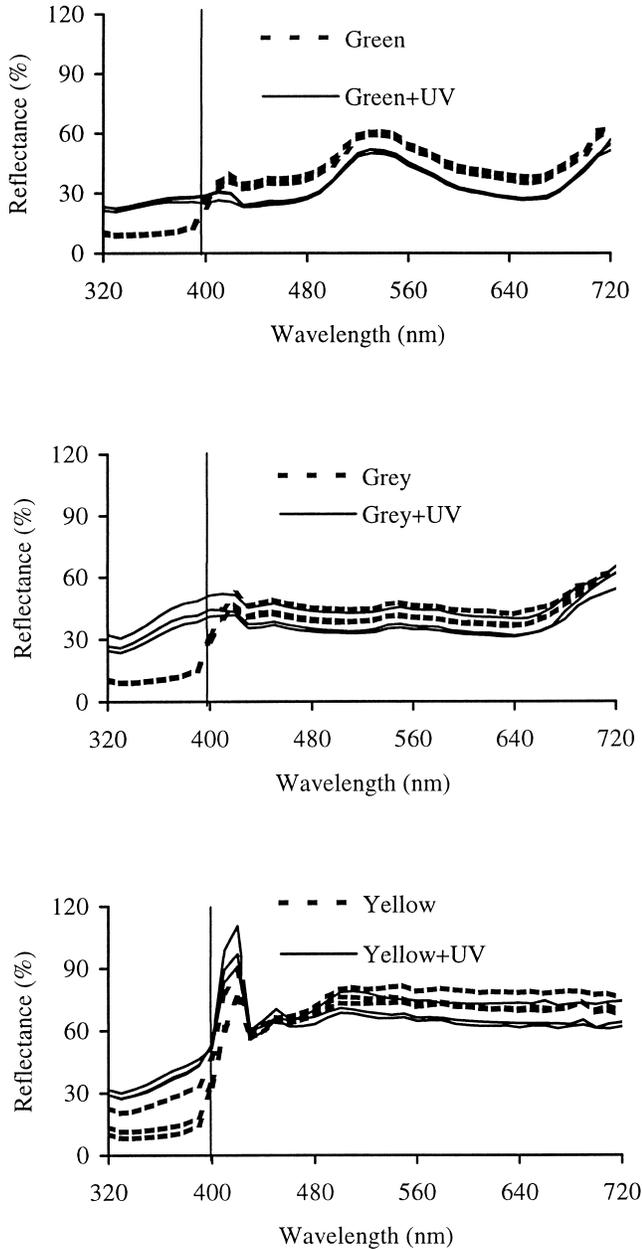


Figure 1
Spectral reflectance of the prey items for the three colors coated with the ultraviolet-reflecting chalk mixture (solid line) and coated with an ultraviolet-absorbing (dotted line) mixture of titaniumdioxide and chalk. Both prey types were measured three times under lighting conditions rich in UV.

ble. For the first group ($n = 13$), the green+UV prey items were made unpalatable, while for the second group ($n = 13$) the green prey items were made unpalatable. We made the almonds distasteful by soaking slices of almond in a mixture of 40 g chloroquine phosphate and one l water for an h, after which we dried the almonds. The concentration of the solution corresponds to that used in previous studies (Alatalo and Mappes, 1996; Lindström et al., 1999). We presented green+UV and green items side by side upon a black tray. The birds underwent four trials, separated by a 20 min pause. During the trials, we offered sequentially six pairs of prey items. During the first trial, we waited until the bird ate both items to make sure that each bird at least tasted an unpalat-

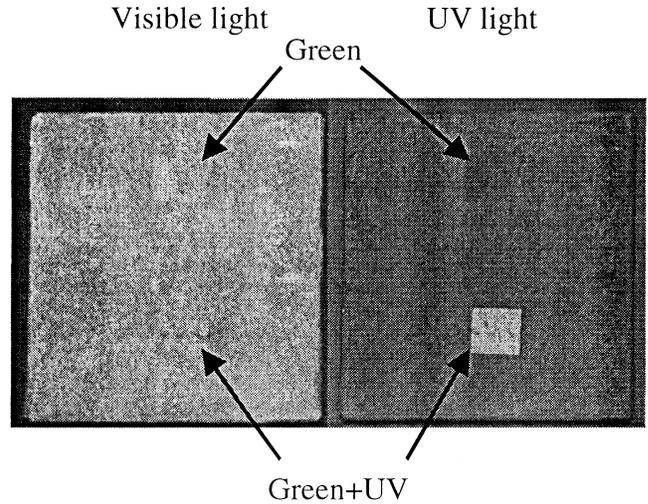


Figure 2
Green and green+UV prey items photographed on a green background without (left picture) and with (right picture) a filter transparent only to ultraviolet. On each tray was placed one ultraviolet-reflecting and one ultraviolet-absorbing prey item. This set-up was used in the control test of UV manipulation.

able prey item. Thus, median of the duration in the first trial was 57 s (green+UV unpalatable) and 54 s (green unpalatable) for consuming both items. In the following three trials after the bird consumed the first item in the pair we allowed the bird a maximum of 30 s to take the remaining prey item.

RESULTS

Control test of the UV manipulation

We tested two prey types used by placing them on the UV-absorbing background and introducing them to the birds. If the treatment was successful in the manipulation of UV then UV-reflecting items should be consumed more, from the UV-absorbing background, than UV-absorbing prey items when in the presence of ultraviolet light. Indeed, under UV light many more green+UV and yellow+UV were eaten compared to when UV light was absent (Wilcoxon matched pair test, $z = -2.46$, $n = 10$, after sequential Bonferroni correction $p = .041$ and $z = -2.43$, $p = .030$, respectively). There was a sim-

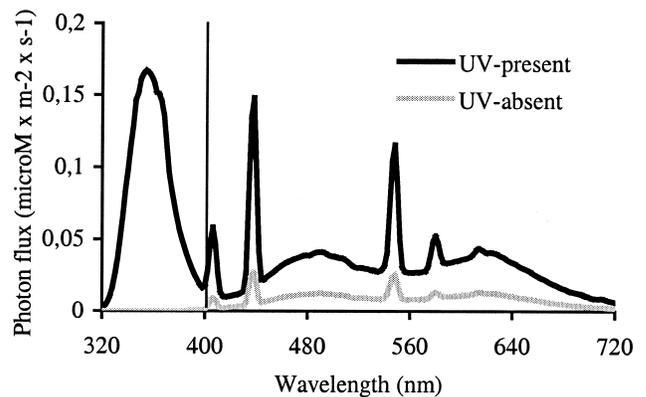


Figure 3
Spectrum of the two light regimes used in the experiment. The black line shows UV-present conditions, which were used in all three experiments. The gray line shows UV-absent conditions used only in the control test of the UV manipulation.

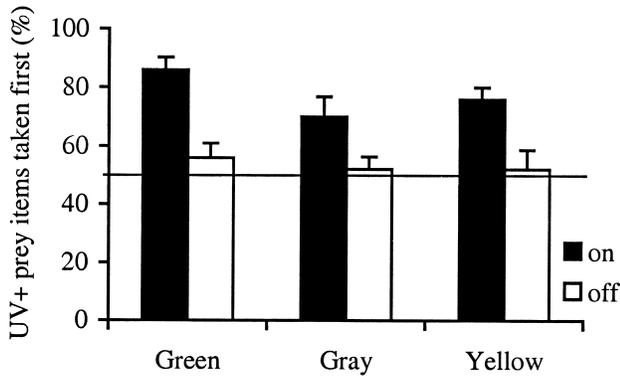


Figure 4
The proportion (\pm SE) of cases in which the birds consumed UV-reflecting prey items first in UV present (on, black columns) or absent (off, white columns) ($n = 10$) conditions in the control test of the UV manipulation. The items were presented on an ultraviolet-absorbing background. Reference line at 50% indicates random expectation.

ilar tendency with the color gray even though the difference was not quite significant (Wilcoxon matched pair test, $z = -1.84$, after sequential Bonferroni correction $p = .066$) (Figure 4). The results showed that bird ate more UV-reflecting prey items than UV-absorbing ones, which suggests that the manipulation succeeded.

Preference experiment

To test whether wild great tits exhibit any preference for UV-reflecting items compared to similar non-ultraviolet reflecting items we presented them with both of these prey types under UV light. Both prey items were highly conspicuous against a black background. There was no significant difference in preferences between UV+ and UV- treated green or gray prey (Wilcoxon matched-pair test, $z = -0.75$, after sequential Bonferroni correction $p = .901$ and $z = -0.34$, $p = .735$, respectively, $n = 36$). Both prey types were consumed in similar proportions. There seemed to be a slight, but not significant, tendency of birds preferring more yellow+UV prey to yellow prey (Wilcoxon matched pair test, $z = -2.35$, after sequential Bonferroni correction $p = .056$, $n = 36$) (Figure 5). These results indicated that there was no avoidance of UV-reflecting items. If anything, there seemed to be a slight preference for yellow+UV.

Learning experiment

The proportion of cases, in which unpalatable items were consumed first, from the items on offer, was used as the dependent variable for each trial. We carried out an Arcsine square root transformation to normalize the data. Two-way ANOVA with repeated measures over the four trials showed a significant main effect ($F_{1,24} = 22.12$, $p < .001$) due to the treatment (green+UV unpalatable versus green unpalatable). This indicated that the proportion of unpalatable items the birds consumed during the trials was lower when green was unpalatable (Figure 6a). There was no significant difference between the trials, indicating that the birds did not learn to avoid unpalatable prey items ($F_{3,22} = 1.87$, $p = .165$). There was also no interaction between the treatment and the trial rank ($F_{3,22} = 0.91$, $p = .454$).

To increase the power of the statistical test, we tested the learning process by comparing the first and last trials separately. When green+UV was unpalatable there was no differ-

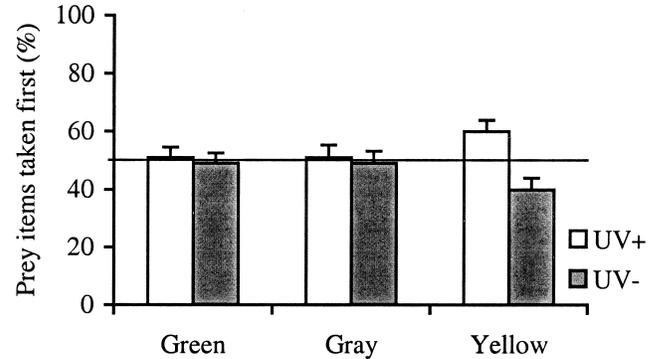


Figure 5
The proportion (\pm SE) of prey items taken first in the preference experiment ($n = 36$). Prey items were presented under UV light on the black tray on which both prey types were equally conspicuous. The white columns represent UV-reflecting prey items and the filled columns represent UV-absorbing prey items. Reference line at 50% indicates random expectation.

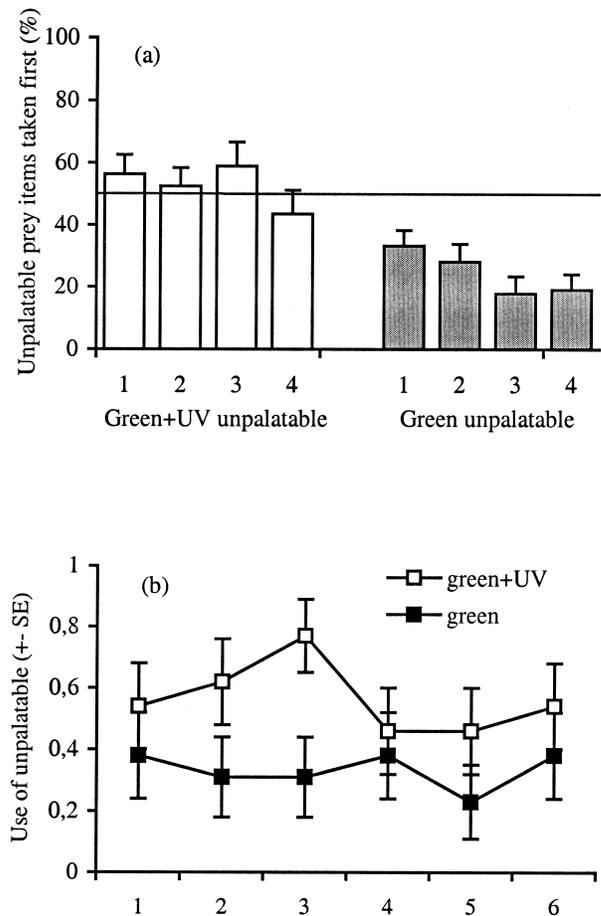


Figure 6
(a) The proportion (\pm SE) of cases in which unpalatable items were consumed first among six presentations in the four trials of the learning experiment ($n = 13$) in the presence of UV. White columns = green+UV distasteful, gray columns = green distasteful. Reference line at 50% indicates random expectation. Error bars represent SE. (b) The scored (palatable taken first = 0, unpalatable taken first = 1) first choice across the six pairs of prey within trial 1 of the learning experiment. The open square = green+UV unpalatable, filled square = green unpalatable.

Table 1

The proportions of unpalatable items taken (\pm SE) before palatable ones within trial four and the proportions of untouched unpalatable items in fourth trial

| | Unpalatable | | |
|-------------|------------------|-----------------|----------------|
| | Green + UV | Green | Red |
| <i>n</i> | 13 | 13 | 10 |
| Taken first | 43.6 \pm 7.7* | 19.2 \pm 4.9 | 13.3 \pm 6.0 |
| Untouched | 48.7 \pm 9.1** | 42.4 \pm 7.9* | 80.0 \pm 7.8 |

The proportions were tested between the learning experiment and the control test of the learning experiment. Both types of green were tested against red.

* $p < .01$; ** $p < .05$.

ence between the first and last trials (paired $t = -1.28$, $df. = 12$, $p = .225$). However, when green was unpalatable (and green+UV was palatable), there was a slight difference between the first and last trials ($t = -2.21$, $df. = 12$, $p = .048$). This difference indicated that the birds had a weak predisposition to learn to distinguish between palatable and unpalatable items on the basis of UV cues, but we stress that pure UV signals as aposematic signals cannot be very effective.

The fact that the starting points of avoidance learning were on different level (Figure 6b) could suggest that there might be avoidance learning within the first trial. To test this we scored the first choice across the six pairs of prey within trial 1 (Figure 6b). If the bird took palatable prey item first it received value of zero. Unpalatable prey chosen first received value of one. There was no interaction between the treatment and the pair rank (GLM: $F_{5,20} = 0.565$, $p = .725$). Furthermore, birds did not learn to avoid unpalatable prey items within trial 1 ($F_{5,20} = 0.752$, $p = .725$) but green unpalatable was avoided relative to green+UV unpalatable ($F_{1,24} = 8.526$, $p = .007$). The result indicated that the lower starting point for green than for green+UV unpalatable prey was not the result of more rapid association of unpalatability within trial 1.

Control test of the learning experiment

To rule out the possibility that the negative result of the learning experiment was due to the setup, we ran a test using the color red which is well known to be used in a warning context. We used the same procedure as in the learning experiment but with a new set of birds. The only difference was the colors used. The proportion (\pm SE) of cases in which the birds consumed red prey items before palatable green items, was, for the four trials: 33.3% (\pm 6.6), 21.7% (\pm 7.5), 18.3% (\pm 8.8), and 13.3% (\pm 6.0). Although the birds exhibited an initial avoidance of red, the birds ($n = 10$) learned to avoid red unpalatable prey items during the experiment ($F_{3,7} = 9.48$, $p = .007$).

When compared with the previous learning experiment the birds ate first significantly less red unpalatable prey items, in the last trial, than green+UV unpalatable prey items (Mann-Whitney test: $Z = -2.643$, $p = .008$) and equal proportion of red as green unpalatable ($Z = -0.835$, $p = .446$). But when we compared the proportion of unpalatable prey that birds refused to eat in the last trial the difference is even clearer (Table 1). The birds left untouched (i.e., refused even to taste) significantly more red unpalatable prey items, in the fourth trial, than green+UV (Mann-Whitney test: $Z = -2.250$, $p = .026$) or green unpalatable items ($Z = -2.753$, $p = .005$). Thereby, the birds exhibited significantly greater rejection of unpalatable prey items in the last trial of the control test than

in the learning experiment. This proves that the inability of the birds to learn in the learning experiment was not due to deficiencies in the experimental design but due to the signal. We can also conclude that the concentration of chloroquine used was aversive enough to produce avoidance learning over the time scale of the experiment if the visual signal is strong enough.

DISCUSSION

We managed to produce UV-absorbing and UV-reflecting signals without greatly affecting the reflectance in the wavelengths above 400 nm. Both prey items appeared very similar in the visible light spectrum but there were clear differences in the UV region. When the UV- and UV+ prey types were presented simultaneously the great tits did not seem to have a clear preference for or an avoidance of UV-reflecting prey items in any of the color combinations used. If anything, the birds consumed slightly, but not significantly more yellow+UV than yellow prey items. This would indicate that there is not a strong avoidance of UV-reflecting prey items.

The birds had difficulties in learning to avoid unpalatable prey items irrespective of whether the signal was UV+ or UV-. In a simultaneous choice experiment, where a bird can compare two prey types side by side, any differences in learning should be easy to find. The poor learning performance of the birds was not due to the experimental design since the birds readily learnt to associate red with unpalatable prey. One possibility is that the UV cues were too weak to be learnt by the birds. Lindström et al. (1999) found that birds learnt to avoid unpalatable signals from palatable ones only when the signals were highly conspicuous. In the present paper, the mean (\pm SE) UV reflectance (320–400 nm) in green+UV was 25% (\pm 0.20) and in green the UV reflectance was 11% (\pm 0.23). Even though the difference in UV between the treatments was rather slight the birds easily detected, in the presence of UV light, UV+ items from the UV-absorbing background.

The result that the birds avoided green unpalatable items in trial 1 of the learning experiment was somewhat unexpected. This avoidance was not due to more rapid avoidance learning of green unpalatable already within trial 1. Although the birds did not exhibit any avoidance of unpalatable items in the green vs. green+UV preference experiment they still might have had some initial preferences for UV+ items. These may appear only in a more critical situation when they are also confronted with unpalatable items. Additionally, the results suggest that birds, if anything, would be more capable of learning to associate UV reflectance with palatable than with unpalatable prey. Natural backgrounds, such as leaves, bark, and soil, absorb UV light (Endler, 1993; Finger and Burkhardt, 1994). Thus the bird might associate UV reflection more easily with something edible than with an inedible item.

We used a non-aposematic color, green, which allowed us to test whether UV cues alone could create the rejection of nasty tasting prey. If UV reflectance indicates unpalatability then birds should have an innate aversion towards UV colors in combination with any color. We found no such preferences in wild adult birds, which have most likely had previous experience of the warning colors used by prey animals and therefore should have exhibited an innate or learned avoidance. Another characteristic of aposematic prey is that the predator must be capable of learning to associate a particular color with inedibility and hence, to avoid catching similar prey at a later date. However, the birds were not capable of learning to avoid unpalatable prey items irrespective of whether they reflected or absorbed UV light. If anything, they seem to associate UV reflectance with palatability. UV cues alone did not seem to effectively signal unpalatability.

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