

Chromaticity in the UV/blue range facilitates the search for achromatically background-matching prey in birds

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A large variety of predatory species rely on their visual abilities to locate their prey. However, the search for prey may be hampered by prey camouflage. The most prominent example of concealing coloration is background-matching prey coloration characterized by a strong visual resemblance of prey to the background. Even though this principle of camouflage was recognized to efficiently work in predator avoidance a long time ago, the underlying mechanisms are not very well known. In this study, we assessed whether blue tits (*Cyanistes caeruleus*) use chromatic cues in the search for prey. We used two prey types that were achromatically identical but differed in chromatic properties in the UV/blue range and presented them on two achromatically identical backgrounds. The backgrounds had either the same chromatic properties as the prey items (matching combination) or differed in their chromatic properties (mismatching combination). Our results show that birds use chromatic cues in the search for mismatching prey, whereupon chromatic contrast leads to a ‘pop-out’ of the prey item from the background. When prey was presented on a matching background, search times were significantly higher. Interestingly, search for more chromatic prey on the matching background was easier than search for less chromatic prey on the matching background. Our results indicate that birds use both achromatic and chromatic cues when searching for prey, and that the combination of both cues might be helpful in the search task.

Keywords: visual search; crypsis; predation; avian vision; luminance; colour

1. INTRODUCTION

Search for food is one of the most essential tasks in the animal kingdom and a large variety of animal species rely on their visual abilities in order to locate food sources or prey. In plant–animal interactions, food sources for pollinators and seed dispersers are often easily visible. Some plant species produce very colourful and highly detectable flowers or fruits because they depend on animals to disperse their seeds or pollens (e.g. Borges *et al.* 2003; Schaefer & Schmidt 2004; Cazetta *et al.* in press). For insectivorous and carnivorous species, however, the localization of food can be a much harder task since their prey seeks to minimize the risk of being eaten. One of the most widespread ways to avoid detection by visually hunting predators is the development of prey camouflage coloration that hinders predators from detecting the prey (Thayer 1909; Cott 1940).

Probably, the most evident example of camouflage coloration is background matching (Cott 1940; Edmunds 1974; Endler 1978, 1984; Merilaita *et al.*

1999, 2001; Ruxton *et al.* 2004; Houston *et al.* 2007; Sherratt *et al.* 2007). Background-matching coloration is characterized by a strong visual resemblance of an animal to the background both in colour and pattern. By blending into the background prey can efficiently decrease the conspicuousness to predators. However, visually hunting predators searching for background-matching prey can still detect the prey if they are able to perceive the shape of the prey. If prey coloration includes high-contrast markings, such as in disruptive coloration, shape detection can be hindered through markings that create false boundaries or break up the body outline (Thayer 1909; Cott 1940; Merilaita 1998; Cuthill *et al.* 2005; Schaefer & Stobbe 2006; Stobbe & Schaefer 2008). Because background-matching prey lacks such markings, it has been argued that background-matching prey is more likely to be given away by its outline than prey with disruptive coloration (Thayer 1909; Cott 1940; Stevens & Cuthill 2006).

High similarity of prey to background in all visual features (e.g. colour, pattern) is a basic precondition for efficient background-matching coloration. Numerous studies, mainly carried out with human subjects, have demonstrated that if an object differs from the background in a single salient feature such as colour, luminance, orientation or motion, it will generate a ‘pop-out’ effect and will be found easily (e.g. Nothdurft 1991, 1993; Mueller *et al.* 1995; Baldassi & Burr 2004). Thus, it can be assumed that background-matching prey

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coloration is most efficient if it shows strong similarity to the background in all visual features that might reveal the location of the prey. Search for prey that has a surface that is not marked with any features standing out from the background is a demanding task for predators as it requires the ability to detect the outline of the prey. In general, there are two distinct cues that can be used for detection of the shape of prey with high similarity to the background. These cues are based on the detection of edges that indicate the position of a prey. First, depending on the orientation and placement of a prey on a background, it can cover parts of background pattern elements. Resulting discontinuities at the prey edge can then reveal the shape of the prey. Second, if the three-dimensional shape of the prey even slightly sticks out from the background, then the body edges will be emphasized due to the shadows created at the body outline (Thayer 1909).

It has been suggested that edge detection mechanisms mainly rely on achromatic cues (e.g. Osorio *et al.* 1999a). Changes in surface luminance are thought to provide reliable information about the end of one object and the beginning of another object. In fact, it has been demonstrated that some species concentrate on achromatic cues in object detection tasks (e.g. Livingstone & Hubel 1988; Osorio *et al.* 1999a; Jones & Osorio 2004). Thus, it might be assumed that predators predominantly focus on achromatic characteristics of background and prey and largely ignore colour when searching for background-matching prey. However, several studies have shown that insects use both achromatic and chromatic cues depending on the size of and the distance to the food source (e.g. Giurfa *et al.* 1997; Giurfa & Vorobyev 1998; Spaethe *et al.* 2001; Kelber 2005). Hence, it might as well be the case that both achromatic and chromatic cues play a role in the search for background-matching prey. As yet, the relative role of achromatic and chromatic cues for detecting background-matching prey is unknown.

In this study, we compared search performance for prey that achromatically matched the background, but either matched or deviated from the background with respect to chromatic spectrum. For this purpose, we trained wild-caught blue tits (*Cyanistes caeruleus*) to search for artificial prey items on two different backgrounds. The colour vision of these birds extends into the ultraviolet (UV) range (Hart *et al.* 2000), and while one of our background and prey patterns stimulated equally all colour receptors (corresponding to 'bird grey') the other stimulated equally in the medium wavelengths and the long wavelengths, but less in the UV range and more in the short wavelength (SW; blue part of the spectrum) range. The two patterns used for the two backgrounds and the two prey types were identical in number and arrangement of elements. Both the isoluminant (i.e. identical in achromatic properties) but chromatically different prey types were presented on both backgrounds.

We hypothesize that if the birds use chromatic information in the search for the prey, then they should relatively easily find the prey when it is presented on the mismatching background. Owing to the chromatic differences between the surface of

the prey and the background, prey items are expected to generate a pop-out effect. However, when the prey matches the background with respect to both achromatic and chromatic characteristics, the search should be based on the detection of the outline of the prey, revealed by achromatic cues caused by shadows or by discontinuity of the surface (i.e. partly occluded pattern elements). This is likely to be more demanding than the simpler filtering of a chromatic cue, and therefore may require a different, slower search mode. Furthermore, any asymmetries, such as the one matching prey-background combination being more difficult to find than the other matching combination, would suggest that the degree of chromaticity and/or the specific spectral properties of the prey and background patterns do also influence the search.

2. MATERIAL AND METHODS

For our study we trained 27 wild-caught blue tits to search for artificial prey items. The birds were captured with mist nets and kept individually in indoor cages (80 × 60 × 40 cm³) at Tovetorp Zoological Research Station (Stockholm University) in southeastern Sweden (58°56' N, 17°08' E). The room temperature was kept constant at 16°C, and the light : dark rhythm was adjusted to the prevailing day length (with approx. 30 min dawn at 07.00 and approx. 30 min dusk at 18.00). The birds were provided with suet, sunflower seeds, peanuts and water *ad libitum*. The experiments were carried out between February and March 2007 and were performed with permission from the Swedish ethical board in Linköping (Dnr: 56-05).

(a) Backgrounds and prey

The two patterns used for the backgrounds and prey items were created using the software COREL DRAW v. 11 (Corel Corporation, Ottawa, Ontario, Canada). Subsequently, they were printed with a laser printer (HP LaserJet 4000 Series PS with 1200 dpi resolution) on two kinds of paper (Soennecken Brilliant, Branion LogServe GmbH, Overath, Germany; Elite linen notepaper, Cologne, Germany), which differed in their reflectance spectra. While the first paper (from now on referred to as the achromatic background and prey) showed an even reflectance spectrum and a relatively high reflection in the UV range, the second paper (from now on referred to as the chromatic background and prey) had peak reflectance in the blue part and low reflectance in the UV part of the spectrum (figure 1). We printed the two papers with geometrically identical patterns that contained five differentially shaped elements in equal numbers. The elements were displayed in four different luminance shades: white (i.e. no printer ink) and three shades of grey. Thus, each background included 20 different elements in equal numbers, presented on an intermediate background shade (figure 2). The arrangement of elements was identical on every background presented to the birds.

Because the 'white' elements were not printed they showed the same reflectance spectra as the papers. To control for avian vision, we took five measurements each of all shades from both the papers with a spectrometer (AvaSpec-2048 fibre optic spectrometer). However, one of the papers showed high reflectance in the blue part of the spectrum, which may be indicative of fluorescence. To avoid any biases in contrast calculations due to fluorescence, we did not use an external light source in the measurements, but measured radiance of all shades under the illuminating light source used in

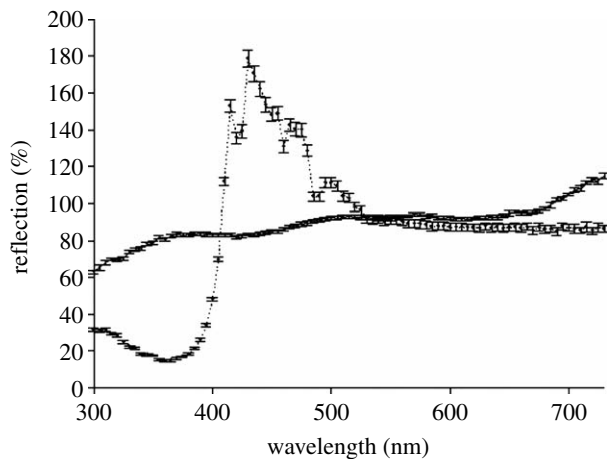


Figure 1. Reflectance spectra of the unprinted (white) elements in the achromatic (solid curve) and in the chromatic background (dotted curve) measured with an Ocean Optics USB 2000 spectrometer with a PX-2 pulsed xenon light source. Shown are mean values and standard errors (each $n=5$).

the experiment (for an irradiance spectrum of the light source see figure 1 in the electronic supplementary material). However, it should be noted that subsequent contrast calculations provided comparable results regardless of the method of spectral measurements (direct reflectance measurement with an external light source or radiance measurement under illuminating light source), indicating that fluorescence did not play a determinant role in this set-up. Before measuring ambient light and radiance of the papers, the spectrometer was calibrated with an AvaLight-HAL Tungsten light source. Rather than measuring radiance, we actually measured irradiance using a cosine-corrected probe. However, because all measurements were made at the same distance and each paper filled the majority of the field of view of the cosine probe, our irradiance measures should be directly proportional to radiance. Subsequently, we calculated resulting reflectance spectra by dividing the irradiance values by the irradiance of the illuminating light in 5 nm steps between 300 and 700 nm. Chromatic (based on the excitation of all four cone types) and achromatic (based on the excitation of the avian double cones) contrast values between grey shades were calculated following Vorobyev & Osorio (1998) and Siddiqi et al. (2004). Contrast values less than 1 just noticeable difference (JND) indicate that two colours are indistinguishable and values greater than 1 JND indicate increased long-distance detection (Schaefer et al. 2006). For calculation of cone catches, we used the cone sensitivities of blue tits identified by Hart et al. (2000). For both backgrounds and prey types, we calculated the contrast between pattern elements (i.e. contrast within a pattern type, 'within-pattern contrast') as well as the contrast between corresponding pattern elements in both pattern types ('between-pattern contrast').

Since achromatic contrast between pattern elements can demonstrably influence the efficiency of camouflage (e.g. Stevens et al. 2006; Fraser et al. 2007), we adjusted the backgrounds and prey types so that the four different shades of grey (elements and background) showed equal relative achromatic contrast to the white (unprinted) shade in both backgrounds (achromatic within-pattern contrast: all $t < 2.1$, d.f. = 8 for each comparison, all $p > 0.05$; for detailed contrast values see table 1 in the electronic supplementary material). This adjustment resulted in the following grey shades, here expressed in percentage of black (i.e. 100% is pure black and 0% is white/unprinted) as defined for the printer setting:

the ground shade of the achromatic paper was 60 per cent black and the elements were 45, 70 and 85 per cent black; the ground shade of the chromatic paper was 55 per cent black and the elements were 40, 65 and 80 per cent black.

Additionally, the comparison of achromatic contrasts between corresponding elements of both background and prey types revealed that they were almost isoluminant (between-pattern contrast (mean achromatic contrast \pm s.e. between corresponding elements): 0–0% -1.1 ± 0.7 JND, 40–45% 0.1 ± 0.3 JND, 55–60% 0.5 ± 0.5 JND, 65–70% -0.04 ± 1.7 JND, 80–85% 2.0 ± 2.6 JND). Thus, we were able to rule out the possibility that overall luminance of background or prey-influenced search times.

Owing to the different chromatic characteristics of the two papers (figure 1), the chromatic background and prey showed slightly higher chromatic contrasts between the unprinted elements and the different shades of grey than did the achromatic background and prey (see table 1 in the electronic supplementary material for details). However, there was no significant difference between the patterns of the two papers (chromatic within-pattern contrast: all $t < 1.6$, d.f. = 8 for each comparison, all $p > 0.05$).

Importantly, the chromatic contrast between corresponding elements of the two patterns was very high in comparison with achromatic contrast between corresponding elements (between-pattern contrast (mean chromatic contrast \pm s.e. between corresponding elements): 0–0% 19.0 ± 0.5 JND, 40–45% 13.2 ± 2.8 JND, 55–60% 16.9 ± 2.9 JND, 65–70% 14.8 ± 2.7 JND, 80–85% 11.8 ± 2.4 JND). This comparison points out the only difference between the two printed papers, namely that the chromatic background and prey were more chromatic than the achromatic background and prey.

Prey items were triangular ($W \times H$: 1.5×1.0 cm²) and contained six pattern elements each so that the density of elements was equal to that in the background. The prey items matched either the achromatic or the chromatic background (figure 2).

(b) Training of the birds

Prior to the experiment, the blue tits were trained to search for the prey items by associating them with a food reward (a piece of organic peanut) that they covered. Training sessions began the day after capture. All birds were trained individually and went through three training steps. To ensure foraging motivation, every training and experimental session started with 60 min of food deprivation in the experimental cage. The experimental cage was made of plywood ($W \times H \times D$: $55 \times 90 \times 70$ cm³) and was lit from the ceiling with two high-frequency fluorescent lamps that had a spectral distribution similar to that of daylight (15 W, BIOLight, Narva). The door of the cage was equipped with an observation window (10×12 cm²), which was covered with a one-way see-through plastic sheet. The birds could thus be observed from the outside, but were unable to see the observer from the inside. To minimize disturbance, the ceiling lights of the experimental room were always shut off during the time of food deprivation and experiments. The experimental boards were slid into the experimental cage from a narrow opening on the bottom of its long side. On the opposite side of the opening, a perch was available 20 cm beneath the ceiling. During the whole time in the experimental cage, the birds had free access to water and the room temperature was kept constant at 16°C.

In training step 1, the blue tits were accustomed to the prey items. For this purpose, two prey items of each kind plus one unprinted triangle of each paper type (i.e. in total six prey items) were placed on a 5×7 cm² piece of brown corrugated

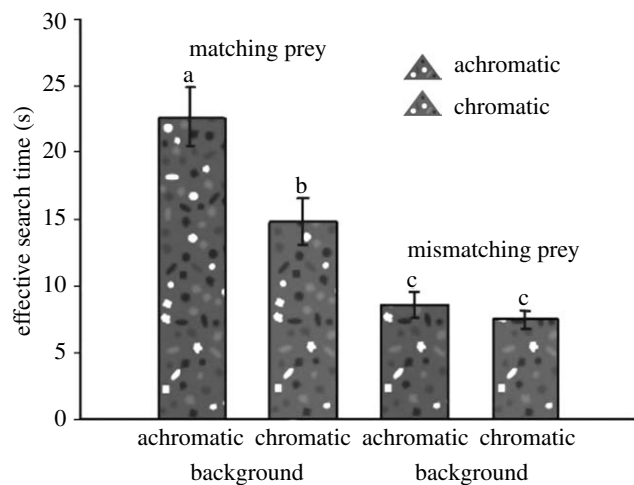


Figure 2. Search times of blue tits for both prey types on both backgrounds. Shown are mean values and standard errors ($n=27$). The letters above the bars denote the results of the *post hoc* comparisons so that the bars with different letter differ significantly from each other (see §2 for details). The filling of the bars each represent the printing on the achromatic and chromatic background. Also displayed are the corresponding prey items. Note that although the differences appear very subtle, due to the use of two different papers and the difference in colour vision between blue tits and humans the birds experienced a clearer difference.

cardboard on which they were all clearly visible. The unprinted prey items had a piece of peanut glued on top, one of each experimental prey types were glued to the cardboard from one tip and the piece of peanut was glued to their underside and was thus partly visible. Additionally, one of each experimental prey types was glued from one tip to cover a hole in the cardboard that the piece of peanut was sunk into. In training step 2, we raised the level of difficulty by covering the two halves of the cardboard with the two backgrounds and by using only printed prey items. On each background type both prey types were present. One prey item was lightly glued to the background and covered a hole in the cardboard containing a piece of peanut, one tip of the second prey item was lifted up to encourage the birds to search for prey. Training step 3 was arranged in the same way as step 2, except that the board was A4 sized and all prey items were glued at all three tips. The position of the prey items was always chosen randomly, but so that no prey item crossed the border between the two backgrounds. Overall, advancement to the next step took place as soon as the birds had managed to complete a training step within 1 hour. The day after completing training step 3, the blue tits proceeded to the experiment. Both training sessions and experiment started by repeating the previous completed training step.

(c) Experimental set-up

One prey item was placed on each A4-sized experimental board during the experiments. Each of the 27 birds used in the experiment was presented with both backgrounds and both prey items. The prey items were oriented and placed at random. The only restriction was that prey items were located at least 2 cm from the board edge. Each prey-background combination, arranged in random order, was repeated three times (12 boards in total per bird). For each experimental board, effective search time (the time a bird spent with active searching for the prey on the board) was recorded until the bird pecked at the prey item and tore it off. The bird was then allowed to eat the food reward before the experimental board

was replaced with the next. Effective search time was defined as the time the bird spent on or close to the board (having its head over the board) and searched for the prey item with its head oriented parallel to the board or downwards.

To exclude the possibility that birds had an aversion to one of the prey items, we also measured search times for prey on an exposing background that was mismatching to both prey types with respect to pattern geometry and reflectance spectrum. Therefore, we randomly chose 20 birds after completion of the experiment and presented them with both prey types on plain brown cardboard (in the same way as in the experiment, i.e. one prey item per board). If the birds showed an aversion to one of the prey types, they were expected to show a delay before they attacked it. Otherwise, we expected the birds to find both prey types rather fast. Each bird was presented with both prey types and this procedure was repeated three times, i.e. with six boards in total.

(d) Statistical analyses

To achieve normal distribution and homoscedasticity, we applied ln-transformation on the search times from the experimental set-up. We analysed the transformed search times from the experimental set-up with repeated-measures ANOVA. Subsequent *post hoc* comparison between groups was carried out using paired *t*-tests. To control for a possible type I error due to multiple comparisons, we used an adjusted α value of 0.007 instead of 0.05. However, all our significant *p* values remain significant after this adjustment. The search times from the set-up controlling for aversion against one of the prey types were normally distributed and were analysed with paired *t*-test. Statistical analyses were made with the free software package R 2.2.0 for Windows (<http://www.r-project.org>).

3. RESULTS

Our predation experiment with artificial prey items and backgrounds revealed that the search times of the blue tits were significantly longer on matching backgrounds than on mismatching backgrounds (interaction between prey and background: $F_{1,26} = 64.27$, $p < 0.001$; figure 2). However, birds took on average approximately 35 per cent longer time to find prey on the achromatic background than on the chromatic background (factor background: $F_{1,26} = 7.86$, $p = 0.006$). The prey type as such did not strongly affect search time (factor prey: $F_{1,26} = 3.21$, $p = 0.08$). *Post hoc* comparisons presented in figure 2 show that the increased search times on the achromatic background were mostly caused by the matching prey and background combination. The difference between the backgrounds was significant only when the prey matched the background, whereas for mismatching prey the search times did not differ significantly between the backgrounds. All following conclusions and discussions are based on the results of the *post hoc* comparisons.

The birds did not show aversion towards either prey type. When presented on the exposing brown background, the birds found the prey very rapidly compared with the search times on the experimental backgrounds. Moreover, the birds did not show any differences in search time before attack between achromatic and chromatic prey (1.8 ± 0.2 s and 1.7 ± 0.1 s, respectively; $t = 0.58$, d.f. = 19, $p = 0.57$).

4. DISCUSSION

Our experiment demonstrates that birds easily found prey that chromatically differed from the background. Regardless of the presented prey–background combination, i.e. the chromatic prey on the achromatic background or the achromatic prey on the chromatic background, search times were very fast. This outcome suggests that search was performed in a so-called ‘pre-attentive’ search mode, in which the whole background is scanned in parallel for potential targets (i.e. parallel search; Treisman & Gelade 1980). Owing to the difference in reflection in the UV/SW part of the spectrum between prey and background, the prey items probably ‘popped out’ from the background and consequently were highly conspicuous to the birds. This result provides further evidence that the blue tits use chromatic cues in search tasks as previously also shown for bees and chicks (e.g. Giurfa *et al.* 1997; Giurfa & Vorobyev 1998; Osorio *et al.* 1999a; Spaethe *et al.* 2001).

It has been known for a long time that animals use background matching, i.e. visual resemblance to their background, to avoid predation (e.g. Wallace 1889), but how this principle of concealment works and how prey appearance should be adjusted to maximize background matching is not known very well (e.g. Merilaita & Lind 2005). Previous studies have shown that similarity in pattern geometry and luminance between the prey and its background influences the efficacy of background-matching colour patterns (Merilaita *et al.* 2001; Stevens *et al.* 2006). In our experiment, birds were able to detect mismatching prey very fast due to the differences in the chromatic properties between the prey and background. Birds found both mismatching prey equally fast indicating that colour differences to the background generally increase predation risk. Thus, our study provides additional evidence that colour is an important aspect of background matching (see also Théry & Casas 2002).

Search for matching prey was as expected more difficult for the birds than search for mismatching prey. In the matching prey–background combinations, birds needed to detect the outline of the prey in order to be able to localize it on the background. The cues available to the blue tits to find prey on a matching background were the same in both the backgrounds. Since prey items were placed on the backgrounds at random, this typically resulted in discontinuity of the background patterning, because they partially covered some of the background elements. This fact and possibly slight shadows around the prey edges generated useful cues for prey detection on both backgrounds. However, since there were no obvious cues, such as difference in colour or lightness, between the prey surface and the background that revealed the position of the prey, birds presumably switched from parallel search to serial search. In serial search attention is focused on the potential targets, serially identifying them as real targets or so-called distractors (Treisman & Gelade 1980).

The result that search times for the matching prey differed between the two prey–background combinations indicates that the chromatic difference between the two patterns influenced the detection of the well-camouflaged prey items. Even though the cues

available for edge detection are solely achromatic cues in both prey–background combinations, birds seem to be influenced by the chromatic properties of background and prey as well. In the present study, the chromaticity of background and prey was high in the chromatic prey–background combination, because reflection of the pattern elements was very low in the UV range and very high in the SW range. Owing to the spectral properties of papers available for our experiment, we could not create a chromatic prey–background combination in which chromaticity is produced in the medium or long wave range. Hence, we are not able to draw the conclusion that chromaticity in general makes search for background-matching prey easier than search solely based on achromatic cues. It is possible that the observed faster search times for chromatic background-matching prey are caused by the specific spectral properties of the achromatic and chromatic background and prey, i.e. high-UV reflection might somehow increase search times or high reflection in the SW range might decrease the difficulty of the search task. Given that it is currently unknown how chromatic stimuli influence processing of visual information by birds, the reason for decreased search times for chromatic prey on a chromatic background remains to be clarified.

In general, chromaticity constitutes an important signal parameter for foraging birds. It has been shown that birds and primates attend primarily to chromatic and not to achromatic cues when searching for fruits (Sumner & Mollon 2000, Schaefer *et al.* 2006; Cazetta *et al.* in press). Furthermore, several studies indicate that prey species are often more camouflaged with respect to chromatic than to achromatic cues (Théry *et al.* 2005; Stuart-Fox *et al.* 2006). For several reasons, chromaticity produced in the UV/blue range of the spectrum might play a special role for passerine birds. Håstad *et al.* (2005) demonstrated that passerines primarily signal to conspecifics in the UV/blue range because signalling in this range increases conspicuousness to other passerine birds. At the same time, it decreases conspicuousness to many avian predators of passerines because most raptors are less sensitive to light in this spectral range (Ödeen & Håstad 2003). Moreover, the UV/blue structural plumage colours often serve as quality-indicating signals in mate choice providing reliable information about, for example, territory quality (Keyser & Hill 2000), reproductive effort (Siefferman & Hill 2003), parasite load (Doucet & Montgomerie 2003) or male competitive ability (Siefferman & Hill 2005). In particular, UV coloration is an important sexually selected trait in the blue tit, the avian predator that we studied. Blue tits mate assortatively according to the degree of UV ornamentation (Andersson & Andersson 1998), and variation in UV ornamentation is correlated to fertilization success (Delhey *et al.* 2007). Spectral variation at SWs is suggested to be encoded by an opponent mechanism that directly compares signals from UV cones to those from SW cones (Osorio *et al.* 1999b), and visual signals in the UV/blue range might be particularly effective if birds are very sensitive to differences in the chromaticity in this spectral range. However, to date, it remains unknown if chromaticity

in the UV/blue range is of greater importance for foraging passerine birds than chromaticity in medium or long wavelengths.

In summary, our study shows that the blue tits base their search for background matching prey on both achromatic and chromatic cues. Moreover, search times were significantly lower when the background and prey was more chromatic, having low UV reflectance and high reflectance in the SW range. We suggest that future studies should examine whether this result is also applicable to chromatic patterns when chromaticity is produced in other parts of the spectrum.

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REFERENCES

- Andersson, S. J. & Andersson, M. 1998 Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. B* **265**, 445–450. (doi:10.1098/rspb.1998.0315)
- Baldassi, S. & Burr, D. C. 2004 'Pop-out' of targets modulated in luminance or colour: the effect of intrinsic and extrinsic uncertainty. *Vis. Res.* **44**, 1227–1233. (doi:10.1016/j.visres.2003.12.018)
- Borges, R. M., Gowda, V. & Zacharias, M. 2003 Butterfly pollination and high-contrast visual signals in a low-density distylous plant. *Oecologia* **136**, 571–573. (doi:10.1007/s00442-003-1336-y)
- Cazetta, E., Schaefer, H. M. & Galetti, M. In press. Why are fruits so colorful? The relative importance of achromatic and chromatic contrasts for detection by birds. *Evol. Ecol.* (doi:10.1007/s10682-007-9217-1)
- Cott, H. 1940 *Adaptive coloration in animals*. London, UK: Methuen.
- Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Párraga, C. A. & Troscianko, T. S. 2005 Disruptive coloration and background pattern matching. *Nature* **434**, 72–74. (doi:10.1038/nature03312)
- Delhey, K., Peters, A., Johnsen, A. & Kempenaers, B. 2007 Fertilization success and UV ornamentation in blue tits *Cyanistes caeruleus*: correlational and experimental evidence. *Behav. Ecol.* **18**, 399–409. (doi:10.1093/beheco/arl096)
- Doucet, S. M. & Montgomerie, R. 2003 Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behav. Ecol.* **14**, 503–509. (doi:10.1093/beheco/arg035)
- Edmunds, M. 1974 *Defence in animals*. New York, NY: Longman.
- Endler, J. A. 1978 A predator's view of animal colour patterns. *Evol. Biol.* **11**, 319–364.
- Endler, J. A. 1984 Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22**, 187–231. (doi:10.1111/j.1095-8312.1984.tb01677.x)
- Fraser, S., Callahan, A., Klassen, D. & Sherratt, T. N. 2007 Empirical test of the role of disruptive coloration in reducing detectability. *Proc. R. Soc. B* **274**, 1325–1331. (doi:10.1098/rspb.2007.0153)
- Giurfa, M. & Vorobyev, M. 1998 The angular range of achromatic target detection by honey bees. *J. Comp. Physiol. A* **183**, 101–110. (doi:10.1007/s003590050238)
- Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. & Menzel, R. 1997 Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *J. Comp. Physiol. A* **180**, 235–243. (doi:10.1007/s003590050044)
- Hart, N. S., Partridge, J. C. & Cuthill, I. C. 2000 Retinal asymmetry in birds. *Curr. Biol.* **10**, 115–117. (doi:10.1016/S0960-9822(00)00297-9)
- Håstad, O., Victorsson, J. & Ödeen, A. 2005 Differences in color vision make passerines less conspicuous in the eyes of their predators. *Proc. Natl Acad. Sci. USA* **102**, 6391–6394. (doi:10.1073/pnas.0409228102)
- Houston, A., Stevens, M. & Cuthill, I. C. 2007 Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behav. Ecol.* **18**, 769–775. (doi:10.1093/beheco/arm039)
- Jones, C. D. & Osorio, D. 2004 Discrimination of oriented visual textures by poultry chicks. *Vis. Res.* **44**, 83–89. (doi:10.1016/j.visres.2003.08.014)
- Kelber, A. 2005 Alternative use of chromatic and achromatic cues in a hawkmoth. *Proc. R. Soc. B* **272**, 2143–2147. (doi:10.1098/rspb.2005.3207)
- Keyser, A. J. & Hill, G. E. 2000 Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav. Ecol.* **11**, 202–209. (doi:10.1093/beheco/11.2.202)
- Livingstone, M. & Hubel, D. 1988 Segregation of form, color, movement, and depth—atomy, physiology and perception. *Science* **240**, 740–749. (doi:10.1126/science.3283936)
- Merilaita, S. 1998 Crypsis through disruptive coloration in an isopod. *Proc. R. Soc. B* **265**, 1059–1064. (doi:10.1098/rspb.1998.0399)
- Merilaita, S. & Lind, J. 2005 Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. B* **272**, 665–670. (doi:10.1098/rspb.2004.3000)
- Merilaita, S., Tuomi, J. & Jormalainen, V. 1999 Optimization of cryptic coloration in heterogeneous habitats. *Biol. J. Linn. Soc.* **67**, 151–161. (doi:10.1111/j.1095-8312.1999.tb01858.x)
- Merilaita, S., Lyytinen, A. & Mappes, J. 2001 Selection for cryptic coloration in a visually heterogeneous habitat. *Proc. R. Soc. B* **268**, 1925–1929. (doi:10.1098/rspb.2001.1747)
- Mueller, H. J., Heller, D. & Ziegler, J. 1995 Visual search for singleton feature targets within and across feature dimensions. *Percept. Psychophys.* **57**, 1–17.
- Nothdurft, H. C. 1991 Texture segmentation and pop-out from orientation contrast. *Vis. Res.* **31**, 1073–1078. (doi:10.1016/0042-6989(91)90211-M)
- Nothdurft, H. C. 1993 Saliency effects across dimensions in visual search. *Vis. Res.* **33**, 839–844. (doi:10.1016/0042-6989(93)90202-8)
- Ödeen, A. & Håstad, O. 2003 Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* **20**, 855–861. (doi:10.1093/molbev/msg108)
- Osorio, D., Miklósi, A. & Gonda, Z. 1999a Visual ecology and perception of coloration patterns by domestic chicks. *Evol. Ecol.* **13**, 673–689. (doi:10.1023/A:1011059715610)
- Osorio, D., Vorobyev, M. & Jones, C. D. 1999b Colour vision of domestic chicks. *J. Exp. Biol.* **202**, 2951–2959.
- Ruxton, G. D., Sherratt, T. N. & Speed, M. 2004 *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford, UK: Oxford University Press.
- Schaefer, H. M. & Schmidt, V. 2004 Detectability and content as opposing signal characteristics in fruits. *Biol. Lett.* **271**(suppl. 5), S370–S373. (doi:10.1098/rsbl.2004.0191)

- Schaefer, H. M. & Stobbe, N. 2006 Disruptive coloration provides camouflage independent of background matching. *Proc. R. Soc. B* **273**, 2427–2432. (doi:10.1098/rspb.2006.3615)
- Schaefer, H. M., Levey, D. J., Schaefer, V. & Avery, M. L. 2006 The role of chromatic and achromatic signals for fruit detection by birds. *Behav. Ecol.* **17**, 784–789. (doi:10.1093/beheco/arl011)
- Sherratt, T. N., Pollitt, D. & Wilkinson, D. M. 2007 The evolution of crypsis in replicating populations of web-based prey. *Oikos* **116**, 449–460. (doi:10.1111/j.0030-1299.2007.15521.x)
- Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M. & Summers, K. 2004 Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J. Exp. Biol.* **207**, 2471–2485. (doi:10.1242/jeb.01047)
- Siefferman, L. & Hill, G. E. 2003 Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behav. Ecol.* **14**, 855–861. (doi:10.1093/beheco/arg063)
- Siefferman, L. & Hill, G. E. 2005 UV-blue structural coloration and competition for nest boxes in male eastern bluebirds. *Anim. Behav.* **69**, 67–72. (doi:10.1016/j.anbehav.2003.12.026)
- Spaethe, J., Tautz, J. & Chittka, L. 2001 Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proc. Natl Acad. Sci. USA* **98**, 3898–3903. (doi:10.1073/pnas.071053098)
- Stevens, M. & Cuthill, I. C. 2006 Disruptive coloration, crypsis and edge detection in early visual processing. *Proc. R. Soc. B* **273**, 2141–2147. (doi:10.1098/rspb.2006.3556)
- Stevens, M., Cuthill, I. C., Windsor, A. M. M. & Walker, H. J. 2006 Disruptive contrast in animal camouflage. *Proc. R. Soc. B* **273**, 2433–2438. (doi:10.1098/rspb.2006.3614)
- Stobbe, N. & Schaefer, H. M. 2008 Enhancement of chromatic contrast increases predation risk for striped butterflies. *Proc. R. Soc. B* **275**, 1535–1541. (doi:10.1098/rspb.2008.0209)
- Stuart-Fox, D., Whiting, M. & Moussalli, A. 2006 Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. *Biol. J. Linn. Soc.* **88**, 437–446. (doi:10.1111/j.1095-8312.2006.00631.x)
- Sumner, P. & Mollon, J. D. 2000 Chromaticity as a signal of ripeness in fruits taken by primates. *J. Exp. Biol.* **203**, 1987–2000.
- Thayer, G. H. 1909 *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern*. New York, NY: MacMillan.
- Théry, M. & Casas, J. 2002 Predator and prey views of spider camouflage. *Nature* **415**, 133. (doi:10.1038/415133a)
- Théry, M., Debut, M., Gomez, D. & Casas, J. 2005 Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behav. Ecol.* **16**, 25–29. (doi:10.1093/beheco/arh130)
- Treisman, A. M. & Gelade, G. 1980 A feature-integration theory of attention. *Cognit. Psychol.* **12**, 97–136. (doi:10.1016/0010-0285(80)90005-5)
- Vorobyev, M. & Osorio, D. 1998 Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. B* **265**, 351–358. (doi:10.1098/rspb.1998.0302)
- Wallace, A. R. 1889 *Darwinism. An exposition of the theory of natural selection with some of its applications*. London, UK: Macmillan & Co.