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Original Article

Hide and seek: properties of prey and background patterns affect prey detection by blue tits

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We studied the effects of visual appearance of background and similarity between background and prey patterning on prey detection and camouflage. Although increased similarity with background (background matching) is known to impede prey detection, the relative importance of different aspects of visual similarity has received little interest. We used blue tits (*Cyanistes caeruleus*) as predators and trained them to search for artificial prey items presented on printed background plates. We particularly investigated the effect of the density and the shape of the elements constituting the background and the prey patterning. Our experiment shows that increase in the density of elements in the background caused an increase in search times of all prey types. We also found that compared with fully background-matching prey, prey patterning that sported a mismatching element shape and, interestingly, also prey patterning that mismatched the element density of the background decrease prey search time and, hence, deteriorated camouflage. There was no difference in search time between the shape- and the density-mismatching prey categories. We conclude that element-dense backgrounds are more protective both for background-matching prey and background-mismatching prey than backgrounds with low element density. Further, our results suggest that even if prey patterning consists of elements that closely match the visual elements in the background, high-level crypsis through background matching only arises if the density of the elements is also similar between the prey patterning and the background. These findings are important when considering prey habitat choice and the evolution and limitations of background matching and signaling coloration.

Key words: **camouflage, crypsis, detection, predation, prey coloration, prey search.**

INTRODUCTION

Protective coloration constitutes a widespread means to decrease predation risk and has a variety of different forms (Ruxton et al. 2004). A common form of protective coloration in prey is cryptic coloration. Animals relying on cryptic coloration use their body colors and patterns to decrease the risk of being detected (Stevens and Merilaita 2009). Background matching, meaning visual similarity between the colors and patterns of an animal and its background, provides a way of decreasing the risk of being detected.

Despite the fact that background matching appears to be a very widespread form of antipredator adaptation, surprisingly few empirical studies have addressed it directly. Little is known about the aspects of the visual appearance of the background that are necessary to match in order for a color pattern to provide an effective concealment (Merilaita and Stevens 2011). For example, flatfish and cuttlefish are known to be able to spectacularly adjust their body patterning to resemble background patterns and objects in shape (e.g., Ramachandran et al. 1996; Hanlon 2007). However, considering prey detection by predators, we do not know much about how important it is to match the specific shapes of single elements constituting the visual background and how important a more general resemblance, such as matching the density of elements, is for effective prey camouflage. Evaluation of the importance of various aspects of color patterns in background matching is important for understanding the function and the evolution of background-matching coloration. Such knowledge is also needed when one attempts to estimate the level of crypsis or conspicuousness of body coloration and visual signals.

Behavior ecological research on both cryptic coloration and protective coloration in general has mainly focused on the properties of prey coloration and the responses it induces in the predator (e.g., Lindström et al. 2001; Cuthill et al. 2005; Merilaita and

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Lind 2006; Stevens et al. 2007; Rowland et al. 2008). Moreover, it is well established that the visual relation between the prey and its background (i.e., their similarity or difference) is important when considering the efficacy and function of different types of protective coloration. However, recent research indicates that to fully understand predators' responses to protective coloration, and particularly prey detection, it is necessary to also take into account the effect of visual properties of the background by itself. Thus, it has been proposed that not only the similarity between a prey and its visual background (i.e., level of background matching) but also the amount of visual information in the background will determine how easy or difficult it will be to detect the prey, and for this reason, the visual properties of the background are probably important for the function and evolution of protective coloration (Merilaita 2003). Basically, this means that some visual aspects of the background may act as noise for detection when a predator is looking for cues that are useful in the detection of prey. Accordingly, it has been shown that the detection of a target shape presented among distractors (i.e., nontarget shapes) by human subjects is influenced not only by the similarity between the target and the distractors but also by the variability among and the number of the distractors present in the background (Duncan and Humphreys 1989). In experiments on human visual psychology, the subjects often search for particular symbols among other symbols, which is—to some extent—different from the search of cryptic prey items. However, in a biologically more relevant setting, using blue tits (*Cyanistes caeruleus*), a natural predator of insects, presented with actual, patterned prey items on patterned backgrounds, we have found that prey detection time increases with increasing diversity and complexity of the shapes of the elements constituting the background patterning (Dimitrova and Merilaita 2010, 2012). Similarly, it has been shown that increased lightness range (i.e., contrast) of the background patterning increases prey search time (Dimitrova et al. 2009). In addition to these studies, Bond and Kamil (2006) have suggested that grain size in the visual background influences search efficacy in blue jays (*Cyanocitta cristata*). In sum, there is increasing evidence that some visual properties of the background, independent of the degree of target–background similarity, can be very important in prey search and probably also for the function of visual signals.

Neither background matching nor visual complexity of background is an univocal property in the sense that several different aspects of visual appearance may contribute to these to varying extents. To understand how they affect prey (and signal) detection and its ecological and evolutionary consequences in nature, it is necessary to conduct systematic studies to identify those aspects in the appearance of prey coloration and visual backgrounds that have important effects on detection. Such studies have so far not been common. However, some of our previous studies (Dimitrova and Merilaita 2010, 2012), as well as the present study, have been conducted for this purpose.

In the present study, we specifically focused on the density of elements constituting a pattern and conducted and studied background matching and the effect of background on prey concealment using an experiment in which we trained wild-caught blue tits to search for artificial prey. Numerous natural visual backgrounds are patchworks comprising sets of objects, particles, or other elements. Examples of these are vegetation, leafworks, bark, rocks covered by lichen or patches of moss, pebbles, fallen leaves or needles, and so on. For this reason, variation in density of the elements constituting a visual background is relevant within and among many types of backgrounds. Density of the elements constituting the background has so far not received attention in the context of prey search. However, we would expect that, in the same way as other properties that contribute to background complexity and influence the amount of visual information in the background, this property may be important when prey detectability and background matching are considered. Our experiment answers 3 questions. 1) Does the density of visual elements in the background influence prey detection? If each visual element constitutes a piece of visual information that can distract the viewer, then we would expect prey search in a high–element-density background to be more difficult than prey search in a low–element-density background. 2) In prey camouflage based on resemblance to a background consisting of such visual elements, is the prey color pattern primarily selected to match the density or the geometric shape of the visual elements, or is it necessary to match both of these visual aspects? If only one of these aspects, for example, geometric shape, is important in background matching, it would suggest that background pattern matching is a relatively versatile adaptation that could be useful under a range of different conditions. 3) If a high-density background makes prey search more difficult, does it also mean that such background is more "forgiving" for deviations from high degree of matching? In other words, does the increase in the difficulty of the search task caused by the properties of the background also mask deviations from high background matching of prey color pattern or is it mainly the highly background-matching prey that benefit from the effect of the background? If the former is true, it could suggest that selection for background matching would be less intense in high-density backgrounds than in low-density backgrounds.

MATERIALS AND METHODS

General procedure

In total, 24 wild blue tits (*C. caeruleus*) were used as predators and were trained to search on artificial backgrounds for artificial prey items that consisted of a piece of printed paper covering a small piece of peanut as a reward. We used blue tits because they are common in the study area and throughout Europe and because they are a visually hunting omnivorous avian species eating various insects such as moths and butterfly larvae. Blue tits and other passerine birds probably impose a significant selection pressure on many camouflaged insects.

Although technically more elaborate methods have been used in some studies on prey detection and predator psychology (e.g., Bond and Kamil 2002, 2006; Blaisdell and Cook 2005), our straightforward method of presenting prey items on background plates is particularly suitable for our purpose and provides several benefits. The laboratory environment enables full control over the search background and direct observation of predator behavior. Yet, the birds only need a relatively brief habituation for this setup, resulting in short time in captivity and comparatively large numbers of replicates.

The blue tits had been captured with mist nets and kept individually in indoor cages ($80 \times 60 \times 40\,cm^3$) at Tovetorp Research Station (Stockholm University) in southeastern Sweden (lat 58°56′N, long 17°08′E). To enable bird capture at the research station during the winter season, there were 3 daily supervised feeding stations with suet balls, sunflower seeds, peanuts, and hemp seeds. The room temperature was about 18 °C and the light:dark rhythm (with 30-min dawn and dusk) was adjusted according to the prevailing day length. The home cages were equipped with 3 perches, and the birds had free access to suet, sunflower seeds, peanuts, and water.

The birds were kept in captivity for 14 days (maximum), before they were ringed (license no. 619 from the Bird Ringing Center, Swedish Museum of Natural History) and released in the area of capture. All birds retained their health during captivity and at time of their release. Many of the individuals were recaptured later during the season at the feeding stations and they were in good condition. The experiments were conducted between February and March of 2010, with permission from the Swedish ethical board in Linköping (no. 62-08). All bird transportation was conducted in dark cloth bags according to the terms of our ethical and bird-ringing permissions.

The general procedure of our experiment was similar to what we have used in earlier experiments (e.g., Dimitrova and Merilaita 2010, 2012). However, all the birds had previously been used in another experiment on prey camouflage (Merilaita and Dimitrova 2014) with similar training and experimental procedure. We chose to reuse these birds in another experiment to minimize the total number of wild birds that we would need to capture and to minimize the amount of training needed before the blue tits could go through the current experiment. Importantly, the backgrounds and the prey items differed considerably in appearance between the 2 studies. The ground color of both the backgrounds and the prey items in the previous experiment was white, whereas in the present experiment, it was gray; moreover, the patterning of the backgrounds and prey items differed between the experiments. Furthermore, the prey items in the previous experiment were square, whereas in the present experiment, they were triangular. Therefore, we are confident that the blue tits' previous experience did not affect the outcome of our current experiment. The day after a blue tit had completed the previous experiment, it was randomly assigned to a treatment group in the current experiment and the training with the new background and prey items started.

Backgrounds and prey

To study the effect of density of elements (i.e., number of elements per unit area) constituting the patterning of the visual background, we created 2 different backgrounds, which differed in their number of elements (a low-density background (hereafter termed LBg) and a high-density background (hereafter termed HBg; Figure 1). Our backgrounds correspond to 2D representations of environments that are made up of a set of objects, particles, or other elements. To enable controlled manipulation of the degree of background matching of prey items on our backgrounds, we only used a limited number of shapes for the elements constituting the backgrounds and did not allow the elements to overlap (because that would have distorted their shapes).

To study background matching and the effect of prey color pattern, we also created 3 categories of prey items: 1) a prey category that matched both the shape and the density of pattern elements in the background (hereafter called MP for matching pattern); 2) a prey category that mismatched the element shapes but matched the element density of the background patterning (hereafter termed DMP for density-matching pattern); and 3) a prey category that matched the element shape but mismatched the density of elements in the background patterning (hereafter named SMP for shape-matching pattern; Figure 1).

Figure 1
The element shapes used in the experiment. (A) The 4 element shapes found only in the background. (B) The 3 element shapes found both in the background and in the prey patterning. (C) The 3 element shapes found only in the prey items that had element mismatch with the background.

The backgrounds were created with the software Corel Draw 11 (Corel Corporation), and the prey items were created by using a purpose-written program in Matlab R2008b (Mathworks). For each prey item, the program chose the exact placement of the pattern elements randomly but without allowing overlap (Figure 2A,B). This prey pattern variation resulted in a search task for the blue tits that simulated foraging on several prey types simultaneously, something that the omnivorous blue tits are used to in nature, especially during the winter months when food is scarce. We wanted the search task to be difficult enough, so that any possible differences in search times would be detectable, but not too difficult so that the birds would lose their motivation to search for the prey items. Therefore, the choice of size, shape, and density of the pattern elements of the backgrounds and the prey items was based on a preliminary test with blue tits that were trained similar to the experimental birds but that were excluded from the experiment. The size of the prey and the number of elements on the prey items and the backgrounds were adjusted so that the element density was equal in the background and in the prey categories matching the element density of a background. All prey items and backgrounds were reproduced with a laser printer (HP LaserJet 4000 Series PS with 1200 dots per inch resolution) on white copying paper (Canon Office).

The 2 backgrounds of A4 size ($21 \times 29\,cm^2$) had a patterning consisting of 7 element shapes (Figure 2C,D). Of these element shapes, 4 were found only in the background patterning (Figure 1A), whereas 3 were used in both the prey patterning and the background (Figure 1B). The shade of the gray ground color of the backgrounds and prey was adjusted so that it roughly corresponded to a luminance that was the mean of the white and black elements, as experienced by blue tits (see Dimitrova et al. 2009). On the LBg, in total, there were 1246 elements and on the HBg, there were 2492 elements (Figure 2C,D). In each background, one-half of the element shapes were black and the other half were white. All background elements were randomly oriented. However, because we addressed questions about the effect of density mismatch, we placed the elements with roughly even density over the entire background (Figure 2C,D). Each printed background was glued on an equal-sized corrugated cardboard, using solvent-free glue stick (Scotch, 3M), to form the experimental boards.

The prey items were triangular (height × width: $18 \times 12\,mm^2$) and had the same gray ground color as the backgrounds. To increase the generality of our results and to decrease the possible effects of predator learning and search image formation, element shapes, placement, and orientations were varied among prey items belonging to the same prey category (Figure 1B,C and 2A,B). Thus, hereafter, when referring to prey with matching element shapes, this includes any combination of 2 of the 3 background-matching element shapes used in the experiment (Figure 1B). The density- and shape-matching prey category (MP) had 2 different, randomly chosen background-matching element shapes, one of each (in total, 2 elements per prey item) when the prey was presented on the LBg, and 2 of each (in total, 4 elements per prey item) when the prey was presented on the HBg. The second prey category matched the pattern element density of the background but mismatched background element shapes (DMP; Figure 2A,B). Thus, one of the element shapes (1 element when presented on the LBg and 2 elements when presented on the HBg) was not present

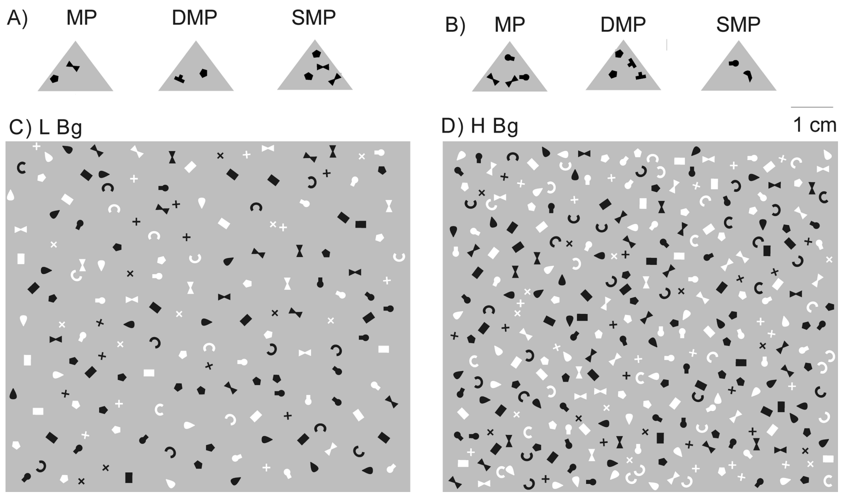

Figure 2
Examples of the prey categories and the backgrounds. Prey category MP had both background-matching element density and shapes, DMP had matched element density but one mismatching element shape, and SMP had only matching element shapes but mismatched element density relative to the background. One example of the prey items from each of the 3 categories (A) in the low-density background and (B) in the high-density background is shown. For each prey item, the matching and mismatching elements were randomly chosen among the shapes depicted in Figure 1A, B, after which they were randomly placed and oriented. Samples of the patterning of (C) the low-density background (LBg) and (D) the high-density background (HBg) are shown.

in the background (Figures 1C). The third prey category had background-matching element shapes but mismatch of the density of the background elements (SMP; Figure 2A,B). On the LBg, the prey had 4 elements and was similar to the element shape- and density-matching prey (MP) on the HBg. On the HBg, the density-mismatching prey had only 2 background-matching elements. Notice that the element density was identical between the DMP (black elements) and the respective background (black-and-white elements) regardless of the element color. Ignoring the color of the elements and focusing on their total densities was justified by a previous experiment, in which search times did not differ among gray-and-white, black-and-white, and black-gray-and-white preys when presented on a and black-gray-and-white background (Dimitrova and Merilaita 2010).

Training and experimental procedure

The experimental cages were made of plywood (width × height × depth: $55 \times 90 \times 70\,cm^3$) and were lit from the ceiling with 2 natural-light–imitating fluorescent lamps (15 W, BIOlight, Narva). An observation window ($10 \times 12\,cm^2$) was covered with a 1-way see-through plastic sheet, and because the experimental room was kept dark when a bird was in an experimental cage, it could not see the observer. There was always access to water *ad libitum* in the cage, and the temperature was maintained at about 18 °C. A perch was located 20 cm below the ceiling, and on the opposite side, near the floor, there was an opening, through which the experimental boards could be inserted. Every training session and the experiment session were preceded by a 45- to 60-min period without food in the experimental cage.

The purpose of the training was to teach the birds to associate the prey items with the reward hidden underneath them and thereby to induce them to search for the artificial prey items. Because the blue tits had already been used in another experiment with similar training and experimental procedure, we only needed a brief training that introduced the blue tits to the new prey items and the backgrounds at the start of the present experiment. This was done in 2 steps. In the first step, we introduced the prey categories to the birds on a plain brown A4-sized corrugated cardboard, on which the prey items were easy to detect. We made 3 randomly placed holes, in which a piece of organically grown peanut (ca. $2 \times 2 \times 2\,mm^3$) was placed as a food reward for a bird that found the prey item and tore it off the background. The holes were then covered with the prey items, one from each prey category. All prey items were lightly glued from 3 points. In the second step, we made the prey items cryptic, by covering the A4-sized cardboard with the high-density background or the low-density background, depending on the background that the blue tit was designated to. We made 6 randomly placed holes for the food reward and covered them with the prey items, 2 from each prey category. A tip of one of the prey items was slightly bent up to initiate searching. A bird advanced to the next step if it had found all prey items on the preceding training step within 1 h. Otherwise, it had to redo that step in the next training session.

The actual experiment started the day after the bird had completed training step 2. For the presentation of prey items in the experiment, 1 randomly oriented prey item was lightly glued at 3 points on each experimental board. The prey items covered a randomly placed hole with a piece of peanut as a food reward. All prey items were placed at least 2 cm away from the board edge. During the experiment, each bird was only presented with 1 type of background, either the LBg or the HBg. On the assigned background, each bird was presented with all 3 prey categories 4 times. This resulted in 12 successive representations for a bird. For each bird, we randomized the order of the prey categories but made sure that equal number of birds started the experiment with each prey category.

For each presentation, the observer (M.D.) recorded the effective search time, that is, the time during which the blue tit actively searched for a prey item on an experimental board. The timing was stopped when the bird had found the prey item and pecked it to tear it off. The bird was then allowed to eat the reward before the board was replaced.

Statistical analyses

To achieve normal distribution and homoscedasticity, we applied logarithmic transformation on the effective search times, suggested by the Box–Cox analysis. When analyzing the data, we used the means of the effective search times of each prey category for each bird, thus resulting in 3 values per bird. The transformed effective search times were analyzed with repeated-measures Anova with IBM SPSS Statistics version 19.0 for Windows. We used prey category as the within-subject factor and background as the between-subject factor. When necessary, paired *t*-tests with corrected α-values according to sequential Bonferroni method (Sokal and Rohlf 1995) were performed as post-hoc tests.

RESULTS

We found a significant difference in effective search time between the 2 backgrounds ($F_{(1,22)} = 10.96$; $P = 0.003$; Figure 3). Search times were consistently longer on the HBg compared with that on the LBg. There was also a significant difference between the 3 prey categories ($F_{(2,44)} = 8.75$; $P = 0.001$). The interaction between background and prey category was not significant ($F_{(2,44)} = 1.28$; $P = 0.29$).

We used post-hoc tests to further analyze the differences between the 3 prey categories. Because the interaction between prey category and background was not significant, we pooled the birds used in the 2 different backgrounds and used paired *t*-tests to test for differences among the prey categories. Thus, 2 out of the 3 pairwise comparisons were significant even after the sequential Bonferroni correction (Figure 3). The fully background-matching MP prey category was more difficult to detect than the shape-matching SMP prey category ($t_{(23)} = 3.28$; $P = 0.003$; corrected $\alpha = 0.025$). The MP category was also more difficult to detect than the density-matching DMP prey category ($t_{(23)} = 4.11$; $P < 0.0001$; corrected $\alpha = 0.017$). There was no significant difference in the search times between the DMP and the SMP prey categories ($t_{(23)} = 0.62$; $P = 0.54$).

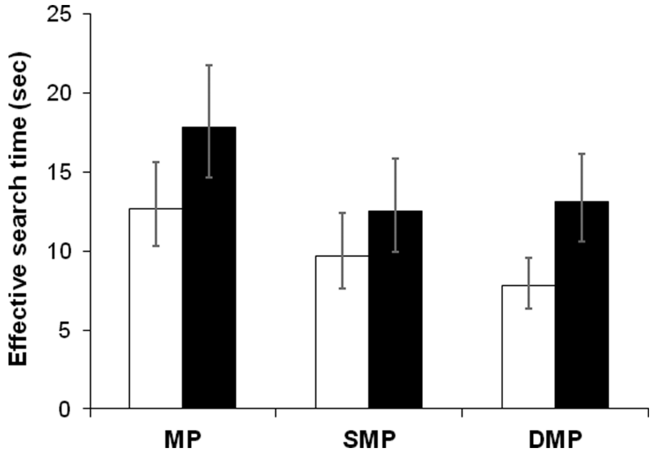

Figure 3
The effective prey search time (s) of blue tits. In this experiment, 12 birds were presented the 3 prey categories on the LBg background (white bars), and another 12 birds were presented the 3 prey categories on the HBg background (black bars). The 3 prey categories had background-matching element density and shapes (MP), background-matching element shapes but mismatching density (SMP), or background-matching density but partly mismatching element shapes (DMP). Whiskers are back-transformed confidence intervals.

DISCUSSION

Our experiment showed that an increase in the density of pattern elements in the background increased the blue tits' search times consistently for all 3 prey types. This result is in accordance with the theoretical prediction that the amount of visual information in the background can make the detection of prey more difficult or slower compared with a background that contains a smaller amount of visual information (Merilaita 2003). The mechanistic explanation of this result might be that a predator looking for the body outline of the prey has to process a larger amount of visual edges when the density of the elements in the background is high than when the density of the same is low. Alternatively, high-contrast elements may have a distractive effect on the predator, an effect that has been demonstrated in a previous experiment with blue tits (Dimitrova et al. 2009) and that could be strengthened by the increase in element density. Such distractive effect can arise if the elements compete for visual attention during the search for the visual cues of the prey or if the blotches cause lateral masking (i.e., impaired perception of peripheral stimuli when a distracting stimulus is present; Desimone and Duncan 1995; Wertheim et al. 2006; Dimitrova et al. 2009; Merilaita et al. 2013). Either of these 2 mechanistic explanations would decrease the search efficacy by increasing the number of prey the birds fail to detect or by forcing the birds to decrease their search rate (Gendron and Staddon 1984; Dukas and Clark 1995).

In our previous experiments with blue tits, we have shown that other visual aspects of the background also influence the difficulty of prey search. Prey search times increase with the level of background complexity both in terms of diversity of shapes and complexity of shapes (i.e., the ratio of perimeter to the square root of area) of the objects, particles, or other elements that constitute the background (Dimitrova and Merilaita 2010, 2012). The present study shows that another property of backgrounds that contributes to visual complexity and amount of visual information (or noise), the density of elements constituting the background, also influences prey detection. In addition, increased lightness range (i.e., achromatic contrast between background elements) has been shown to increase prey search times (Dimitrova et al. 2009). Thus, in practice, variation in all of the different aspects of visual backgrounds that we have looked into so far has turned out to be a potentially important factor with respect to prey detection. Collectively, these results point toward important effects that have not been investigated in animals searching for camouflaged prey or predator–prey interactions in general. Importantly, these effects of the visual properties of backgrounds are likely to have behavioral, ecological, and evolutionary consequences. For example, variation in 1 or several aspects of backgrounds influencing visual detection could induce differences among environments in the intensity and direction of the selection shaping antipredator strategies, prey coloration, and also animal signals in general. Results from a comparative study and an evolutionary simulation show that prey living in a visual environment that facilitates concealment are more likely to evolve toward camouflage, whereas prey in a more exposing environment are more likely to evolve warning coloration (Merilaita and Tullberg 2005). Moreover, variation in the exposing or concealing properties of various backgrounds may induce behavioral responses, for example, by influencing the patch choice by prey and predators (Kjernsmo and Merilaita 2012).

In addition to the effect of the background on prey search, our experiment also addressed background matching. It was clear that the birds had more difficulty in finding the prey belonging to the category matching both shape and density of the elements in the background patterning than in finding the prey categories mismatching either one of these aspects. It may not be very surprising that the prey that sported a mismatching pattern element shape was easier to detect than the background-matching prey, considering that birds are known to be able to discriminate nonidentical shapes (Blaisdell and Cook 2005). Our intuitive expectation was that matching element shapes even in densities equaling one-half or twice the element density in the background patterning would have provided more effective protection than the prey pattern containing mismatching elements. Therefore, we find it interesting that our experiment did not reveal a pronounced difference between the prey that had mismatched element shape and the prey that had mismatched element density. However, it is important to bear in mind that the patterning of our prey items differed even within the same prey category with respect to shapes, placement, and orientation of the markings. It seems likely that this variation has impeded any learning or search image formation (cf. Pietrewicz and Kamil 1979; Bond and Kamil 2002; Dimitrova and Merilaita 2012), which might have been particularly harmful to an invariable prey with a mismatching element shape.

The significant role of pattern element density for highly successful background matching is a central finding of this study. First, we can conclude that simply possessing elements that closely match in shape and color the elements constituting the visual background does not suffice and should therefore not be considered indicative of high degree of background matching. Second, our results suggest that although nonpatterned colorations such as uniform green, brown, or gray appear to be common in arthropods as well as in other prey taxa and may yield some benefit through background matching due to their resemblance of the average or dominant tint of the background, they probably do not yield very high protection in flecked backgrounds (i.e., against backgrounds that are heterogeneous on a scale smaller than the size of the prey). This is also in accordance with findings in cuttlefish, which regulate their colors and patterning for camouflage: When adjusting its camouflage, the common cuttlefish (*Sepia officinalis*) not only imitates the general color of a background but also responds to high-contrast visual edges in the background (Kelman et al. 2007; Zylinski et al. 2009). In vertebrate predators, such as our blue tits, edge detectors of low-level vision enable perception of spatial frequency (Mather 2006; Zylinski et al. 2009). Our result regarding pattern element density suggests that spatial frequency is an important factor in maximization of background matching. Moreover, the results from a predation experiment conducted by Bond and Kamil (2006) suggest the importance of spatial frequency.

On average, the backgrounds, which also contained white elements, were somewhat lighter than the gray-and-black prey, and due to the number of elements, the prey with 4 marks was darker than the prey with 2 marks. These differences in average luminance of the prey did not, however, appear very important (i.e., the prey with 2 marks, although deviating less from the average lightness of the HBg, was more easily detected on that background than the prey with 4 marks). This may not be very surprising, because there was local variation in the lightness of the background due to the random placement of the black and the white elements and because the actual colors constituting the prey patterning matched a subsample of the colors constituting the background (i.e., none of the prey colors were mismatching; see also Dimitrova and Merilaita 2010).

We also asked whether a background that makes the search for prey more difficult would be more forgiving for deviations from high degree of background matching than a background in which it is easier to detect the prey. We, however, did not find any support for this. When compared with the highly matching prey category, our analysis did not suggest any smaller disadvantage of mismatching (for either of the mismatching prey category) in the high-density background than in the low-density background.

In general, our results regarding background matching suggest that there are no shortcuts in maximization of background matching with respect to shapes and densities of markings or proportions of shades, but in order to provide a high level of protection, a color pattern has to match the background with respect to all these aspects. This indicates that conditions for successful background matching may be rather stringent.

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REFERENCES

Blaisdell AP, Cook RG. 2005. Two-item same-different concept learning in pigeons. Learn Behav. 33:67–77.

Bond AB, Kamil AC. 2002. Visual predators select for crypticity and polymorphism in virtual prey. Nature. 415:609–613.

Bond AB, Kamil AC. 2006. Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. Proc Natl Acad Sci USA. 103:3214–3219.

Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga CA, Troscianko TS. 2005. Disruptive coloration and background pattern matching. Nature. 434:72–74.

Desimone R, Duncan J. 1995. Neural mechanisms of selective visual attention. Annu Rev Neurosci. 18:193–222.

Dimitrova M, Merilaita S. 2010. Prey concealment: visual background complexity and prey contrast distribution. Behav Ecol. 21:176–181.

Dimitrova M, Merilaita S. 2012. Prey pattern regularity and background complexity affect detectability of background-matching prey. Behav Ecol. 23:384–390.

Dimitrova M, Stobbe N, Schaefer HM, Merilaita S. 2009. Concealed by conspicuousness: distractive prey markings and backgrounds. Proc Biol Sci. 276:1905–1910.

Dukas R, Clark CW. 1995. Searching for cryptic prey: a dynamic model. Ecology. 76:1320–1326.

Duncan J, Humphreys GW. 1989. Visual search and stimulus similarity. Psychol Rev. 96:433–458.

Gendron RP, Staddon JER. 1984. A laboratory simulation of foraging behavior: the effect of search rate on the probability of detecting prey. Am Nat. 124:407–415.

Hanlon R. 2007. Cephalopod dynamic camouflage. Curr Biol. 17:R400–R404.

Kelman EJ, Baddeley RJ, Shohet AJ, Osorio D. 2007. Perception of visual texture and the expression of disruptive camouflage by the cuttlefish, *Sepia officinalis*. Proc Biol Sci. 274:1369–1375.

Kjernsmo K, Merilaita S. 2012. Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. Proc Biol Sci. 279:4192–4198.

Lindström L, Alatalo RV, Lyytinen A, Mappes J. 2001. Predator experience on cryptic prey affects the survival of conspicuous aposematic prey. Proc Biol Sci. 268:357–361.

Mather G. 2006. Foundations of perception. Hove (UK): Psychology Press.

Merilaita S. 2003. Visual background complexity facilitates the evolution of camouflage. Evolution. 57:1248–1254.

Merilaita S, Dimitrova M. 2014. Accuracy of background matching and prey detection: predation by blue tits (*Cyanistes caeruleus*) indicates intense selection for highly matching prey colour pattern. Funct Ecol. doi:10.1111/1365-2435.12248

Merilaita S, Lind J. 2006. Great tits (*Parus major*) searching for artificial prey: implications for cryptic coloration and symmetry. Behav Ecol. 17:84–87.

Merilaita S, Schaefer HM, Dimitrova M. 2013. What is camouflage through distractive markings? Behav Ecol. 24:e1272–e1273.
Merilaita S, Stevens M. 2011. Crypsis through background matching. In: Stevens M, Merilaita S, editors. Animal camouflage: mechanisms and function. Cambridge (MA): Cambridge University Press. p. 17–33.
Merilaita S, Tullberg BS. 2005. Constrained camouflage facilitates the evolution of conspicuous warning coloration. Evolution. 59:38–45.
Pietrewicz AT, Kamil AC. 1979. Search Image Formation in the Blue Jay (*Cyanocitta cristata*). Science. 204:1332–1333.
Ramachandran VS, Tyler CW, Gregory RL, Rogers-Ramachandran D, Duensing S, Pillsbury C, Ramachandran C. 1996. Rapid adaptive camouflage in tropical flounders. Nature. 379:815–818.
Rowland HM, Cuthill IC, Harvey IF, Speed MP, Ruxton GD. 2008. Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. Proc Biol Sci. 275:2539–2545.
Ruxton GD, Sherratt TM, Speed MP. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford: Oxford University Press.
Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. New York: W.H. Freeman.
Stevens M, Merilaita S. 2009. Animal camouflage: current issues and new perspectives. Philos Trans R Soc Lond B Biol Sci. 364:423–427.
Stevens M, Hopkins E, Hinde W, Adcock A, Connolly Y, Troscianko T, Cuthill IC. 2007. Field experiments on the effectiveness of 'eyespots' as predator deterrents. Anim Behav. 74:1215–1227
Wertheim AH, Hooge IT, Krikke K, Johnson A. 2006. How important is lateral masking in visual search? Exp Brain Res. 170:387–402.
Zylinski S, Osorio D, Shohet AJ. 2009. Cuttlefish camouflage: context-dependent body pattern use during motion. Proc Biol Sci. 276:3963–3969.