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Concealed by conspicuousness: distractive prey markings and backgrounds

Marina Dimitrova^{1,*}, Nina Stobbe², H. Martin Schaefer² and Sami Merilaita^{1,†}

¹Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden

²Department of Evolutionary Biology and Animal Ecology, Faculty of Biology, University of Freiburg, Hauptstrasse 1, 79104 Freiburg, Germany

High-contrast markings, called distractive or dazzle markings, have been suggested to draw and hold the attention of a viewer, thus hindering detection or recognition of revealing prey characteristics, such as the body outline. We tested this hypothesis in a predation experiment with blue tits (*Cyanistes caeruleus*) and artificial prey. We also tested whether this idea can be extrapolated to the background appearance and whether high-contrast markings in the background would improve prey concealment. We compared search times for a high-contrast range prey (HC-P) and a low-contrast range prey (LC-P) in a high-contrast range background (HC-B) and a low-contrast range background (LC-B). The HC-P was more difficult to detect in both backgrounds, although it did not match the LC-B. Also, both prey types were more difficult to find in the HC-B than in the LC-B, in spite of the mismatch of the LC-P. In addition, the HC-P was more difficult to detect, in both backgrounds, when compared with a generalist prey, not mismatching either background. Thus, we conclude that distractive prey pattern markings and selection of microhabitats with distractive features may provide an effective way to improve camouflage. Importantly, high-contrast markings, both as part of the prey coloration and in the background, can indeed increase prey concealment.

Keywords: crypsis; predation; dazzle; disruptive coloration; camouflage; background matching

1. INTRODUCTION

Many animals are considered to have cryptic coloration; the adaptive purpose of cryptic coloration is concealment (Poulton 1890). Cryptic coloration has historically constituted an important example of adaptation that has been used to support the theory of natural selection (e.g. Wallace 1889).

Visual similarity between an animal and its environment, nowadays often called background matching, was the only means of concealment that had been recognized before Thayer (1909) proposed his ideas about rufous and secant patterns (now collectively known as disruptive patterns) and distractive markings (also called dazzle markings). Disruptive patterns are thought to obliterate the shape of their bearer, while distractive markings make detection difficult by manipulating the attention of the viewer. Somewhat confusingly, in his renowned book, Cott (1940) did not make a distinction between these two ways to achieve camouflage, but included the idea of distractive markings in his description of shape-obliterating patterns that he called disruptive coloration. However, in light of the present knowledge it seems that these two types of cryptic coloration target different perceptual mechanisms and therefore should be considered distinct principles of concealment (Stevens & Merilaita 2009). While there is now experimental evidence for obliteration of shape (i.e. disruptive patterns; Cuthill *et al.* 2005; Schaefer & Stobbe 2006; Stevens *et al.* 2006;

Fraser *et al.* 2007; Kelman *et al.* 2007), there is still no experimental proof for the idea of distractive markings.

Thayer (1909) suggested that the aim of distractive markings is to reduce ‘...one form’s or detail’s conspicuousness by blazoning of some other detail’. He argued that these ‘meaningless’ markings tend to draw and hold a predator’s attention away from the prey body shape, thus hindering detection or recognition of more informative characteristics, such as the body outline, which could reveal a prey’s presence. These markings should highly contrast with the rest of the prey coloration to be able to draw a predator’s attention towards them. The idea of distractive markings may appear counterintuitive, because it essentially suggests that conspicuous markings may improve inconspicuousness. Possibly because of the seemingly contradictory nature of this idea, distractive markings have received little scientific attention.

The aim of this study was to test whether high-contrast distractive prey markings would decrease the risk of detection for a prey. Further, if such distractive markings on prey facilitate concealment, then we could probably expect similar markings in the background to be even more effective, because of the larger area and possibly larger variation in pattern geometry and colours of the background. Therefore, we tested the efficacy of distractive markings not only by manipulating the prey appearance, but by manipulating the background appearance as well. Specifically, we predicted that if prey concealment is simply determined by background matching, then prey matching the background should be more difficult to detect than a mismatching prey. However, if high-contrast markings do induce a distractive effect, then a prey and a background with such markings will lead to

* Author for correspondence (marina.dimitrova@zoologi.su.se).

† Present address: Environmental and Marine Biology, Åbo Akademi University, 20520 Turku, Finland.

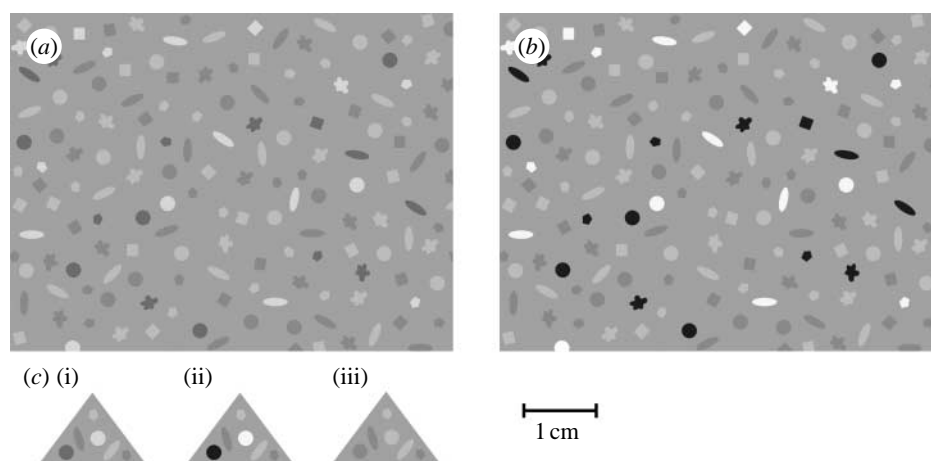


Figure 1. (a) The LC-B and (b) the HC-B differed only in the luminance of the darkest and lightest element shades. (c) The three prey categories: (i) the prey with low-contrast markings (LC-P), (ii) the prey with high-contrast markings (HC-P) and (iii) the generalist prey (G-P) mismatching neither of the backgrounds. Only the luminance of the two circles differs between the three prey categories.

higher prey concealment, even when the prey is not background matching. We tested these predictions with two comparisons. First, we compared a high-contrast range prey (HC-P) and a low-contrast range prey (LC-P) in a high-contrast range background (HC-B) and a low-contrast range background (LC-B). Second, we compared the HC-P with a prey that did not mismatch either background. This third prey type was a background generalist with a pattern consisting of elements that were equally common in both backgrounds.

2. MATERIAL AND METHODS

(a) *General procedure*

We used wild-caught blue tits (*Cyanistes caeruleus*) as predators and trained them to search for artificial prey items, covering a small piece of peanut as a reward, in artificial backgrounds. Both the prey items and the backgrounds were made of paper, allowing an easy manipulation of their patterning. To study the distractive effect of the background, we produced two different backgrounds, which differed in luminance of pattern elements and consequently in contrast range. We produced three different categories of prey: (i) with low-contrast range markings (LC-P); (ii) with high-contrast range markings (HC-P); and (iii) a generalist prey with markings that were equally common in both backgrounds (G-P), thus equally matching both backgrounds (figure 1).

(b) *The predators*

This study was performed with permission from the Swedish ethical board in Linköping (Dnr: 56-05). The experiment was conducted between January and February 2007 at Tovetorp Zoological Research Station (Stockholm University) in Southeastern Sweden (58°56' N, 17°08' E). The blue tits were captured with mist-nets and held in individual cages (80 × 60 × 40 cm³). The room temperature was 15°C, and the light : dark rhythm (with dusk and dawn) was adjusted according to the prevailing day length. The blue tits were provided with suet, sunflower seeds, peanuts and water *ad libitum*. They were kept indoors between 4 and 7 days before they were released in the area of capture.

(c) *The background and the prey*

The artificial backgrounds and prey items were created by using the software COREL DRAW 11 (Corel Corporation) and printed with a laser printer (HP LaserJet 4000 Series PS with 1200 dpi resolution) on white copying paper (Canon Office). We calibrated the printer so that the printed papers' luminance scale would correspond to blue tit vision (Hart *et al.* 2000), such that, for example, 50 per cent white would be half as dark as white paper in the eyes of the blue tits (cf. Stevens *et al.* 2006). We used a spectrometer (Ocean Optics USB 2000 with a PX-2 pulsed xenon light source) to measure the luminance and spectral reflectance of the grey shades and computed the corresponding double-cone and cone catches following Vorobyev & Osorio (1998) and Siddiqi *et al.* (2004). Using a regression between the printer's grey scale and the actual luminance values (double-cone catches), we adjusted the printer to obtain the desired luminance values. All grey scale percentages from here on are related to luminance as perceived by blue tits, such that the shade 100 per cent corresponds to white paper, the shade 0 per cent corresponds to the reflectance of the black ink and the shade 50 per cent corresponds to grey that the blue tits perceived half as dark as the white paper.

Both backgrounds were geometrically identical and had the same number and shape of five elements (figure 1). These five element shapes were divided in four different shades. Two of these shades (35 and 65% white) and the overall ground shade (50% white) were present in both backgrounds. The two backgrounds only differed in the two most extreme shades. In the LC-B, these shades were 20 and 80 per cent white (figure 1a). In the HC-B, these element shades were 0 and 100 per cent white (figure 1b).

For the experiment each printed background was separately attached on A4-sized corrugated cardboard, using a solvent-free glue stick (Scotch, 3M). The shape of the prey was triangular ($W \times H$: 1.5 × 1.0 cm). The same prey pattern was used for all three prey types and the colour patterns were thus geometrically identical, but the shade of the circles differed between the three prey categories (figure 1c). The ground shade of all the prey types was 50 per cent white (as in the two backgrounds). In the first comparison, we used the following two prey categories: LC-P, matching the LC-B (element shades 20, 35, 65 and 80% white); and HC-P, matching the HC-B (0, 35, 65 and

100% white; figure 1c). In the second comparison, we compared the HC-P with a third prey category, which had only the intermediate grey shades (35 and 65% white; G-P, figure 1c) that were common to both backgrounds. Thus, this G-P prey is a background generalist that contains only elements that are present in both backgrounds. For the experiment the prey items were glued lightly from three points to the background boards to cover a randomly placed hole containing a peanut reward (approx. $2 \times 2 \times 2$ mm³).

We assessed the achromatic and chromatic contrasts between our high-contrast and low-contrast treatments by calculating the contrast values between the pairs of differing element shades. Contrast value less than 1 jnd (just noticeable difference) indicates that two shades are indistinguishable, whereas a value of 1 jnd or larger indicates that the viewer can tell apart the two shades; the higher the value, the more likely the viewer is to detect a difference under given conditions (for example distance; Schaefer *et al.* 2006). We found that our manipulation resulted in detectable achromatic contrasts between the lightest shades and between the darkest shades of the high-contrast and the low-contrast treatments. Between the lightest shades of the pattern, there was a low achromatic and no detectable chromatic contrast for blue tits (mean \pm s.e.: 80 versus 100% white: 4.02 ± 0.32 jnds achromatic contrast; 0.66 ± 0.11 jnds chromatic contrast). Because the unprinted paper was not white to the birds, but had a bluish tone, and the printer ink had an evenly flat reflectance, there was a chromatic contrast detectable to the blue tits between the darkest grey and the black of the pattern. However, even here the achromatic contrast was almost four times stronger (0 versus 20% white: 44.75 ± 0.59 jnds achromatic contrast; 12.27 ± 1.08 jnds chromatic contrast).

(d) Training of the birds

Prior to the experiment, the blue tits were trained to search for the prey items by associating them with the pieces of peanut they covered. All training was done in the experimental cages and all the blue tits went through the same procedure. The training procedure was divided into three steps and began the day after a bird was captured. A bird advanced to the next step when it had managed to complete a training step within 1 hour. The day after the completion of the third step, it advanced to the experiment. Both the training and the experiment were started by repeating the previous completed training step. Every training and experimental session was preceded by 60 min without food in the experimental cage. For presentation of prey items during the training, we used 5×7 cm² corrugated cardboard boards for training steps 1 and 2, and A4-sized corrugated cardboard boards for training step 3. The prey items were placed and oriented at random.

In training step 1, the blue tits were familiarized with the prey items. All the prey items were presented in a plain brown background and were thus clearly visible. Four prey items were used per board: one of each experimental prey category and one that was completely white. There were three different levels of difficulty: (1) the white prey item had a piece of peanut glued on top, hence the reward was fully visible; (2) one prey item was glued to the cardboard from one tip, with a piece of peanut glued to its underside—but, because there was no hole in the board, the peanut was partly visible; and (3) two prey items were glued from one point to cover a hole in the cardboard with a piece of peanut in it. In the

second training step, the two halves of the cardboard were covered with the two backgrounds; hence the prey items were now cryptic. A prey item from each category (three per board) was used to cover a hole containing a peanut reward. The prey items were placed so that they did not overlap the border between the two backgrounds. All three tips of the prey were lightly glued to the background except for one prey, for which one tip was lifted up to induce search behaviour in the blue tits. Training step 3 was the same as training step 2, with the exceptions that the board was A4-sized and all three prey items were glued from three points.

(e) The experiment

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 natural light-emitting lamps (15 W, BIOLight, Narva). The observation window (10×12 cm²) was covered with one-way see-through plastic sheet, which hindered the birds in the experimental cage from seeing the observer during the experiment. To minimize disturbance, the experimental room was always kept dark when a bird was in an experimental cage. The experimental boards were slid into the experimental cage from an opening on the bottom of its long side. On the opposite side of this opening, 20 cm beneath the ceiling, was a perch. The temperature in the experimental cage was 16°C. The blue tits had water *ad libitum* in the experimental cage.

In the experiment the blue tits were presented with one prey item on an experimental background board at a time. The prey item was placed and oriented at random on each A4-sized experimental board, with the restriction that the prey item was at least 2 cm from the board edge. Thus, each blue tit was presented with combinations of all three prey categories and both backgrounds in a sequence. In total 33 birds were used in the experiment. Each background–prey combination was repeated three times, resulting in 18 presentations per bird. We arranged six background–prey combinations in a random order, but made sure that equal numbers of birds started the experiment with each background–prey combination. For each experimental board, we recorded the effective search time (the time a blue tit used for actively searching for the prey item on the experimental board) until the bird had found the prey item and pecked at it to tear it off. The bird was then allowed to eat the reward, before the experimental board was replaced with the next. A bird was considered to begin an active search when it landed on or just next to the experimental board (with its head over the board edge) and started to search for the prey item with its head oriented straight or down. If a bird did not manage to find the prey item within 20 min of total search time, the board was taken out and was presented again after the rest of the presentations. In such cases, the effective search time of the second presentation was used in the analysis. However, this only happened with nine experimental boards. On one occasion a bird became frustrated because it was not able to visually detect the prey, and started instead to frenziedly peck at the experimental board. In this case the entire group of six background–prey combinations was presented again after the rest of the presentations, and the effective search time of the second presentation was used in the analysis.

To be certain that the birds did not have an aversion towards any of the three different prey types, we made a control experiment. After completing the experiment,

we randomly chose 20 birds. They were presented with prey items in the same way as in the experiment (i.e. one prey item per board), but on plain brown A4-sized corrugated cardboard boards, thus making all the prey items easy to detect. Thus aversion towards a prey item would be revealed by a delay before ‘attack’. Each bird was exposed to all three prey categories, in total nine boards (three repeats for each prey category).

(f) *Statistical analyses*

To achieve normal distribution and homoscedasticity, we applied ln-transformation on the effective search times, suggested by the Box-Cox analysis. We analysed the transformed effective search times from the experimental set-up with repeated-measurements ANOVA and the transformed effective search times from the ‘willingness to attack’ set-up with one-way ANOVA with SPSS v. 15.0 for Windows. Because parts of the experimental data (e.g. effective search times of HC-P) were used in two comparisons, the risk of type I error was increased. This can be corrected for by using an adjusted α -value of 0.025 instead of 0.05 (Rice 1989). However, all our significant p -values remain significant even after this adjustment.

3. RESULTS

Our first comparison addressed the distractive effect of prey coloration by comparing HC-P and LC-P, each of them matching one of the backgrounds. We found a significant difference in search time depending on prey category ($F_{1,32}=7.72$; $p=0.009$; figure 2). The HC-P was more difficult to detect on both the matching and mismatching backgrounds than the LC-P, supporting the hypothesis of the concealing effect of high-contrast markings. We also found a significant effect of the background contrast range ($F_{1,32}=9.43$; $p=0.004$). Both prey types—the prey with distractive markings (HC-P) and the prey without distractive markings (LC-P)—were more difficult to detect in the HC-B than in the LC-B background (figure 2). The interaction between background and prey category was not significant ($F_{1,32}=0.014$; $p=0.91$). The HC-P was generally more difficult to detect independently of background appearance. This suggests that in the LC-B, where HC-P was mismatching, it gained camouflage through its distractive high-contrast markings and that this distractive effect was stronger than the disadvantage of mismatching the background. The HC-B increased the concealment of both HC-P and LC-P, suggesting that distractive markings in the background are effective as well.

In the second comparison, we tested the search times for the HC-P against the search times of a ‘generalist’ prey (G-P) that did not mismatch either of the backgrounds. Again, we found a significant difference in search time depending on prey category ($F_{1,32}=6.54$; $p=0.015$; figure 3). The HC-P was more difficult to detect than the G-P independently of background contrast range. Also the effect of background contrast range was again significant ($F_{1,32}=7.72$; $p=0.009$). Both prey types HC-P and G-P were more difficult to detect in the HC-B than in the LC-B background (figure 3). The interaction between background and prey category was not significant ($F_{1,32}=0.019$; $p=0.89$). This result suggests that the HC-P with distractive markings does

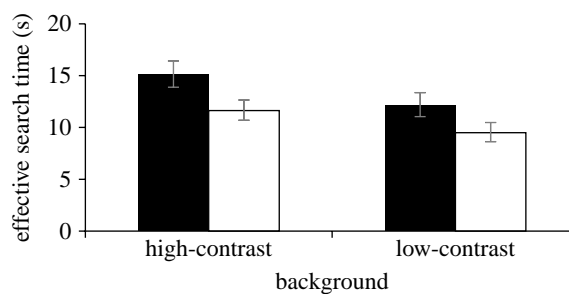


Figure 2. High-contrast markings present in the prey coloration (HC-P; black bar) or in the background (HC-B) increased predator search times and made the prey more difficult to detect compared with a prey without such markings (LC-P; white bar). The whiskers are back-transformed standard errors ($n=33$).

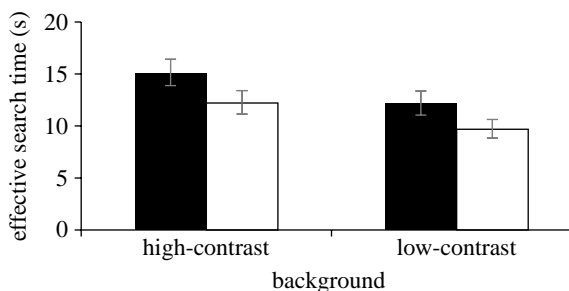


Figure 3. High-contrast markings present in the prey coloration (HC-P; black bar) or in the background (HC-B) increased predator search times when compared with a background generalist prey (G-P; white bar). The whiskers are back-transformed standard errors ($n=33$).

have an advantage when comparing with a prey that does not mismatch either of the backgrounds.

Finally, we did not find any indication of different prevalence for the blue tits to attack any prey of the three prey categories when presented on plain brown boards ($F_{2,18}=0.67$; $p=0.53$). All the prey categories were immediately attacked, with mean effective search times \pm back-transformed s.e. for the HC-P $1.45 + 0.12 / -0.11$ s, for the LC-P $1.38 + 0.11 / -0.11$ s and for the G-P $1.32 + 0.10 / -0.10$ s. Hence, the longer search time of the HC-P in the experiment was not caused by the birds being less willing to attack it.

4. DISCUSSION

We found that high-contrast markings, in accordance with Thayer’s (1909) proposal as part of prey coloration, but also in the background, can indeed increase prey concealment. The HC-P was more difficult to detect than both the LC-P and the G-P. In addition, all three prey types were more difficult to detect in the HC-B than in the LC-B.

We found that the prey with distractive markings (HC-P) was most difficult to detect, even when its distractive markings did not match the background. In addition, our results also support recent studies where the importance of the background appearance *per se* for prey detection has been emphasized (e.g. Merilaita 2003). Specifically, we found that background with distractive markings decreased the risk of detection by birds as visual predators, independently of prey appearance (HC-P, LC-P or G-P). There is natural variation in contrast

range between habitats due to illumination conditions (e.g. directional versus diffuse illumination or dappled versus uniform illumination) and some substrates have higher contrast range (e.g. rocks or tree trunks partly covered with differently coloured moss and lichens) than others. We suggest that high-contrast habitats may favour prey evolution towards camouflage, rather than other anti-predator strategies (Merilaita & Tullberg 2005).

In a recent experiment Stevens *et al.* (2008) studied how long a time dead mealworms pinned on trees and partly covered with triangular pieces of printed paper 'survived' predation by wild birds. The triangles matched the tree trunks, but half of them also had a bright spot. Because these spots did not influence the survival of the mealworms, Stevens *et al.* suggested that distractive markings are not an effective means of concealment. Importantly, in their experiment the birds were not familiar with the triangles and hence did not associate them with the mealworm. Without first showing that the foreign structure (triangle) does not decrease the concealment of the actual target, it is questionable whether their set-up is suitable for testing distractive effect on the target.

Thayer (1909) suggested that distractive markings function by drawing and holding the attention of a viewer from traits that would be useful for detecting or recognizing the prey. From a psychological point of view, this would mean that distractive markings would manipulate attentional mechanisms in visual processing. Visual attention is limited and only a certain amount of information can be processed at one time (Desimone & Duncan 1995). Therefore, different stimuli in the visual field are considered to compete for attention (Desimone & Duncan 1995). The outcome of this competition, i.e. selection of target of attention, depends partly on the features of the stimuli. Brightness appears to be one such feature; there is evidence from human vision that this competition is biased in favour of bright stimuli, so that stimuli with increased relative brightness receive attentional prioritization (Proulx & Egeth 2008). Thus, it is possible that our results could be explained by the lightest markings in the HC-B and HC-P drawing the attention of the birds from the outlines of the prey items.

Lateral masking may provide another explanation for our results. Lateral masking means that the peripheral perception of a visual stimulus is impaired when other stimuli (distractors) are present in its adjacent surroundings (Wertheim *et al.* 2006). It is considered to be caused by lower-level visual processes in contrast to attentional processes that involve higher-order mechanisms. In humans, lateral masking has been found to be stronger with high-contrast distractors than with low-contrast ones (Chung *et al.* 2001). This effect may occur because high-contrast distractors elevate the contrast detection threshold, making it more difficult to detect the target (Chung *et al.* 2001). Thus, in our experiment the high-contrast markings may have interfered through lateral masking with detection or recognition of prey characteristics such as the outline, which has a lower contrast.

Although lateral masking might account for the effect of background markings in our experiment, it appears less likely that it would explain the effect of the prey markings; in the HC-B there were a high number of the distracting markings present, but prey markings alone may not suffice to influence the contrast threshold. This implies that the

effect of high-contrast markings in our experiment is at least partly explained by attention-driven processes. The present set-up does not allow us to discriminate which processes are responsible for the longer search times of the HC-P and in the HC-B. The mechanisms underlying lateral masking and the way they are related to attentional processes are currently not very well understood (Wertheim *et al.* 2006). Also, the current knowledge does not allow us to judge whether our high-contrast elements were distributed densely enough to result in effective lateral masking in a passerine bird such as the blue tit.

The results from our experiment lead to the question of optimization of distractive markings and prey coloration in general. When comparing the predictions from background matching and distractive markings, one realizes that these two appear to be in conflict with each other. Background matching is based on colours and luminance that blend with the background (Endler 1978; Théry & Casas 2002; Ruxton *et al.* 2004), whereas distractive markings use high-contrast elements that do not necessarily match the background. There is probably a limit to how contrasting and, especially, how large such distractive markings can be without increasing prey conspicuousness too much. Thayer (1909) suggested about distractive markings that 'the stronger the pattern appears, the dimmer appear the forms and outlines of its wearer', but he also wrote that distractive markings 'are, in most cases, too small to show except in a very near view—when, by their sharp but isolated and non-committal conspicuousness, they tend to draw and hold the eye's attention'. Thus, the small size of distractive markings might be beneficial for two reasons. First, with small distractive markings a prey would still have a relatively high level of background matching when seen from a distance. Second, the small size of distractive markings may hinder predator search image formation (Bond & Kamil 1998). The small size of the conspicuous markings of the camouflaged comma butterfly (*Polygonia c-album*) and also the silver Y moth (*Autographa gamma*) may possibly function as a distractive marking.

As mentioned in the introduction, both distractive markings and disruptive coloration emphasize high contrast between prey pattern elements. Possibly for this reason, these two mechanistically distinct concealing functions have often been blended (e.g. Cott 1940). However, the optimal location of markings is likely to differ between these two types of coloration. Disruptive markings are expected to touch the outline (Cott 1940; Merilaita 1998; Cuthill *et al.* 2005; Fraser *et al.* 2007), whereas distractive markings probably should not. In this study we placed the distractive markings away from the prey outline so that they would not draw predators' attention towards it. Further, Stevens *et al.* (2006) have shown that the luminance of the elements of disruptive pattern should optimally be within the range of those found in the background (but see Schaefer & Stobbe 2006 for disruption by colours). By contrast with Stevens *et al.* (2006), in our experiment the distractive markings were effective even when they contrasted with the background.

Previous studies have also suggested that optimization of prey camouflage in heterogeneous, patchy habitats can be achieved in different ways, i.e. by having a coloration adapted to one particular patch type or by having a compromised coloration adapted to several patch types

(Merilaita *et al.* 1999, 2001; Houston *et al.* 2007; Sherratt *et al.* 2007). Our results can be interpreted from this point of view as well. The prey with distractive markings was well camouflaged independently of background appearance. This suggests that one way to cope with the problem of visually heterogeneous habitats for cryptic animals may be by using distractive markings.

The use of artificial prey and backgrounds allowed us to specifically investigate the effect of high-contrast distractive markings. We found support for the idea that distractive markings are an effective way of achieving camouflage against avian predators. Birds are important visually hunting predators that affect the natural selection of the appearance of many prey animals. Our results show the plausibility that, in nature, distractive elements, both in prey and backgrounds, may increase prey concealment. As far as we are aware, our results provide the first experimental evidence that distractive markings promote prey camouflage.

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