

Background-matching and disruptive coloration, and the evolution of cryptic coloration

Sami Merilaita* and Johan Lind†

Department of Zoology, Stockholm University SE-10691, Stockholm, Sweden

Cryptic prey coloration typically bears a resemblance to the habitat the prey uses. It has been suggested that coloration which visually matches a random sample of the background maximizes background matching. We studied this previously untested hypothesis, as well as another, little studied principle of concealment, disruptive coloration, and whether it could, acting in addition to background matching, provide another plausible means of achieving camouflage. We presented great tits (*Parus major*) with artificial background-matching and disruptive prey (DP), and measured detection times. First, we studied whether any random sample of a background produces equally good crypsis. This turned out to not be the case. Next, we compared the DP and the best background-matching prey and found that they were equally cryptic. We repeated the tests using prey with all the coloration elements being whole, instead of some of them being broken by the prey outline, but this did not change the result. We conclude that resemblance of the background is an important aspect of concealment, but that coloration matching a random visual sample of the background is neither sufficient nor necessary to minimize the probability of detection. Further, our study lends empirical support to the principle of disruptive coloration.

Keywords: crypsis; disruptive coloration; background matching; evolution; predator–prey interaction

1. INTRODUCTION

A classic example of natural selection is prey coloration that decreases the risk of detection by predators. Here we will call such adaptation cryptic coloration or camouflage (e.g. Cott 1940; Merilaita *et al.* 1999, 2003), but other terms can also be found in literature, such as obliterative coloration (Thayer 1909), concealing coloration (Cott 1940), or *crypsis* (e.g. Edmunds 1974). Two main principles have been suggested for decreasing the risk of detection, namely background matching and disruptive coloration.

One of the principles for decreasing the risk of detection is that of visual resemblance to the background. This is known as background matching (also called cryptic resemblance (Cott 1940) and crypsis *sensu* Endler (1978)). According to this principle, the more similar to the visual background the colours and geometry of a prey colour pattern are in the eyes of the predator, the more difficult it should be for the predator to detect the prey (Cott 1940; Norris & Lowe 1964; Edmunds 1974; Endler 1978). In his often quoted definition Endler (1978, 1984, 1991) proposed that a colour pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat, where the prey is most vulnerable to visually hunting predators. This proposal has been used as a basis for quantification of the degree of camouflage, and it assumes that all random samples of a given background are equally cryptic (Endler 1978, 1984).

Another suggested principle for decreasing the risk of detection is disruptive coloration (Thayer 1909; Cott 1940; Edmunds 1974). According to Cott (1940), it is the

continuity of surface, bounded by a specific contour or outline, which chiefly enables the recognition of objects; so if a surface is covered with irregular patches of contrasted colours and tones, these patches tend to catch the eye of the observer and to draw attention away from the shape which bears them. Such a colour pattern, that aims to hinder detection of the shape of an animal, is called disruptive coloration. There are several ways to use patterns that may result in such an effect (Cott 1940; Merilaita 1998). Marginal pattern elements, touching the outline and differentially blending into the background, may break up the continuity of the outline. Distractive marks aim to draw the attention of the observer away from the outline and other characteristics that facilitate recognition. This may be aided by maximum disruptive contrast within the prey, making the distracting elements stand out strongly. Also, the adjacent distractive marks may aim to give an impression of separate objects instead of a repeated pattern of a single object.

Many prey species bear a resemblance to their visual background (Cott 1940; Norris & Lowe 1964; Endler 1984; Stuart-Fox *et al.* 2004), and there is a substantial amount of evidence to show that risk of detection correlates with the degree of resemblance between prey and background (e.g. Turner 1961; Sandoval 1994; Nystrand & Granström 1997; Merilaita *et al.* 2001). Therefore, it appears somewhat peculiar that Endler's (1978) influential idea of maximization of camouflage based on the random sampling of background has not thus far been tested experimentally. In contrast to background matching, there are significantly fewer studies that have addressed disruptive coloration, and although there is some correlative evidence for it, there is no direct, experimental evidence for disruptive coloration (Merilaita 1998; Ruxton *et al.* 2004; see also § 4).

Here, we test Endler's (1978) idea of crypsis

* Author for correspondence (sami.merilaita@zoologi.su.se).

† Present address: School of Biology, Bute Building, University of St Andrews, St Andrews, Fife KY16 9TS, UK.

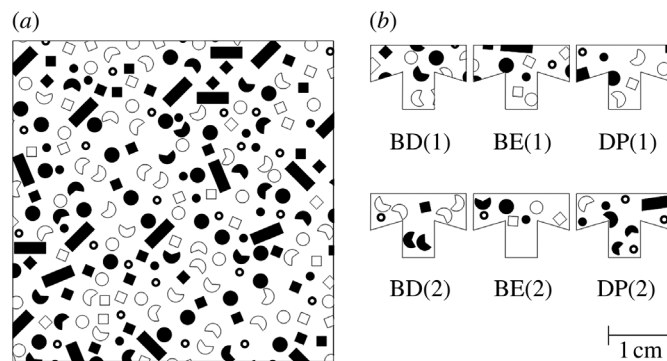


Figure 1. (a) A sample of the background used in the experiment. (b) The six prey used in the experiment. Prey set 1 (top row) had some pattern elements cut by the outline, and prey set 2 (bottom row) had whole elements only. Prey in the left and middle columns had patterns representing random samples of the background (BD was expected to be difficult to detect and BE was expected to be easy to detect), and the right column shows prey with disruptive patterns, DP. Both (a) and (b) are drawn to scale.

maximization through a random sample of the background in a predation experiment using artificial prey and background, and great tits (*Parus major*) as predators. First, we show that coloration representing a random sample of the background is not a sufficient condition for the maximization of background matching, because the variation in probability of detection may be substantial between such colorations. Second, by comparing prey coloration that represents an exact sample of the background with prey coloration that has been created by applying the principle of disruptive coloration, we show that matching a random sample of the background, is also not a necessary condition for a low probability of detection. This also provides experimental evidence for the plausibility of the principle of disruptive coloration.

2. METHODS

(a) *The predators*

To investigate the risk of detection, we used great tits, *P. major*, and had them search for artificial prey (cf. Merilaita *et al.* 2001). Great tits are easy to train and feed on a large variety of prey, which makes them ideal for this type of investigation. The birds were trapped with mist-nets at Tovetorp Zoological Research Station (Stockholm University) in southeast Sweden, where we also performed the experiment. The experiment was performed from October to December 2003. Prior to trials, birds were housed separately, indoors, in holding cages ($80 \times 60 \times 40 \text{ cm}^3$), where we gave them water, suet and sunflower seeds *ad libitum*. We also gave them peanut chips regularly, because these were used during the training and in the experiments. The study was performed with permission from the Swedish ethical board for conducting behavioural research.

(b) *The background*

We made the background with COREL DRAW 10 (Corel Corporation). The aim was to create a background complex enough to make the prey relatively difficult to detect, a prerequisite for detecting differences between different prey of reasonably good camouflage (figure 1a). On the other hand, the background could not be too difficult, because that could result in birds losing their motivation to search for prey. A4 sized ($20 \times 29 \text{ cm}^2$) background boards were then made of printed backgrounds glued to equally sized corrugated cardboard, using solvent free glue stick (Scotch, 3M, Cergy,

France). We used artificial, black-and-white prey and background, and all the prey items and backgrounds used in the experiment were copied from printed originals on the same copying machine with the same toner and paper throughout the experiment.

(c) *The prey*

We wanted the prey to have a characteristic shape that the predators could learn to recognize (figure 1b). Moreover, we did not want the shape to be too simple, partly because shapes of real prey are not simple and partly because visual systems appear to easily complete simple forms when they are only partially visible, making it more difficult to disrupt them. We made the prey colour patterns in COREL DRAW 10 and reproduced them with a copying machine. The prey items were then cut out of the paper to the prey shape. In the experiment, a papery prey item was glued lightly from three points to cover a hole on the background board. In the hole there was a piece of peanut (approximately $2 \times 2 \times 2 \text{ mm}^3$), rewarding a bird that found the prey and tore it off the background.

We required three different prey categories (figure 1b): (i) prey with a pattern randomly sampled from the background which we expected would be difficult to detect, BD, (ii) prey with a pattern randomly sampled from the background which we expected would be easier to detect, BE, and (iii) prey with a pattern element distribution designed by us, using the principle of disruptive coloration, DP. Both categories BD and BE represented examples of background matching based on a random sample of the background. Because we were uncertain about whether pattern elements broken in the sampling would increase the risk of detection, we made two different three-pattern sets. In the first set, the samples were used as such, and thus, there were some pattern elements cut by the outline; whereas in the second set the samples from the background were modified so that half of the elements that broke the outline were deleted and the remaining outline-breaking elements tucked inside the outline to the nearest place, where they would not overlap with another element. Altogether, this resulted in six prey patterns, three with some elements cut by the outline and three with whole elements only (figure 1b).

To make the BD and BE patterns for both the prey sets, we sampled the background by placing the T-shaped outline of the prey at 40 randomly chosen locations with

respect to the x - (0–20 cm) and y -coordinate (0–29 cm) and rotations (1–360°). The patterns for the set with whole elements only was modified as described above. Among these 80 samples, we selected two patterns that appeared difficult to detect, and two patterns that appeared easy to detect, to be used in the experiment. This choice of the background-matching and disruptive patterns was based on our own judgment (i.e. we searched the prey from the background) as well as on pilot experiments, using five birds not included in the experiment.

When designing the disruptive prey (DP), we used pattern elements found on the background, but their distribution was not based on a sample of the background. For each prey set we made 10 different variants and chose one for the experiment as described above. While most of the elements in these two patterns were kept unchanged, the size or shape of a minority were slightly changed for the purpose of enhancing disruption. We modified only a few pattern elements, because we mainly focused on pattern elements distribution (disruptive or sampled from the background) and because pattern elements deviating from those found in the background might increase the risk of detection. In the pattern with some elements broken by prey outline, only the elements cut by the outline differed from the background elements. In the pattern with whole elements only, three elements were transformed. A black quadrangle was turned to a parallelogram and the two lower black, pie-shaped elements were made slightly smaller for a better fit (figure 1*b*).

The outline, and especially its angles, can give away the shape of a prey or any other object (e.g. Palmer 1999). On the other hand, predators have to detect the edges of the prey among all the edges they see, including the edges of the pattern elements. Therefore, for the DP, we attempted to place the pattern elements so that they would act as distractive marks, diverting the predators' attention from the true outline and angles of the prey (Cott 1940). For that reason, we placed elements at the angles of the outline to compete for the predators' attention. Similarly, we used the linear edges of some pattern elements to compete for the predators' attention, by placing them near the prey edges. These were non-parallel, aiming to distract the predator from detecting the orientation of the true edges of the prey. For example, see the parallelogram in the right 'wing' of the DP with inserted elements and the white square of the prey with broken elements in figure 1*b*. In addition, we used some of the pie-shaped elements in an attempt to disrupt the prey surface and change the appearance of the prey shape by creating illusory outlines. For example, see figure 1*b*, where the element in the left 'armpit' of the DP with inserted elements appears to extend the vertical outline along the linear outlines of the element, and the two other 'pies' in the 'tail' of the prey appear to partition off the lower right corner; and also one of the white 'pies' of the DP with broken elements appears to partition off the lower left corner of the tail.

(d) Training procedure

Before being subjected to the experiment, the birds were trained to associate the prey with food. This training was carried out in three steps, with steps 1 and 2 executed in the holding cages. To make the artificial prey attractive, we glued a peanut chip (approximately $2 \times 2 \times 2$ mm³) to the ventral surface of each prey. In step 1, all six prey were used on the bare surface of a piece of brown cardboard (15×21 cm²)

which made the prey very easy to distinguish. Two prey were glued to the cardboard upside down and two prey were glued to the cardboard by just attaching one tip of a 'wing' of the T-shaped prey. This made it display its shape and pattern, but it protruded from the cardboard owing to the peanut chip on its ventral surface. Before the last two prey were attached, two holes were made in the cardboard for the peanut chip. Hence, when these last two prey were glued to the cardboard, their surface was level with the background. The prey types were randomly assigned to the different arrangements on the background. Further, in step 2, the background was first glued to a piece of cardboard (15×21 cm²), and then the six prey were glued to the background after six holes were made. We folded one side of the 'T' of one prey to make it easier to detect, and hence, to stimulate the birds to search for more prey on the background. The last step 3 of the training procedure was similar to step 2, except that it took place in the experimental cage. A bird passed a training step and was qualified for the next step after it had consumed all six prey of a training set within approximately 1 h. We trained 20 birds for the experiment.

(e) Experimental procedure

The experiments were conducted in separate plywood cages ($55 \times 90 \times 70$ cm³). There was always fresh water in the cages. All observations were made through an opening (10×12 cm²), covered with a mosquito net, at the top of the front door. Background boards were inserted through an opening (2×32 cm²) on the bottom of the right side of the cage. It was covered when not in use. A perch was placed on the long side opposite the opening, 20 cm beneath the ceiling, and each cage was lit from above by two lamps (9 W, fluorescent, Philips). To minimize disturbance the room was kept dark.

Before an experiment started, we let the bird acclimatize to the experimental cage for 45–60 min. Because the birds did not have access to food during this time, this also increased their motivation to search for the prey. During the experiment, each prey item was presented singly on a background board. Each bird was presented with all six prey types. We randomized the order of the 6 different prey types, but balanced the overall design so that all prey would be equally represented as first prey in a series, to avoid any directional bias if the birds found the first prey in the experiment less quickly. The six prey types were then presented three times in the same order, resulting in 18 presentations of prey for each bird. The location and orientation of the prey items on the background boards were randomized. When the experiment was completed the bird was returned to its holding cage to take part in another experiment (not discussed in this paper). Shortly after completing both experiments, the bird was released at the trapping site.

For each presented prey, we measured effective search time and used it as an (inverse) estimate of the probability of detection. We defined effective search time as the time a bird spent on the background searching for prey and measured this using a stopwatch (Merilaita *et al.* 2001). If a bird did not find the prey on the background board within 600 s, because the prey was difficult to find or because of low motivation, the background board was taken out of the cage and presented again at the end of the experiment. This happened to nine birds for one prey item, four birds for two prey items and one bird for three prey items. To avoid confounding the bird's loss

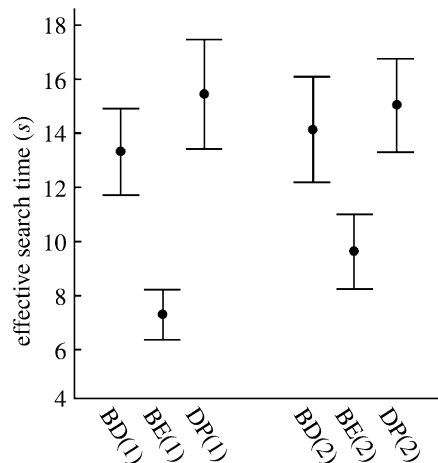


Figure 2. Effective search time (s) of the great tits searching for prey on the background boards (mean \pm s.e.). Prey set 1 had some pattern elements cut by the outline and prey set 2 had whole elements only. BD, background-matching prey expected to be difficult to detect; BE, background-matching prey expected to be easy to detect; DP, prey with disruptive pattern.

of motivation with the prey's probability of detection, we then used the last time measurement (when that particular prey item was found before 600 s had elapsed) in the analysis.

(f) *Statistical analysis*

We calculated the mean effective search time for each bird from the three trials made with each prey type. These values were then log-transformed to attain normally distributed data (Kolmogorov–Smirnov test for normality: $p > 0.12$ for all variables after the transformation). Because each bird looked for all the prey types, we used paired t -tests in the comparisons. To control for the increased probability of obtaining Type I errors when performing multiple comparisons, we used the Dunn–Šidák method to adjust α -levels (Sokal & Rohlf 1995). Statistical tests were performed using SPSS 11 (SPSS Inc.).

3. RESULTS

We found that effective search time, our measure of the probability of detection, varied substantially between prey representing different random samples of the background. Effective search time was significantly longer for the prey categorized as expected to be more difficult to detect than for the prey categorized as expected to be easier to detect. This was true for both the prey with pattern elements broken by the outline (paired t -test: $t_{19} = 3.4$, $p = 0.003$; figure 2) and the prey with whole elements only ($t_{19} = 2.8$, $p = 0.012$). We also found that the DP took longer for the birds to find than did the easier background-matching prey, a result also valid for both prey types (prey with broken elements: $t_{19} = 4.9$, $p < 0.001$; prey with whole elements only: $t_{19} = 3.2$, $p = 0.004$). All these results remained significant after the adjustments of α -levels owing to multiple comparisons. Interestingly, when comparing the prey with disruptive pattern and the more difficult background-matching prey, no significant differences were found (prey with broken elements: $t_{19} = 1.0$, $p = 0.31$; prey with whole elements only: $t_{19} = 0.6$, $p = 0.56$; figure 2).

The general pattern was very similar for prey with and without broken elements. This was shown by repeated measures ANOVA (four levels) with the two types of more difficult background-matching prey and with the two types of prey with disruptive patterns. There was no difference in effective search time between these prey types ($F_{3,57} = 0.7$, $p = 0.56$; figure 2).

4. DISCUSSION

Overall, the results show that our choice of prey and background coloration was successful with respect to difficulty of the detection task, as the birds were able to find the prey but yet the set-up allowed us to find noticeable differences between some of the prey types. The two main results were the following: first, there was a substantial difference in effective search time between the two categories of background-matching prey; and second, the background-matching prey that was more difficult to detect was not more cryptic than the disruptive coloration. The results were similar for the prey with broken and with whole elements on the outline. This may be owing to the fact that there were broken elements in both treatments, because even the prey with only whole elements usually covered partly some pattern elements on the background.

From these results, we can draw the following conclusions about background matching. First, it is clear that all samples of a background did not provide equally cryptic prey coloration, but that some samples were more cryptic than others. Thus, prey coloration matching a random visual sample of the background was not a sufficient condition for minimizing the probability of detection. This clearly disagrees with the idea that a random sample of the background maximizes background matching (Endler 1978, 1984, 1991). Furthermore, the prey with disruptive coloration was equally as cryptic as the prey with the background-matching coloration that was more difficult to detect, suggesting that the coloration providing the best camouflage for a given background need not necessarily be a sample of that background. Therefore, prey coloration matching a random visual sample of the background was not a necessary condition for maximal camouflage. Collectively, it seems that some ideas about background matching have been widely accepted, because they appear intuitively appealing, and not because they rest on proper hypothesis testing (see also Merilaita *et al.* 1999, 2001; Merilaita 2003; Ruxton *et al.* 2004).

One could argue that our interpretation of the results would benefit from an estimation of background matching through the quantification of the similarity of prey coloration and background (cf. Endler 1984), instead of just relying upon search time. However, although some quantifications may sometimes be useful, previous studies (Merilaita *et al.* 1999; Merilaita 2003) together with the present one suggest that they do not necessarily correspond very accurately to the predator's perception, especially when relating to the geometry of colour patterns. Furthermore, an estimation using predators gives, from the evolutionary point of view, a more relevant measure of camouflage than a comparison of background and prey coloration for aspects chosen by the researcher.

The result that the probability of detection varied between different background-matching prey suggests that prey coloration matching a random visual sample of the background maximizes background matching only against very simple and invariable backgrounds. This leads to the obvious question: how, then, is background matching maximized in visually complex habitats? Unfortunately, the existence of a simple rule governing how to maximize background matching on visually complex backgrounds seems unlikely. For one thing, visual background variability, both at large and at small scales, affects the optimization of cryptic coloration. Large-scale variations, such as differences between microhabitats, select for the coloration matching of one of the microhabitats when the microhabitats are very different, but with increasing similarity between the microhabitats it becomes more likely that selection favours a coloration combining the requirements of both microhabitats (Merilaita *et al.* 1999, 2001). Small scale variations in background (i.e. variation among patches smaller than the prey) may affect how accurate a match is required to produce good camouflage (Merilaita 2003).

Also, we can specifically consider why the background-matching prey of our experiment varied in the probability of detection. The experiment was not designed to answer this question, and it is an obvious subject for further studies. However, we may guess that the important aspects of prey pattern, which might include pattern element density or distribution, or average lightness, were more representative of the background in some samples than others, making prey with that pattern less sensitive to their exact placement on the background. Another possible explanation is the overlap between the concepts of background matching and disruptive coloration (Merilaita 1998). It is likely that sampling the background produces patterns that interact differently with prey shape and outline. In other words, prey with different background-matching patterns benefit to a varying extent from the principle of disruptive coloration. Thus, this additional, varying benefit may contribute to the variance in the probability of detection between the different background-matching colour patterns.

That the prey with disruptive coloration and the most cryptic background-matching prey did not differ in probability of detection suggests two things: first, it seems that selection for background matching does not rule out disruptive coloration; second, that our application of the principle of disruptive coloration by the tactical placement of the selected pattern elements resulted in a low probability of detection, lending plausibility to the principle of disruptive coloration. On the other hand, even though we designed the disruptive coloration, it is obviously impossible to tell to what extent the probability of detection of the DP came from the principle of disruptive coloration.

We feel that our inability to determine how significantly our attempt to apply the principle of disruptive coloration increased prey camouflage reflects more general difficulties in the study of disruptive coloration. This is supported by the fact that, although the idea of disruptive coloration is not new, there are only few experimental studies dealing directly with it. A major problem is the identification of disruptive coloration. For instance,

Turner (1961) presented artificial prey on grass to wild birds and called his striped prey disruptive, even though it may simply have matched the background of a mixture of green and dry grass. Silberglied *et al.* (1980) obliterated the white wing stripes supposed to be disruptive in male *Anartia fatima* butterflies, and studied the survival of the manipulated and control butterflies, without finding any significant difference. However, instead of having a disruptive function, the stripe may be a sexual signal (Emmel 1972; Taylor 1973). We can see two reasons for the problems in identifying disruptive coloration. One reason is that, as mentioned above, disruptive coloration and background-matching coloration are not mutually exclusive. It has even been suggested that crypsis based on the random sampling of background would also cover the principle of disruptive coloration (Endler 1978). However, it seems that background-matching and disruptive coloration do not overlap that much, and that these functions may be distinguished at least in some cases (Merilaita 1998). Another, at least equally important, reason may be that no explicit mechanistic basis related to visual information processing has been suggested for disruptive coloration. Thus, disruptive coloration may appear as a somewhat diffuse collection of means, rather than a single, unambiguous way of achieving concealment. More importantly, this may make it rather difficult to formulate easily testable null hypotheses about disruptive coloration. Yet, we feel that it is possible to overcome many of these difficulties. For example, one prediction that may help to distinguish disruptive coloration from background-matching coloration is that the optimization of disruptive coloration should be related to the shape of the prey, whereas background-matching coloration should be independent of body shape. Thus, two prey species with markedly different body shapes using the same habitat may be expected to evolve different cryptic coloration if they rely on disruptive coloration, but not necessarily so if they rely on resemblance to the background.

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