THE ROYAL SOCIETY

Selection for cryptic coloration in a visually heterogeneous habitat

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We studied selection by predators for cryptic prey coloration in a visually heterogeneous habitat that consists of two microhabitats. It has been suggested that the probability of escaping detection in such habitats might be optimized by maximizing crypsis in one of the microhabitats. However, a recent model indicates that a coloration that compromises the requirements of different microhabitats might sometimes be the optimal solution. To experimentally study these hypotheses, we allowed great tits (*Parus major* L.) to search for artificial prey items in two different microhabitats (background boards): small patterned and large patterned. On each board there was one prey item that was either small-patterned, large-patterned or medium-patterned and thus compromised. Search time was used as the measure of crypsis and was on average longer on the large-patterned than on the small-patterned background. On the small-patterned background, the small-patterned prey was more cryptic than the compromised prey, which was in turn more cryptic than the large-patterned prey. On the large-patterned background, the small-patterned prey was least cryptic, but the compromised prey did not differ significantly from the large-patterned prey. The compromised coloration had lower predation risk than the matching colorations. This indicates that in some conditions a compromised coloration might be the best strategy for the prey and has important implications for the study of animal coloration.

Keywords: camouflage; cryptic prey coloration; predation

1. INTRODUCTION

Although cryptic animal coloration (i.e. coloration that decreases the risk of detection) has been one of the classic examples of natural selection (Darwin 1859), our knowledge about what determines the particular appearance of such coloration is scarce. There are still surprisingly few experimental tests about the basic assumptions of optimization of cryptic coloration. Many previous papers have instead focused on predator learning and search image formation (e.g. Pietrewicz & Kamil 1979; Gendron 1986; Kono *et al*. 1998), whereas the studies estimating crypsis in a given species usually have had limited contribution to the theory of cryptic coloration optimization.

One of the less explored areas of crypsis is the optimization of coloration in heterogeneous habitats, which consist of two or more visually different microhabitats (but see Merilaita *et al*. 1999). However, most animals live in these visually patchy habitats. Such habitats are an obvious problem to animals, because crypsis is a background-specific adaptation and increased crypsis in one microhabitat is expected to decrease crypsis in another one (Edmunds 1974; Endler 1978; Sandoval 1994). In heterogeneous habitats, the degree of crypsis was thought to be the highest in microhabitats in which the risk of encountering a predator is highest (Endler 1978, 1984). However, in their recent model, Merilaita *et al*. (1999) showed that this need not always be the case. Crypsis can be optimized as a compromise between the requirements of different microhabitats.

We present an experimental study of a trade-off in crypsis between microhabitats. We offered artificial cryptic prey items to avian predators in a habitat with two artificial backgrounds. This allowed us to manipulate crypsis and create a gradient of matching between prey and background colour patterns. Specifically, we wanted to find out whether a compromised pattern could successfully deceive predators that are adapted to visually detect their prey and how well the compromise works in comparison with prey patterns that match either of the backgrounds.

2. METHODS

(a) *Theoretical background*

The model habitat in Merilaita *et al*. (1999) consisted of two different microhabitats. The optimal combination of crypsis in the microhabitats was supposed to maximize the probability of a prey escaping detection by a predator. They defined this probability as a function of the degrees of crypsis of the prey, the probabilities of occurrence and the probabilities of encountering a predator in the two microhabitats. The model included a trade-off in crypsis between the two visually different microhabitats such that an increased crypsis in one microhabitat was expected to result in a decreased crypsis in the other microhabitat. The trade-off gives the highest possible crypsis an animal can produce in one microhabitat for each value of crypsis in the other microhabitat. It is the shape of this trade-off that largely determines whether the optimal coloration is a compromise between the requirements of the differing microhabitats or exclusively adapted to only one of them. In general, a compromise is the optimal coloration when the trade-off is convex (seen from the origin), but a coloration matching one of the backgrounds is the optimal one when the trade-off is concave. Here, we test whether the expectation that a compromise might have a lower susceptibility to predation than a coloration that matches one of the backgrounds is valid from the predator psychology point of view.

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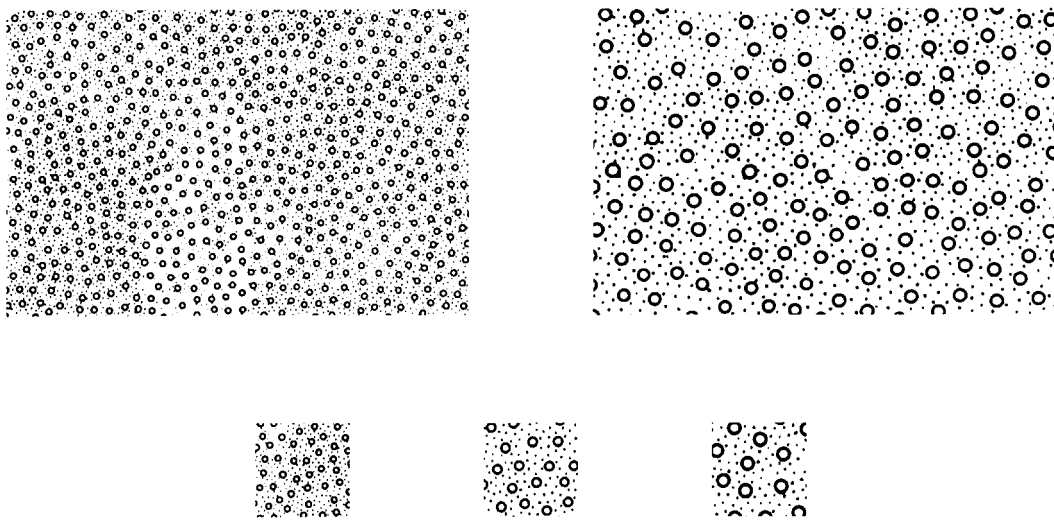
Figure 1. The two large rectangles show the small and large background patterns, and the three small squares show the small, compromised and large prey patterns used in the experiment.

(b) *Predators, prey items and backgrounds*

We used great tits (*Parus major* L.) as predators because they naturally search for insects and seed in their habitat (Alatalo 1982), and they are known to do well as experimental predators (e.g. Lindström *et al.* 1999). We conducted the experiment in October–November 1999 at Konnevesi Research Station in Central Finland (62° 37′ N, 26° 20′ E). We had a permit to catch great tits with mist nets and keep them in captivity for the experiments (from the North Savo Regional Environment Centre, license 0699L0420–254). They were housed individually in 0.6 m × 0.6 m × 1.0 m cages at room temperature and a 12 L : 12 D cycle. We provided the birds with sunflower seeds, peanuts and water *ad libitum*.

We chose to use artificial prey and background patterns to minimize any effects of previous experience and learning on our experimental measure of crypsis. We tested five different sets of prey and background patterns, with varying pattern size, shape and density, in small-scale pilot experiments before choosing the one that was best suited for the manipulation of crypsis. The criterion for choice was that there had to be an observable difference in search time between a prey on a matching and on a mismatching background.

We prepared the prey items and backgrounds from white paper with a black pattern. Only one pattern was used, but it was varied in size (figure 1). As the original pattern, we used Formatt no. 7115 screen (Graphic Products, Beaverton, OR, USA). This was reproduced at different scales using a copying machine with a zoom function. The two background patterns used were 100 and 200% of the original pattern scale. The three prey patterns used were 100, 150 and 200% of the original pattern scale. Consequently, the prey with the 100 and the 200% patterns perfectly matched one of the backgrounds, whereas the prey with the 150% pattern was a compromise between the two backgrounds. Hereafter, we shall refer to the 100% pattern as the small pattern, the 200% as the large pattern and the 150% as the compromised pattern. We prepared all backgrounds and prey items from the same copying paper.

We made the prey by gluing a 5 mm × 5 mm piece of paper onto the underside of a 12 mm × 12 mm piece of the patterned paper. An almond chip (*ca.* 2 mm × 2 mm × 1 mm) was then glued onto the smaller piece of paper. The function of the

smaller piece of paper that was placed between the almond and the larger piece of paper was to prevent oil from the almond being absorbed to the printed side of the prey item. We made the backgrounds (20 cm × 29 cm) of corrugated cardboard covered with the patterned paper. We attached one prey item onto each background board. On each randomly chosen site of attachment, a hole for the almond was made so that the prey item would not protrude. To further ensure the flatness of the prey items and to make them immobile, three of their corners were lightly glued onto the background.

(c) *Training the birds*

We prepared the birds for the experiment using stepwise training to search for and consume the artificial prey on the background boards. During the familiarization and training sessions other food was removed from the cage. If any of these steps took longer than 2 h, we interrupted it and fed the bird. First, we familiarized the birds with the food. We started the procedure by offering the birds pieces of almond chips. After they had started to consume almond, we gave them five pieces of almond chips each glued on a 12 mm × 12 mm piece of white paper so that they would associate the piece of paper with food. Because these birds were also used in another experiment (Lyytinen *et al.* 1999) that was carried out after this one, they were next trained to consume pieces of almond chips enveloped between two 12 mm × 12 mm pieces of brown paper. Note that in the training for the other experiment, the prey items were monochrome brown and they were offered on a white background. Therefore it most probably did not influence the ability of the birds to detect the prey used in our experiment.

In the first pre-experiment training session, we gave the birds six prey items (two of each of the three prey types used in the experiment) on a 10 cm × 15 cm brown background. Three of these prey items (one of each type) were sunk into the background as described above, whereas the other three were not. Instead, these items were glued from one corner only, such that they would strikingly protrude and the piece of almond would be easy to find. This helped the birds to learn to recognize and to consume the prey items.

In the second pre-experiment training session we again offered the birds six prey items (two of each of the three prey

types), but this time in succession on both of the backgrounds used in the experiment. The background size was again 10 cm × 15 cm and each piece of almond was sunk on the background so that all prey items were flat.

(d) *Experimental procedure*

We did the experiment in matt-black cages that were 50 cm wide, 70 cm deep and 96 cm high. Each cage was lit by one 18 W fluorescent tube attached in the ceiling. On one wall there was an opening through which the background boards with prey items could be placed. On the opposite wall there was a perch at 30 cm height. We observed the behaviour of the birds through a 10 cm × 15 cm window. The window was covered with mosquito net and the observer room was kept dark so that the observer would not disturb the birds. The birds were acclimatized to the cages either by carrying out the second pre-experiment training session there or by keeping a bird there for 1 h with food and water before the experiment. Before starting the experiment, we removed food from the cage and each bird was deprived of food for a period of 0.5–2 h.

We used 23 trained birds. During the experiment each bird was presented with all six possible combinations of the two backgrounds and the three prey types a total of three times, resulting in 18 presentations. We presented the two backgrounds systematically in turn (the first one was chosen randomly), and the order of the prey types was randomized in each of the three series of six presentations. Thus, our experimental environment corresponds to a heterogeneous habitat that consists of two microhabitats in which the prey has equal probabilities of occurrence and equal probabilities of encountering a predator. Because we presented the different prey types and the backgrounds an equal number of times to the birds before and during the experiment, and the combinations of prey and background were presented in random order, we do not expect there to be any confounding effects of biased learning in our experimental measurement of crypsis. Neither is it likely that the predators formed search images because we presented several prey types and backgrounds in a rapid sequence (Pietrewicz & Kamil 1979).

During each presentation we used a stopwatch to record the effective search time, that is the time a bird spent on the background board searching for a prey. We used the effective search time as a measure of crypsis. We set the maximum effective search time to 180 s because we wanted to ensure that the experiment would not be too exhausting for the birds (180 s effective search time corresponded to a total time of *ca.* 0.5 h). Furthermore, the search motivation of the birds decreased with time, so that by 180 s the birds had little motivation left. However, the 180 s limit was reached only twice, once for a large-patterned prey on a large-patterned background and once for a small-patterned prey on a small-patterned background.

(e) *Statistical analysis*

For each bird, we calculated the mean effective search time for the three trials made with each prey type on each background. We used a repeated-measures ANOVA with planned comparisons when comparing the degree of crypsis of the prey types on a background. We used logarithmic transformation or non-parametric methods when necessary owing to the distribution of the data. We used sequential Bonferroni adjustment to correct for the type I error due to repeated testing (Rice 1989).

We graphically solved for the colour pattern that maximizes the probability of escaping detection in our experimental envir-

onment using the model of Merilaita *et al.* (1999). We first plotted the mean search time of each prey type on one background against the mean search time on the other background to show the trade-off in crypsis between the two microhabitats. Next, we found the point furthest from the origin where the slope, determined by the probabilities of occurrence of the prey and the probabilities of encountering a predator in the two microhabitats, touches or crosses the trade-off curve. The slope was −1, as these probabilities were equal for both backgrounds and all prey types in our experiment. A line with this slope gives a set of points with equal probability of escaping detection in the whole habitat, based on different combinations of crypsis in the two microhabitats. Because crypsis increases with the distance from the origin, and because the trade-off consists of the best possible combinations of crypsis in the two microhabitats that an animal can achieve, the outermost point where a line with this slope touches or crosses the trade-off curve gives the best colour pattern possible for the habitat.

We tested whether the shape of the trade-off curve was convex or concave by the following method. First, we solved the equation of the line through the mean search times of two prey types. Then we calculated the shortest distance to the line for each of the 69 points of the three prey types. For those points below the line, a negative value was assigned. If the three prey types corresponded to a linear trade-off curve, no significant differences in the distance would be expected among them. Here, we used Friedman's non-parametric test for repeated measurements.

3. RESULTS

On the small-patterned background, the three prey types differed in crypsis as would be expected from their degree of background matching. Search time was significantly longer for the small-patterned prey than for the compromised prey (repeated-measures ANOVA with logarithmic transformation, planned comparisons, $F_{1,22} = 16.2$, $p = 0.0006$; figure 2). For the large-patterned prey, search time was significantly shorter than for the compromised prey ($F_{1,22} = 11.9$, $p = 0.0023$; figure 2).

However, on the large-patterned background the search time did not differ significantly between the compromised and the large-patterned prey ($F_{1,2} = 0.87$, $p = 0.36$; figure 2). But, again, search time was significantly longer for the compromised prey than for the least matching prey, which this time was the small-patterned type ($F_{1,22} = 15.1$, $p = 0.0008$; figure 2). All the significant differences remained highly significant ($p < 0.01$) after the sequential Bonferroni correction.

Generally, on both backgrounds, search time increased with increasing background-matching to the prey colour pattern and, thus, there was a trade-off in crypsis between the backgrounds. The shape of the trade-off proved to be convex. The equation of the line through the mean search times for the large-patterned and the compromised prey was $y = -0.37x + 26.03$ (with search time on the small-patterned background on the *x*-axis and on the large-patterned background on the *y*-axis). The mean of the shortest distance to this line was 0.00 for the large-patterned prey, −0.01 for the compromised prey and −7.05 for the small-patterned prey. The small-patterned prey lay significantly below the line of linear expectation (Friedman's test, $\chi^2 = 6.52$, $n = 23$, d.f. = 2, $p = 0.038$), which indicates that the trade-off was convex.
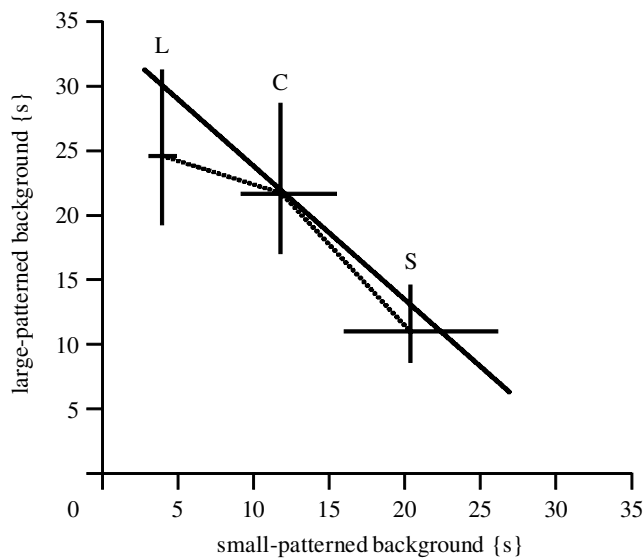
Figure 2. The crypsis of the three prey types on the two backgrounds measured as mean search times (with 95% confidence intervals after logarithmic transformation) in seconds, giving the trade-off in crypsis between the microhabitats. Prey types: L, large patterned; C, compromised; S, small patterned. The slope of the straight line is determined by the probability of encountering a predator and the probability of occurrence of prey in each microhabitat. The optimal coloration in a given environment is the one touching this line, which in this case is the compromised coloration.

The graphical solution for the optimization of cryptic colour pattern in our experimental environment is shown in figure 2. Because the three prey types corresponded to a convex trade-off curve, the best of the three prey colour patterns that maximizes the probability of escaping detection by a predator was the compromised colour pattern.

The average search time per prey item for all three prey types was significantly longer on the large-patterned background ($\overline{X} \pm$ s.e. $= 19.1 \pm 2.8$ s) than on the small-patterned background (12.0 ± 1.7 s) (paired t-test with logarithmic transformation, $t = 2.91$, $n = 23$, $p = 0.0080$). This indicates that the large-patterned background made detection more difficult than the small-patterned background. Because the average difference in search time between the most and the least matching prey type did not differ significantly between the two backgrounds (Wilcoxon matched-pairs test, $\mathcal{Z} = 0.75$, $n = 23$, $p = 0.46$), this result is not an artefact due to different ranges of distribution of crypsis on the two backgrounds.

4. DISCUSSION

Our results show that the compromised colour pattern had lower predation risk than the two matching colour patterns. The high crypsis of the small and the large pattern on their matching backgrounds did not compensate for their low crypsis on the mismatching background and, therefore, their overall probability of escaping detection was lower than in the compromised colour pattern. This result indicates that in some habitats a compromised colour pattern might be the best strategy for cryptic animals. Here, we manipulated the scale of a colour pattern, but we believe that it is reasonable to

assume that the result applies to the shapes and colours of cryptic colour patterns as well. A prerequisite for this result was the convex shape of the trade-off curve in crypsis between the two microhabitats.

There are three factors that shape the trade-off in crypsis (Merilaita *et al.* 1999). First, visual difference between the microhabitats sets the physical constraint for the simultaneous maximization of crypsis in them. Second, biological constraints, such as a lack of genetic variation or the high costs of producing a colour pattern, can hinder selection, resulting in phenotypes that would physically be the best possible ones. Third, it is the perception of a predator that ultimately determines the success of any cryptic animal coloration against a given background. Here, we manipulated prey colour pattern and the visual difference between the microhabitats and let predators judge the outcome. The patterns differed only in size. Although it was enough to induce clear differences in susceptibility to predators between the small-patterned and the large-patterned prey, the difference was not too big for the compromised prey to be successful. Owing to the quality of the perceptual abilities of the predators, that is their visual acuity (Endler 1978) and, in this case possibly more likely, their ability to distinguish between patterns when searching (Kiltie & Laine 1992), it was especially difficult for them to detect the mismatch between the patterns of the compromised prey and the large-patterned background.

We cannot tell how common compromised cryptic colour patterns are because this aspect of crypsis has not been explored in nature (but see Shreeve (1990) and Merilaita *et al.* (1999) for some probable examples of them). However, visual heterogeneity of habitats is the rule rather than the exception, indicating that conditions favouring the occurrence of compromised cryptic colour patterns might be widespread. Interestingly, it has been suggested that also some mimetic colour patterns might be compromised owing to multiple models (Edmunds 2000). On a more general level, compromises are obviously expected to be common among colour patterns that combine different functions, such as crypsis together with signalling or thermoregulation (Endler 1978, 1980).

An interesting point is that the crypsis of our prey types did not vary symmetrically between the two backgrounds, although variation in the pattern geometry was symmetrical. The search times were, on average, longer on the large-patterned background than on the small-patterned background. Also, the difference in search time between the compromised prey and the matching prey was less on the large-patterned background than on the small-patterned background. This indicates that the prey probably gained more protection from the large-patterned background and that equally close matching, as on the small-patterned background, was not required for a relatively high crypsis. There are at least two possible explanations that might contribute to this observation. First, the large-patterned background might be a more difficult visual environment for the searcher. The literature about crypsis mainly stresses the relationship between background and prey coloration as the determinant of crypsis (Endler 1978; Edmunds 1990; Guilford 1992). However, it might also be possible that visual characteristics of the background (such as heterogeneity or

complexity of background elements) *per se* affect the detectability of prey by distracting the predator and that backgrounds vary in this respect. Second, the scale of pattern on the large-patterned background in relation to the size and shape of prey might be such that the outline of the prey items is not as easily detected on it as on the small-patterned background. In this way, the large-patterned background might have increased the protection of the prey through disruptive coloration (Cott 1940; Merilaita 1998). When searching for the prey, the birds apparently used the outline of the prey, in addition to the pattern, as a cue and often bent down to view the surface of the background board to find prey by its contour.

To conclude, when estimating the crypsis of animal coloration one should not neglect the possibility of the coloration having evolved as a compromise for the requirements of different backgrounds. Thus, an optimal cryptic coloration for a habitat might be one that has not maximized crypsis in any of the microhabitats that constitute the habitat as a whole.

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