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Crypsis through disruptive coloration in an isopod

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The white-spotted colour morph of the marine isopod *Idotea baltica* appears cryptic on the brown alga *Fucus vesiculosus* with its white-coloured epizoites *Electra crustulenta* and *Balanus improvisus*. This study shows that the crypsis of this coloration is achieved through disruptive coloration rather than through background matching. Crypsis through background matching requires that the sizes and the shapes of the pattern elements should closely resemble those of the visual background. Comparisons between the white spots of the isopods and those of their natural background contradicted this prediction. Disruptive coloration, which aims to obscure the true form of the animal by partly blending with the background and distracting the attention of the viewer from the contour of the animal to unessential patterns, presupposes more marginal elements than expected by the pattern element distribution in the background, and also highly variable and complex elements. Comparison between the observed spot distribution and simulated individuals with randomly distributed spots showed that the spots in these isopods do indeed touch the body outline more often than expected. Furthermore, the spots were highly variable and complex.

Keywords: background matching; camouflage; crypsis; disruptive coloration; *Idotea baltica*

1. INTRODUCTION

The function of cryptic animal coloration is to decrease the probability of detection. This function can usually be identified easily, but the mechanisms by which it is achieved are often unclear. Furthermore, we can seldom tell why a cryptic coloration has its specific appearance.

Cryptic coloration in many cases can be traced back to the visual habitat of the animal wearing it. Resemblance in colours and patterns between an animal and its background, that is background matching (Cott 1940; Edmunds 1974; Endler 1978), is an often postulated method of attaining crypsis. According to Endler's (1978, 1991) definition of crypsis, which stresses the importance of background matching, a cryptic prey coloration should resemble a random sample of the visual background in size, shape and colour at the time and place of highest predation risk. He also derived a method for quantifying background matching based on a comparison between the colours and patterns of the animal and its background (Endler 1984). This principle for quantifying background matching of different colour patterns has subsequently been applied in several studies (see, for example, Kiltie 1992; King 1992; Westmoreland & Kiltie 1996).

Because edges and boundaries play a central role in visual recognition (Tovée 1996), another way to achieve camouflage is through disruptive coloration (Cott 1940; Edmunds 1974), by obscuring the contour and the true form of the animal. This can be attained in two ways: first, some parts of the animal blend into the background so that its surface is broken up into meaningless shapes, and second, the attention of the viewer is drawn to unessential patterns. Both ways result in an impression of something completely different from the actual bearer of the colour pattern in shape or even in number (Cott 1940).

Studies of cryptic colorations have seldom considered the possible role of disruptive patterns (but see Beatson 1976; Silberglied *et al.* 1980; Endler 1984; Armbruster & Page 1996; Marshal & Messenger 1996). The most thorough description of this phenomenon can still be found in Cott (1940), where he proposed certain principles for what constitutes disruptive coloration.

1. Disruptive marginal patterns are elements of the pattern interrupted at the margin. While some colours at the body outline merge to the background, others break up a continuous contour and distort its characteristic form.
2. Differential blending of a pattern makes some elements of the animal coloration closely match the background, while others stand out as distracting marks and break up the continuity of the surface.
3. Adjacent, distracting elements should be variable and complex to give an impression of a series of separate objects, instead of a repeated simple pattern of one object.
4. Maximum disruptive contrast, that is, maximal contrast between the components of the animal coloration, makes the distracting elements stand out even more strongly and prevents recognition by drawing the attention of an observer to themselves, so that the outline and the parts of the animal merging into the background pass unnoticed.

To enable the distinction between the importance of background matching and the disruptive role of the coloration (which need not to be mutually exclusive) the following predictions about the distribution, the geometry,

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and the colours of the pattern can be derived from the principles set out in the previous section.

1. The elements of a background matching pattern are expected to be distributed according to pattern element distribution in the background. Instead, a higher number of marginal pattern elements (i.e. elements touching the body outline) than expected from the pattern element distribution in the background would suggest a disruptive pattern.
2. The size and the shape of the elements of a background matching pattern should equal the size and the shape of the visual elements in the habitat. The elements of a distracting patchwork of a disruptive pattern should be highly variable and complex to give the impression of separate objects.
3. The colours of a background matching pattern should be a random sample of the background colours. The colours of a disruptive pattern should also be, at least partly, a sample of the colours of the background, but on the other hand there should be contrasts between the colours.

In this paper I present a study on camouflage in a colour polymorphic marine isopod, *Idotea baltica*, focusing on the geometry of the white-spotted phenotype called *albafusca* (see figure 1). In the *albafusca* individuals the ground colour of the back produced by melanophores contrasts with a variable number of white spots, which vary in size and shape. The spots often touch the body outline and sometimes reach laterally across the animal. *Albafusca*-patterned isopods appear cryptic on the brown alga *Fucus vesiculosus* with its white epizoites, the bryozoan *Electra crustulenta* and the barnacle *Balanus improvisus* (Salemaa 1978).

To distinguish if *albafusca* is employing background matching and disruptive coloration to achieve crypsis, I analysed the size and the shape of the spots of this colour pattern and of the spots found in the habitat. Furthermore, I created a method of testing if the proportion of marginal spots deviated from random expectation. As far as I know, this is the first attempt to distinguish between the importance of background matching and disruptive coloration by a quantitative analysis.

2. METHODS

Idotea baltica has five heritable colour morphs which, to the human eye, appear to be cryptic (Tinturier-Hamelin 1963; Salemaa 1978). At the south-western coast of Finland, in the vicinity of the Archipelago Research Institute of the University of Turku (60° 14′N, 21° 60′E), where the animals used in this study were collected, the white-spotted *albafusca* is abundant being, after the uniform colour morph, the second most common morph in males, and in females these two morphs are about equally common (Jormalainen *et al.* 1995). *I. baltica* inhabits the brown alga *F. vesiculosus* and can change its ground colour by chromatophore responses to match the different colours of the alga, but the white spots of the patterned individuals always remain unchanged (Tinturier-Hamelin 1963; Jormalainen & Tuomi 1989). *I. baltica* is preyed on by visually searching fishes like eelpout (*Zoarces viviparus*) and perch (*Perca fluviatilis*) (Salemaa 1978; Jormalainen *et al.* 1995).

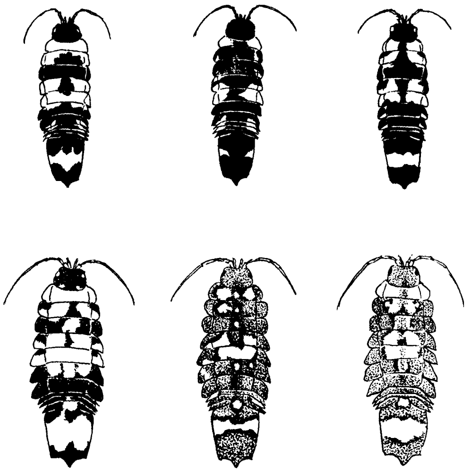

Figure 1. Some of the *I. baltica* females (upper row) and males (lower row) used in this study (not to scale).

(a) *Testing for the match in pattern geometry*

The analysis of background matching basically followed the procedure outlined by Endler (1984). Between 16 and 29 June 1995 I collected 303 isopods from one location and photographed all the white-spotted *albafusca* individuals. I also collected *F. vesiculosus* thalli from the same site and photographed 109 *E. crustulenta* colonies and 54 *B. improvisus* individuals picked at random. I digitized the pictures, and did an analysis on a Macintosh computer using the public domain NIH Image program (developed at the US National Institutes of Health and available on the Internet at `http://rsb.info.nih.gov/nih-image/`) to measure the lengths of the isopods and the areas and perimeters of their spots and the area and perimeter of *E. crustulenta* and *B. improvisus*. For each isopod I also recorded the total number of spots, and the number of marginal spots (i.e. spots touching the body outline of the animal). I analysed the background matching of the *albafusca* pattern by comparing the area of the spots with that of the epizoites. To compare the shape of the spots on the isopods and the epizoites, respectively, I created an index of roundness (I_R):

$$I_R = \left(\frac{P^2}{4\pi A}\right) - 1$$

where P is perimeter and A is area of a spot. $I_R = 0$ when the spot is circular, and, independently of spot area, takes larger values the more complex the shape is, that is, the longer the perimeter is in relation to the area of the spot.

To test for differences in variability between spots on *I. baltica* and epizoites I employed corrected coefficients of variation (CV*; Sokal & Braumann 1980; Sokal & Rohlf 1995). I compared CV* of the epizoite samples against the mean CV* of the isopod individuals using the Student's *t*-test after logarithmic transformation for normality.

(b) *Testing for the distribution of the spots*

If the *albafusca* morph shows a disruptive pattern employing marginal patterns, the elements of this pattern should touch the body outline of the animal more often than expected by the distribution of the visual elements in the background. Because in suitable microhabitats the exact placement of the epizoites *E. crustulenta* and *B. improvisus* seems to be random, I used random distribution as a null hypothesis for the distribution of the spots on the isopods. To find out the exact null hypothesis

Table 1. *Mann–Whitney U-tests for size and colour pattern characteristics between female and male isopods used in the analysis*

($\bar{x}\pm$s.e. are given for females ($N=64$) and males ($N=15$).)

	females	males	U	p
length	15.3 ± 0.2 mm	20.0 ± 0.3 mm	2	<0.001
spot area	2.9 ± 0.4 mm^2	2.3 ± 0.6 mm^2	391	0.27
spot number	7.4 ± 0.5	11.9 ± 2.0	314.5	<0.05
total area of spots/(length)^2	0.069 ± 0.005	0.043 ± 0.006	281	0.013
spot shape complexity	2.4 ± 0.2	2.3 ± 0.7	309	0.033

for the distribution of the spots I designed a computer program to simulate randomly arranged spots. The number of marginal spots is affected by the area and the total number of the spots. These were obtained from the individuals measured in the image analysis (see previous paragraph).

The simulation used a 0.25 mm × 0.25 mm grid. The outline coordinates of an average size model individual (length 15.3 mm and area 57.8 mm^2 for females and 20.0 mm and 105.0 mm^2 for males, respectively) were mapped on the grid. The areas of all the spots of each individual from the image analysis data were first standardized to correspond to the model individual by multiplying with the square of the mean body length and dividing by the square of the body length of the individual, and were then entered into the program.

The program started the spot simulation for an individual by choosing random coordinates for the first pixel within the given outlines. New random coordinates were generated until all the pixels of each spot had been acceptably placed. Coordinates were accepted if they were situated side by side with some of the previously accepted pixels of the same spot. If the coordinates were already occupied or situated side by side with a pixel belonging to another spot, they were rejected. The natural spots are irregular and variable in shape, but never string-like, branched or disrupted. To obtain clusters of pixels that resemble natural spots in shape, each neighbouring, previously accepted pixel increased the probability of acceptance of a new pixel by 25%. Thus, a new pixel with a previously accepted pixel on all four sides was always accepted, whereas a new pixel with only one previously accepted pixel by its side had only a 25% chance of being accepted. When all the pixels of a spot had been chosen, the creation of the next spot began, and this was repeated until all the spots of an individual had been created. For each simulated individual the program recorded the total number of spots and the number of spots touching the outline. Using the data of the spots of real individuals (64 females and 15 males), the simulation was repeated 30 times for each individual, to produce 2370 simulated isopods. Finally, I compared pairwise the number of marginal spots of each real individual with the mean number of marginal spots of its simulations using Wilcoxon signed-ranks tests. Because the body shape differs between the sexes, both the simulations and the comparisons were done separately for females and males.

3. RESULTS

(a) *Testing for the match in pattern geometry*

The tests for differences in pattern geometry between females and males are collated in table 1. Although females were significantly smaller than males, the mean area of the spots on an individual did not differ significantly between the sexes. On the other hand, males (minimum = 3, maximum = 26) had significantly more spots than females (minimum = 2, maximum = 23). The total area of white spots related to the square of the length of an individual was significantly larger in females than in males, indicating that females had more white per unit area. Furthermore, the mean spot shape of individuals was significantly more complex in females than in males.

To test if the area and the shape of the white spots on the isopods differed from the area and the shape of the white spots of the background, I randomly chose a single spot from each individual isopod so that they would be statistically independent replicates. Spots on the isopods ($\bar{x}\pm$s.e. = 2.4 ± 0.3 mm^2, $N=80$) were significantly smaller than *E. crustulenta* colonies (115.5 ± 10.3 mm^2, $N=109$; Mann–Whitney U-test: $U=92$, $p<0.001$) and *B. improvisus* individuals (34.4 ± 2.4 mm^2, $N=54$; Mann–Whitney U-test: $U=4$, $p<0.001$; figure 2). The comparison of shape, based on the index of roundness, showed that the shape of the spots of females (2.4 ± 0.2, $N=64$) was significantly more complex than the shape of *E. crustulenta* colonies (1.0 ± 0.06, $N=109$; Mann–Whitney U-test: $U=751$, $p<0.001$) and *B. improvisus* (0.2 ± 0.02, $N=54$; Mann–Whitney U-test: $U=5$, $p<0.001$; figure 3). Also the shape of the spots of males (2.3 ± 0.7, $N=15$) was more complex than the shape of *E. crustulenta* colonies (Mann–Whitney U-test: $U=425$, $p=0.003$) and *B. improvisus* (Mann–Whitney U-test: $U=6$, $p<0.001$; figure 3). The spots of the isopod individuals were on average more variable than *E. crustulenta* colonies ($t=3.27$, d.f. = 108, $p<0.001$) and *B. improvisus* individuals ($t=20.1$, d.f. = 53, $p<0.001$) in area and in shape (*E. crustulenta*: $t=1.84$, d.f. = 108, $p=0.034$; *B. improvisus*: $t=4.56$, d.f. = 53, $p<0.001$).

(b) *Testing for the distribution of the spots*

A comparison between real and simulated isopods revealed that, in both sexes, the number of marginal spots in real isopods was significantly larger than expected by chance alone (Wilcoxon's matched-pairs test: females, $z=5.29$, $N=64$, $p<0.001$; males, $z=2.24$, $N=15$, $p=0.023$; see figure 4).

Although the number of marginal spots did not differ significantly between the sexes (females, $\bar{x}\pm$s.e. = 5.5 ± 0.4, $N=64$; males, 7.1 ± 1.4, $N=15$; Mann–Whitney U-test, $U=443.5$, $p=0.65$), females had proportionally more marginal spots than males (females, 74 ± 3.0%; males, 54 ± 6.3%; Mann–Whitney U-test: $U=229.5$, $p=0.017$) because the total number of spots was on average smaller in females than in males. The mean area of the marginal spots for both sexes (2.9 ± 0.3 mm^2) was larger than the mean area of other spots (1.4 ± 0.3 mm^2;

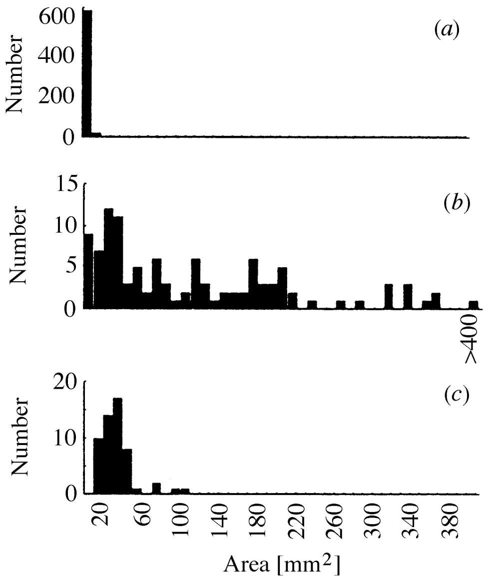

Figure 2. Frequency distribution of the area (mm^2) of the white spots on (*a*) *I. baltica* and the epizoites *E. crustulenta* (*b*) and *B. improvisus* (*c*).

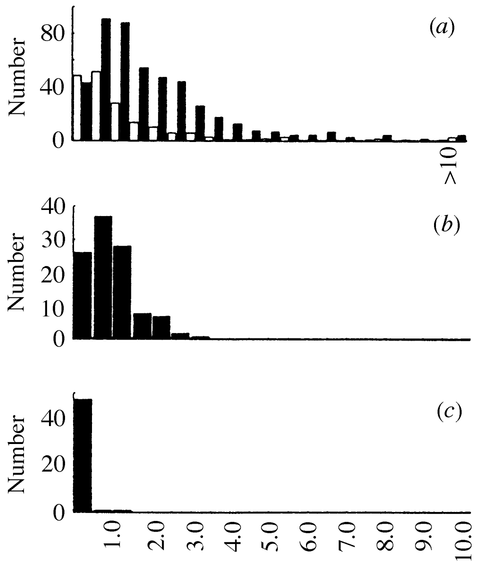

Figure 3. Frequency distribution of the shape of the white spots on (*a*) male (white bars) and female (black bars) *I. baltica*, and the epizoites (*b*) *E. crustulenta* and (*c*) *B. improvisus* based on the index of roundness (see text).

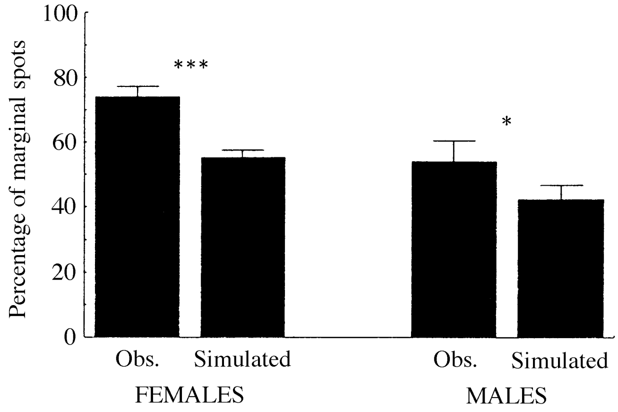

Figure 4. Observed and average simulated frequencies of marginal spots as percentages for females and males ($\bar{x}$ + s.e.; *$p<0.05$; ***$p<0.001$).

Wilcoxon signed-ranks test: $z=3.79$, $N=55$, $p<0.001$). The mean index of roundness of the marginal spots was also larger, indicating that they were more complex in shape ($2.3\pm0.1\,\mathrm{mm}^2$) than the other spots ($1.8\pm0.3\,\mathrm{mm}^2$; Wilcoxon's signed-ranks test: $z=3.06$, $N=55$, $p<0.002$).

4. DISCUSSION

My analyses of spot geometry suggest that the *albafusca* morph achieves crypsis by disruptive coloration rather than by background matching (table 2). This conclusion is supported primarily by the larger than expected number of marginal spots, suggesting that they serve to obscure the form of the isopod rather than to match spots in the background. Furthermore, the complexity and variability of the spots may further increase this disruptive effect by giving the impression of a series of separate objects which do not reveal the shape of the isopods.

The size of the white spots of *albafusca* was significantly smaller than those of the background, although the size of the isopods would allow much larger spots. The shape was also found to differ, with the spots of the isopods being more complex than those of the background. The spots of the isopods were, on average, more variable both in area and in shape than those of the background. These results strongly suggest that natural selection has not maximized the background matching of pattern in *albafusca*. However, this study reflects the particular situation of adult *I. baltica*, but owing to the growth of the organisms other life history stages should be considered. *B. improvisus* larvae settle in late summer (Blom & Nyholm 1961), that is at about the same time as *I. baltica* are born in the northern Baltic (Jansson & Matthiesen 1997), but owing to the relatively fast growth of *B. improvisus* the overlap in area and shape is probably very small throughout the respective life cycles of the two species. Also, the new *E. crustulenta* colonies start emerging in late summer (Borg 1947). Although the spots of adult *albafusca* individuals deviated from the typical area and shape of *E. crustulenta* colonies, some overlap was evident and may exist also with the white spots of juveniles during autumn. The possibility that *albafusca* also gains a certain amount of benefit by background matching therefore cannot be excluded.

When comparing the principles of background matching and disruptive coloration it is obvious that background matching should be highly background specific, because it should be faithful in size and shape to the visual elements in the habitat. Thus, if background matching were to alter because of changes in the dimensions of the pattern owing to growth (King 1992), or because of variations in the visual background, disruptive coloration may be a better option. The variation in coverage of *F. vesiculosus* by the epizoites between sites, between thalli, and within a thallus causes unpredictability in the visual habitat, which may have

Table 2. *Predictions for different traits of pattern elements from crypsis through background matching and through disruptive coloration, and observed traits for the white-spotted colour morph of* I. baltica

trait of pattern elements	prediction from background matching	prediction from disruptive coloration	observed
distribution	same as in the background	more marginal spots than expected by chance	more marginal spots than expected by chance
area	same as in the background	—	smaller than in the background
shape	same as in the background	complex	more complex than in the background
variation in area	same as in the background	high	higher than in the background
variation in shape	same as in the background	high	higher than in the background
colours	same as in the background	same as in the background, contrasted	same as in the background, contrasted

prevented close background matching, and instead selected for disruptive coloration in *albafusca*.

The sexual differences in the appearance of *albafusca* are probably related to the *albafusca* morph being more frequent among females than among males. Female *I. baltica* are more likely to occur on epizoite covered parts of *F. vesiculosus* than males (Merilaita & Jormalainen 1997), and therefore both the *albafusca* pattern itself and a strong expression of it should be favoured in females.

To summarize, the *albafusca* spots did not closely match the white spots of the background in area or shape. Instead, they touched the body outline more often than expected, and were more variable and complex than the background spots, as predicted by crypsis through disruptive coloration. Although the appearance of this coloration can be a product of both mechanisms, collectively, these results indicate that selection in this case has favoured crypsis through disruptive coloration over close background matching.

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