

Commentary

## Disruptive and cryptic coloration

Camouflage may be achieved in three ways: crypsis, disruptive coloration and masquerade (Endler 1981). Cryptic prey resemble random samples of the visual background (Endler 1978, 1981, 1984), minimizing their signal/noise ratio (S/N). Disruptively coloured prey contain some highly conspicuous as well as cryptic pattern elements. The conspicuous elements distract the predator's attention and break up the body outline, making detection of the prey difficult (Thayer 1909; Cott 1940; Stevens & Cuthill 2006). In masquerade, the prey is detected as distinct from the visual background but not recognized as edible (Endler 1981), for example by resembling a leaf (Thayer 1909). The two ways of avoiding detection, crypsis and disruptive coloration, appear contradictory (Merilaita & Lind 2005), because crypsis relies on minimizing the S/N, while disruptive coloration relies on keeping S/N high.

This issue of *Proceedings B* contains two elegant papers on the interaction between disruptive coloration and crypsis (Schaefer & Stobbe 2006; Stevens *et al.* 2006). Following Cuthill *et al.* (2005), these authors constructed artificial prey with pattern elements that stimulated bird eyes in known ways (allowing visual contrast predictions), attached a mealworm to each moth-like stimulus for a reward, and presented these prey to wild birds by attaching them to tree trunks and recording disappearance. The stimuli consisted of some patches that were similar to and other patches that contrasted with the visual background. In disruptive ('edge') patterns, contrasting patches cut across the edges of the 'wings', while in the non-disruptive ('inside') patterns, the contrasting patches were away from the edges of the wings. Like Cuthill *et al.* (2005), the two new papers found that the disruptive pattern resulted in higher 'survivorship' (significantly lower rates of removal by the birds) than the inside pattern. These new papers go further in examining the joint effects of contrast and outline disruption on fitness.

Schaefer & Stobbe (2006) presented the prey against two different visual backgrounds: birch and oak bark with moss. In the first two experiments, the brown and pink colours of the stimuli were similar to a real moth, while in the third a novel colour (blue) was used. Schaefer & Stobbe (2006) predicted that the advantage of disruptive patterns would be greater when disruptive patches had higher contrast, and that disruptive contrast with the visual background increases fitness even if it decreases crypsis. On birch, the cryptic non-disruptive form did worse than the others. On oak, the edge forms and the cryptic (brown) inside form did equally well but better than the more conspicuous pink inside form. This suggests that on some backgrounds the joint effects of disruption

and crypsis are better than a poorly cryptic and non-disruptive pattern, and that the disadvantage of having more contrast is mitigated by having the contrasting components disruptive. In tests with the novel colour, both disruptive and non-disruptive blue forms had the same fitness as the other forms on birch, but the disruptive form with blue did better on oak and moss. It is possible that neophobia towards novel colours (Mappes *et al.* 2005) may have interacted with disruptive coloration to increase the fitness of the novel coloured forms. More work is needed on neophobia, camouflage and visual background effects.

Schaefer & Stobbe (2006) report a significant difference in fitness depending upon whether background contrast was chromatic or achromatic. When the cryptic form had similar chromatic but lower achromatic contrast than the disruptive form, its fitness was lower than most of the disruptive patterns. When the cryptic form had lower chromatic but similar achromatic contrast, there was no fitness change. This suggests that chromatic contrast is more important than achromatic contrast in avoiding predation when patterns are disruptive. Schaefer & Stobbe (2006) suggested that this may explain why insects and reptiles are often more cryptic chromatically than achromatically. This needs further study.

Stevens *et al.* (2006) varied background contrast against oak bark. They explored only achromatic differences because the achromatic visual channel is known to be used in texture and possibly shape discrimination by birds, and because light brown and black might be similar to warning colours (as may be the pink and the novel blue used by Schaefer & Stobbe 2006). Non-disruptive patterns with all components matching the background had higher fitness than non-disruptive patterns in which some patches contrasted with the backgrounds, indicating that crypsis predicts fitness in the absence of disruptive patches. Most importantly, disruptive patterns worked best if all of the components matched the backgrounds. These cryptic-disruptive stimuli had a higher fitness than disruptive patterns in which one component mismatched the background. A combination of disruptive coloration and crypsis works better than either does alone. If all pattern components contrast with the background then the body outline and shape are relatively easy to detect, but if part of the pattern was indistinguishable from that of the background, then body edge detection is much more difficult (Merilaita & Lind 2005; Stevens & Cuthill 2006). This may explain the minimal effect of novel colours in Schaefer & Stobbe (2006), where all colours contrasted more strongly with the background than in their other experiments. Future investigations should address the effects of varying degrees of within-pattern and pattern-background contrast in both the chromatic and achromatic channels.

The accompanying articles can be viewed at <http://dx.doi.org/doi:10.1098/rspb.2006.3614> and <http://dx.doi.org/doi:10.1098/rspb.2006.3615>.

Moth species that rest in only one or two visual background microhabitats are known to be much more cryptic than species which rest in several visual backgrounds; microhabitat choice allows greater crypsis to evolve (Endler 1984); the same should be true for habitat specialists and generalists. This suggests that although purely cryptic species may be less at risk to predation, they may be constrained to fewer habitats than if they were less cryptic (Merilaita *et al.* 1999; Ruxton *et al.* 2004). Disruptive coloration may be a way to allow higher survival on the more variable visual backgrounds experienced by generalists because it works on more visual backgrounds. It may also allow foraging in more places because disruptively patterned species do not have to restrict foraging to where they are most cryptic (Ruxton *et al.* 2004; Sherratt *et al.* 2005). There is probably a three-way tradeoff between habitat specialization, crypsis and disruptive coloration, and this too should be investigated.

These papers show that predator avoidance is not just a matter of background matching, and that we need to take account of both visual and cognitive processes (Guilford & Dawkins 1991; Stevens & Cuthill 2006). Prey can be detected by their body outline, which is extracted by edge-detecting neurons. Disruptive coloration may have evolved because it confuses the edge-detectors, making computational inferences about prey shape difficult if not impossible (Osorio & Srinivasan 1991; Stevens & Cuthill 2006). Edges in natural scenes produce various kinds of luminance and chromatic gradients. False gradients are common in animal colour patterns, leading to misleading appearance of shape, even when they do not disrupt the body outline (Thayer 1909). False gradients can be enhanced by reverse gradients, making the false edges easier to detect than real gradients, further misleading the predators (Osorio & Srinivasan 1991). If colours were used for aposematic, social or sexual signalling, the design should be different, with signalling part edges accentuated rather than disrupted (see diagrams in Cott 1940, pp. 94–95). Colour pattern geometry needs further study.

Predator search modes can affect the evolution of camouflage, as exemplified by polymorphism of undefended prey. Selective attention and other mechanisms lead to frequency-dependent selection, favouring rarer forms and hence polymorphism. This allows mixed strategies of habitat or microhabitat usage (Bond & Kamil 2006), restricting the individual but not the lineage to fewer habitats. Greater detection difficulty leads predators to change from parallel (multiple field) to serial (single field) search. Because only serial searches are enhanced by selective attention, polymorphism becomes more likely as detection probability declines (Bond & Kamil 2006). The spatial scale of the visual background affects detection probabilities, and hence determines whether or not prey become visual background specialists or generalists (Bond & Kamil 2006). If prey evolve to habitat specialists or even polymorphic specialists, then disruptive coloration may not provide any added benefit, but if prey evolve towards generalists, then disruptive components may spread because they allow the use of more places that are safe for cryptic generalists. Alternatively, monomorphic generalists may evolve to polymorphic specialists without disruption. These observations indicate the importance of considering both the visual and cognitive

abilities of both predators and prey in order to understand the evolution of prey coloration. The studies in this issue of *Proceedings B* reveal that the subject of camouflage has a rich complexity that will repay much future work.

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