

Hiding in plain sight

Thomas N. Sherratt, Arash Rashed and Christopher D. Beatty

Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada

Although the principles of disruptive colouration are widely believed to explain a variety of animal colour patterns, there has been no field evidence that it works to reduce the detection rates of natural prey. In a recent paper, Cuthill *et al.* successfully address this shortfall, separating the benefits of background matching from those of disruptive colouration. Their results provide the first definitive field support for this long-recognized phenomenon and suggest several new avenues of research.

Avoiding detection

Organisms are thought to use several different techniques to avoid being detected by predators. Thus, they can adopt colours and patterns that match their general backgrounds (background matching or crypsis [1]), or can evolve a resemblance to an uninteresting element of their environment, such as a twig or leaf (masquerade [2]). More controversially, they can be darker on their dorsal regions than on their ventral regions, rendering their body shapes less three-dimensional in appearance (countershading [3]). Another related and potentially ubiquitous means of avoiding detection is that of disruptive colouration [4], in which appropriate markings can create false boundaries, or hide existing ones, thereby rendering the detection of characteristic shapes more difficult. The principle has been used by artists and the military for decades (Box 1; Figure 1a), but, until now, evidence of its effectiveness in protecting prey in the natural world has been absent. Thus, the only previous field experiment conducted on disruptive colouration was by Silberglied *et al.* [5], who experimentally obliterated the white (and potentially disruptive) wing stripe on the palatable butterfly *Anartia fatima* (Figure 1b) and found that these modified individuals did not survive any better or worse than did controls. As Silberglied *et al.* lamented 'Few concepts in the theory of adaptive coloration are as well accepted, but as poorly documented, as that of disruptive coloration' [5]. With the recent publication of a paper by Innes Cuthill and colleagues [6], our understanding is at last beginning to improve.

Testing the effectiveness of disruptive colouration

Hugh Cott's principle of maximum disruptive contrast [4] proposes that disruptive markings have the greatest effect in obscuring bodies, or parts of bodies, when there is a high contrast in the tone between different components of a

pattern. Cuthill *et al.* [6] interpreted Cott's insights to derive two key predictions: (i) patterns on the edge of the body should be more effective in enhancing concealment than are equivalent patterns placed randomly but away from the edge; and (ii) highly contrasting colours should be more effective than should those of low contrast.

Cuthill *et al.* consider their work to be 'field psychophysics', but any parent wishing to make their Easter egg hunts a little more challenging might do well to learn its lessons. The authors pinned artificial moth-like prey (dead mealworms on top of coloured paper triangles; Figure 1c) onto oak trees in mixed deciduous woods in the south of England. These mealworms were frequently attacked by birds, but they were also occasionally consumed by slugs

Box 1. Disruptive coloration and the art of war

Abbott Thayer, identified by many as the founder of modern military camouflage, was a painter and natural historian who did much to raise awareness of the ways in which organisms avoid detection [13]. At the outset of World War I, the French experienced heavy casualties because their soldiers wore red trousers as part of their uniform. Traditionally, soldiers had been dressed in bright colours to make them appear more menacing to the enemy [14]; with the development of more accurate, longer-range and faster-firing weapons at the end of the 19th century, soldiers now needed to be unseen.

In response to this need, the French established the first *section de camouflage* in 1915, and British and American camouflage units followed. These units, whose members were known as camoufleurs, comprised an eclectic mix of artists, biologists and military strategists, brought together to develop techniques for hiding soldiers, ships and other military apparatus from the enemy. These units developed a variety of camouflage techniques, some of which utilized the principles of countershading and disruptive coloration.

A prominent technique for protecting ships (known as 'dazzle' painting) was created by British camoufleur Norman Wilkinson. Wilkinson realized that a moving target, such as a ship, would be impossible to hide against its background. 'Dazzle' utilized complex patterns painted in high-contrast colours (Figure 1a, main text) to obscure the outline and orientation of a ship. These patterns made it difficult for German U-boats to determine the distance and heading of ships, and thus target them with torpedoes [15].

Camoufleur units were also active during World War II (WWII). Indeed, the biologist and artist Hugh Cott was a key contributor to military camouflage techniques, serving as chief instructor of the Middle East Camouflage School during the war. British artist and naturalist Peter Scott was also involved in WWII naval camouflage strategies and noted that some of the ships of the Royal Navy were camouflaged so well that vessels occasionally collided [16]. In spite of the introduction of technologies such as radar, modern military camouflage techniques still make use of biological themes, including disruptive coloration to help break up the object outlines. Recent advances in camouflage design utilize both background matching techniques and 'symmetry axis' disruptive patterns, which break up the axes of symmetry of a person or object rather than its outline.

Corresponding author: Sherratt, T.N. (sherratt@ccs.carleton.ca).

Available online 9 June 2005

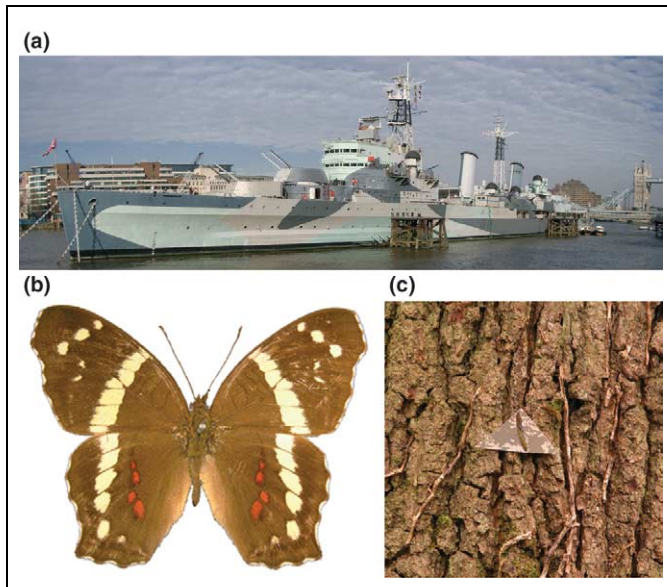


Figure 1. Examples of potentially disruptively patterned objects: (a) HMS Belfast demonstrating the ‘dazzle’ painting style used to confuse the enemy; (b) the butterfly *Anartia fatima*, studied by Silbergeld *et al.* in their early field work on the advantages of disruptive coloration [5]; and (c) an artificial moth of the type used by Cuthill *et al.* in their recent study [6]. Reproduced with permission from Phil Heneghan (a), Gerald Legg (b) and Martin Stevens (c).

and spiders. Two experiments were conducted, each of which compared the ‘survivorship’ of different types of artificial moth (e.g. one type with wing edges obscured, other types with no wing edges obscured) over 24 h as part of a temporal randomized block design. Of course, the mealworm itself will have formed an internal contrast with the wing, but each of the treatments were similar in this regard and it is likely that birds would have taken much longer to associate the prey items with food had the mealworms been placed underneath.

In the first experiment, five different types of artificial moth were pinned out. Three of the moth types were brown and black, with patterns selected to resemble ridged oak bark. Colour matches to natural bark were verified by spectrophotometry, coupled with modeling the predicted photon catches of an insectivorous bird. However, the three moth types differed as to how their edges were obscured. Thus, an ‘Edge’ moth consisted of brown prey with black markings allowed to overlap their triangular border; an ‘Inside 1’ moth was the same type of bi-coloured prey with markings displaced inwards (often leaving an artificial brown border); and an ‘Inside 2’ moth consisted of prey with randomly selected markings with no edge overlapping. Solid brown prey and solid black prey were used as monochrome controls. A second experiment set out to compare the survivorship of ‘Edge’ and ‘Inside 2’ forms generated by using high-contrast colours (‘EH’, ‘IH’) and low-contrast colours (‘EL’ and ‘IL’) as well as monochromatic forms that were the average colour of the two contrast types (‘AH’ and ‘AL’).

The results were dramatic. Using Cox proportional hazards survival regression (a ‘semi-parametric’ method for analyzing census data), the authors found that the artificial moths exhibiting markings overlapping their edges (‘Edge’) survived significantly better than did the other forms, whereas ‘Inside 2’ moths survived

significantly better than did ‘Inside 1’ moths. Monochrome artificial moths fared worst of all. Moreover, whereas the ‘EH’ and ‘EL’ moths survived significantly better than did the other forms of moth in experiment 2, the ‘EH’ moths survived better than did the ‘EL’ moths.

What are we to make of these results? They are consistent with the view that patterns preventing the recognition of actual body shapes help to reduce detection, and that highly contrasting colours enhance this disruptive effect. Indeed, one might argue from the results of experiment 2 that obscuring the edge might be more important than adopting high contrast *per se*, at least for these prey types. Similarly, it was reassuring to see that the ‘Inside 2’ moths tended to survive better than did the ‘Inside 1’ moths (which exhibited a false internal boundary without obscuring the real one). The monochrome treatments survived worst of all, presumably because their overall degree of background matching was less. Through its elegant design (particularly the attempt to differentiate background matching from disruptive colouration) and high amounts of replication, this is the best field study to date on the selective advantage of disruptive colouration.

Prospects

Many challenges lie ahead. One problem is sifting through the bewildering array of potential examples of disruptively patterned organisms (e.g. [7]), which range from mollusks, crustaceans and insects to snakes, fish, birds and mammals, to evaluate whether their markings have arisen to disrupt visual perception. Manipulative field trials are one way forward, but would necessarily be limited to a few key examples. Recent work of Merilaita [8] on the quantitative distribution and location of markings in the marine isopod *Idotea baltica*, as well as manipulative laboratory experiments on artificial prey with great tits *Parus major* [9] offer another way forward, whereas comparative studies (e.g. [10]) might shed light on the factors (e.g. type of habitat) that particular forms of patterning tends to be associated with.

Another challenge will be to elucidate whether disruptive patterns can still be effective if prey are symmetrical in appearance, as many moth species appear to be. There are also many challenges for theoreticians. If disruptive patterns increase conspicuousness, then what is the nature of the tradeoff between disruption and background matching? Does disruptive patterning enable its carrier to exploit a greater range of habitats than can an organism with background matching? Furthermore, what factors determine the scale of the blotches used to break up an outline (too large a pattern might enable an observer to elucidate shape more readily, but too small a pattern might increase the overall contrast)? More importantly, how variable are the disruptive marks within species, and do these systems exhibit frequency dependence as shown for classically cryptic prey [11]? Thus, if all members of the same species adopt exactly the same form of disruptive colouration, then specialist predators might learn to recognize their features.

Conclusions

Disruptive colouration has been taught in biology classrooms throughout the world, and there is a widespread belief that it

works. Although its techniques have long been exploited, there is increasing recognition of the need to test the theory as it applies to animal patterns [12]. With Cuthill *et al.*'s work, we have some of the best insights yet into the adaptive significance of disruptive patterns in the natural world.

Acknowledgements

We thank Graeme Ruxton, Dave Wilkinson and members of the Carleton University Evolution Discussion Group for comments.

References

- Endler, J.A. (1984) Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* 22, 187–231
- Allen, J.A. and Cooper, J.M. (1985) Crypsis and masquerade. *J. Biol. Ed.* 19, 268–270
- Ruxton, G.D. *et al.* (2004) What, if anything, is the adaptive function of countershading? *Anim. Behav.* 68, 445–451
- Cott, H.B. (1940) *Adaptive Coloration in Animals*, Meuthen
- Silbergeld, R.E. *et al.* (1980) Disruptive coloration in butterflies: lack of support in *Anartia fatima*. *Science* 209, 617–619
- Cuthill, I.C. *et al.* (2005) Disruptive coloration and background pattern matching. *Nature* 434, 72–74
- Chiao, C-C. *et al.* (2005) Disruptive body patterning of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. *Biol. Bull.* 208, 7–11
- Merilaita, S. (1998) Crypsis through disruptive coloration in an isopod. *Proc. R. Soc. Lond. B Biol. Sci.* 265, 1059–1064
- Merilaita, S. and Lind, J. (2005) Background matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. Lond. B Biol. Sci.* 272, 665–670
- Stoner, J.C. *et al.* (2003) Ecological and behavioral correlates of coloration in artiodactyls: systematic attempts to verify conventional hypotheses. *Behav. Ecol.* 14, 823–840
- Bond, A.B. and Kamil, A.C. (2002) Visual predators select for crypticity and polymorphism in virtual prey. *Nature* 415, 609–613
- Ruxton, G.D. *et al.* (2004) *Avoiding Attack: the Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*, Oxford University Press
- Thayer, G.H. (1909) *Concealing-colouration in the Animal Kingdom*, Macmillan
- Fussell, P. (2002) *Uniforms: Why we Wear What we Wear*, Houghton Mifflin
- Behrens, R.R. (2002) *False Colors: Art, Design and Modern Camouflage*, Bobolink Books
- Scott, P. (1961) *Eye of the Wind*, Hodder and Stoughton

0169-5347/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.tree.2005.05.010

Are scared prey as good as dead?

Barney Luttbeg and Jacob L. Kerby

Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA

Predators affect prey and their resources by changing the density and traits (e.g. morphology and behavior) of those prey. Ecological studies and models of community dynamics, however, typically only incorporate how changes in prey densities, rather than their traits, affect community dynamics. In a recent meta-analysis, Preisser *et al.* show that trait effects are as large, if not larger than density effects. This strongly suggests that trait effects should be integrated into empirical and theoretical studies.

The significance of fear

Historically, ecologists have characterized species interactions by the density effects that species have on each other. For example, when carnivores consume herbivores, they directly reduce herbivore densities and might indirectly affect plant densities by reducing or shifting herbivory (Box 1). Predators not only eat their prey, but also scare them [1]. By scaring prey and causing them to alter their traits, such as foraging effort or defensive morphologies, predators can have significant impacts on prey and their resources. For example, herbivores hiding from carnivores might feed less on plants, thus decreasing their own growth and reproduction, and increasing plant densities. A recent meta-analysis by Preisser *et al.* of

166 studies from 49 publications is the best evidence yet that trait effects are generally important and could rival and even exceed the importance of density effects [2].

Although the existence of trait effects has been well documented [3,4], their importance and extent are still largely unclear. Human experience suggests that changes caused by the fear of events might have larger effects on our

Box 1. Terminology and primary mechanisms of effects

Preisser *et al.* used the terminology of density- and trait-mediated interactions for both direct and indirect effects and distinguished between the two by noting whether the effects were for two- and three-level food chains, respectively [2]. In other papers, indirect effects have been referred to as density- and trait-mediated indirect interactions [4]. We define the terminology used here as follows:

- **Density effects:** consumptive effects resulting from predators killing prey.

Direct density effects: changes in prey density caused by predation.

Indirect density effects: changes in the resource density of the prey caused by predation reducing prey density.

- **Trait effects:** non-consumptive effects resulting from changes in prey behavior or morphology in response to predation risk.

Direct trait effects: changes in prey density caused by changes in prey behavior or morphology in response to predation risk. It is caused primarily by prey starving, emigrating, or being consumed more often by other predators.

Indirect trait effects: changes in the resource density of the prey resulting from changes in behavior or morphology of prey. It is caused primarily by prey reducing their foraging, switching their diets, or emigrating.

Corresponding author: Luttbeg, B. (bluttbeg@ucdavis.edu).

Available online 26 May 2005