# Disruptive coloration and background pattern matching

Innes C. Cuthill[1], Martin Stevens[1], Jenna Sheppard[1], Tracey Maddocks[1], C. Alejandro Párraga[2] & Tom S. Troscianko[2]

[1]School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK

[2]Department of Experimental Psychology, University of Bristol, Woodland Road, Bristol BS8 1TN, UK

Effective camouflage renders a target indistinguishable from irrelevant background objects. Two interrelated but logically distinct mechanisms for this are background pattern matching (crypsis[1,2]) and disruptive coloration: in the former, the animal's colours are a random sample of the background[1,2]; in the latter, bold contrasting colours on the animal's periphery break up its outline. The latter has long been proposed as an explanation for some apparently conspicuous coloration in animals[3,4], and is standard textbook material. Surprisingly, only one quantitative test of the theory exists, and one experimental test of its effectiveness against non-human predators6. Here we test two key predictions: that patterns on the body's outline should be particularly effective in promoting concealment and that highly contrasting colours should enhance this disruptive effect. Artificial moth-like targets were exposed to bird predation in the field, with the experimental colour patterns on the 'wings' and a dead mealworm as the edible 'body'. Survival analysis supported the predictions, indicating that disruptive coloration is an effective means of camouflage, above and beyond background pattern matching.

The pioneers of modern military camouflage were both artists and keen observers of nature[7]. For example, the work of Thayer, who proposed the theory of countershading[8] and developed Bates's ideas on disruptive coloration in animals[3], was influential in persuading the US government to form a special camouflage unit during the First World War (ref. 7). Thayer's theory of 'ruptive' coloration, that contrasting colours on an object help to break up its outline, is such a central feature of military camouflage — and similar patterns in the animal kingdom seem so obviously designed to fulfil the same role[4] — that it is easy to assume that what deceives humans deceives other animals. Yet it is unwise to extrapolate from human perception to that of other animals[9–11], and there are many other explanations for colour patterns presumed by Thayer and successors to be camouflage[3,4,12,13]. Before accepting that disruptive coloration has a role in anti-predator defence, two conditions must hold: that the distribution of colour patterns matches that predicted by the theory, and that these distributions reduce the detectability of prey to predators. There has only been one test of each condition. In one[5], the spots on a marine isopod were shown to touch the body outline more often than predicted by background matching, which is consistent with the theory of disruptive coloration. In the other[6], there was no effect on survival of experimentally removing the wing-stripes of a nymphalid butterfly that is highly palatable to birds, a finding inconsistent with the theory, although the methods might have unintentionally made the butterflies more similar to a co-occurring unpalatable species[14] or altered their palatability directly. Clearly there is a pressing need for further empirical research before we can accept what has been described[4] as "certainly the most important set of principles relating to concealment".
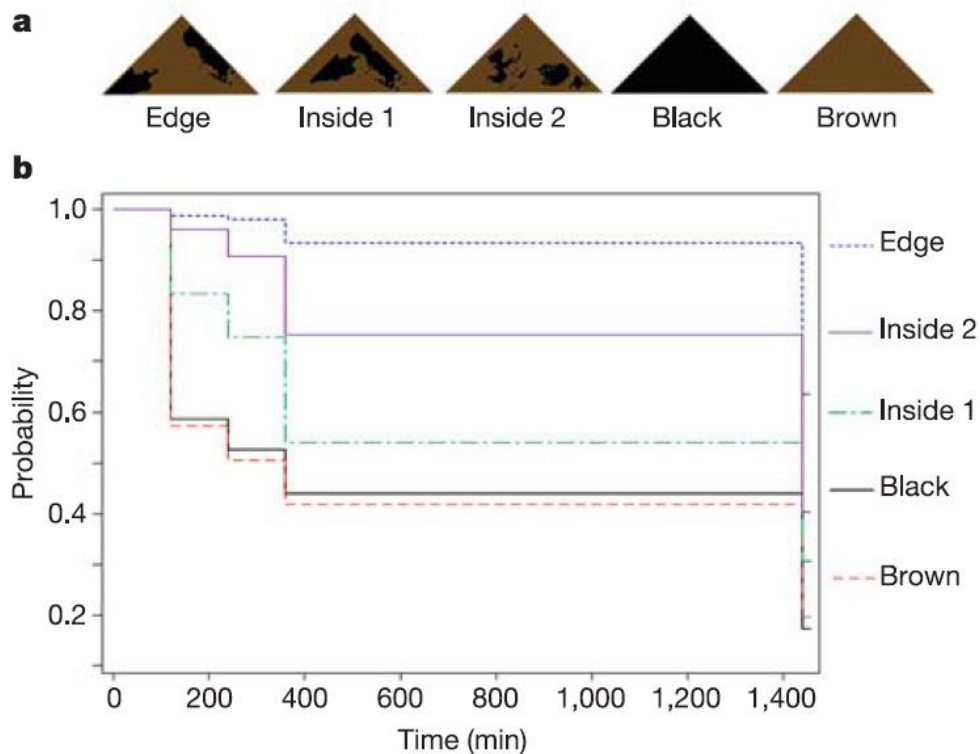
***Figure 1*** *Patterns placed on the body's outline enhance survival. **a**, Examples of 'moth' targets in experiment 1; **b**, survival curves. The differences between treatments were significant (Wald = 138.92, d.f. = 4, P < 0.001) in the order Edge > Inside 2 (Wald = 16.03, d.f. = 1, P < 0.001) > Inside 1 (Wald = 11.01, d.f. = 1, P = 0.001) > Black or Brown (Inside 1 versus Black, Wald = 13.33, d.f. = 1, P < 0.001; Inside 1 versus Brown, Wald = 13.11, d.f. = 1, P < 0.001); there was no difference between the latter monochrome treatments (Wald = 0.00, d.f. = 1, P = 0.992).*

We tested two predictions[5] arising from previous work[3,4]: first, that patterns on the body's edge should be more effective than equivalent patterns placed randomly; second, that highly contrasting colours should be more disruptive than those of low contrast. In each case, provided that the colours and patterns on the prey were equally common in the background, the theory of background pattern matching[1,2,15] would predict no difference in the effectiveness of the camouflage. Our artificial targets (see Methods), with their coloured 'wings' and edible 'bodies', were not designed to mimic any real lepidopteran, and the oak tree trunks on which they were pinned were merely a convenient complexly patterned substrate against which birds might detect prey. Thus, our experiments are best thought of as 'field psychophysics' rather than a study of moth predation risk.

In experiment 1, targets were dark brown with black markings designed, with regard to bird vision, to match the real patterns of dark and light on heavily ridged, mature, oak bark. There were five treatments (Fig. 1): markings overlapping the edges of the 'wings' ('Edge'), the exact same markings displaced inwards so that no edges were overlapped ('Inside 1'), other randomly selected markings placed so as not to overlap edges ('Inside 2'), monochrome brown, and monochrome black. The three bicoloured treatments all possessed life-sized pattern elements randomly sampled from the background, and so should have been equally cryptic in terms of background pattern matching (and better camouflaged than mono- chrome brown or black). Similarly, no difference would be predicted if bicoloured targets gained a crypsis advantage because, when viewed from a distance, predators would not be able to discriminate between the two colours and so would see a spatially averaged dark brown. Only the theory of disruptive

coloration predicted that treatment Edge should survive better than the other bicoloured treatments. This prediction was fulfilled (Fig. 1). Treatment Inside 2 was included because of the possibility that moving the pattern elements present in treatment Edge from the periphery of the 'wings', to form treatment Inside 1, created pattern elements with straight lines that themselves could have enhanced conspicuousness. This indeed seemed to be so, because treatment Inside 2 survived better than Inside 1, which lacked these straight edges to the pattern elements (Fig. 1). The inwards displacement of pattern elements in Inside 1 also tended to enhance the outline of these targets, thus having the opposite effect to disruptive coloration. Nevertheless, all bicoloured treatments survived better than mono- chrome black or brown, indicating that background pattern matching was, as expected, itself effective as camouflage (Fig. 1).
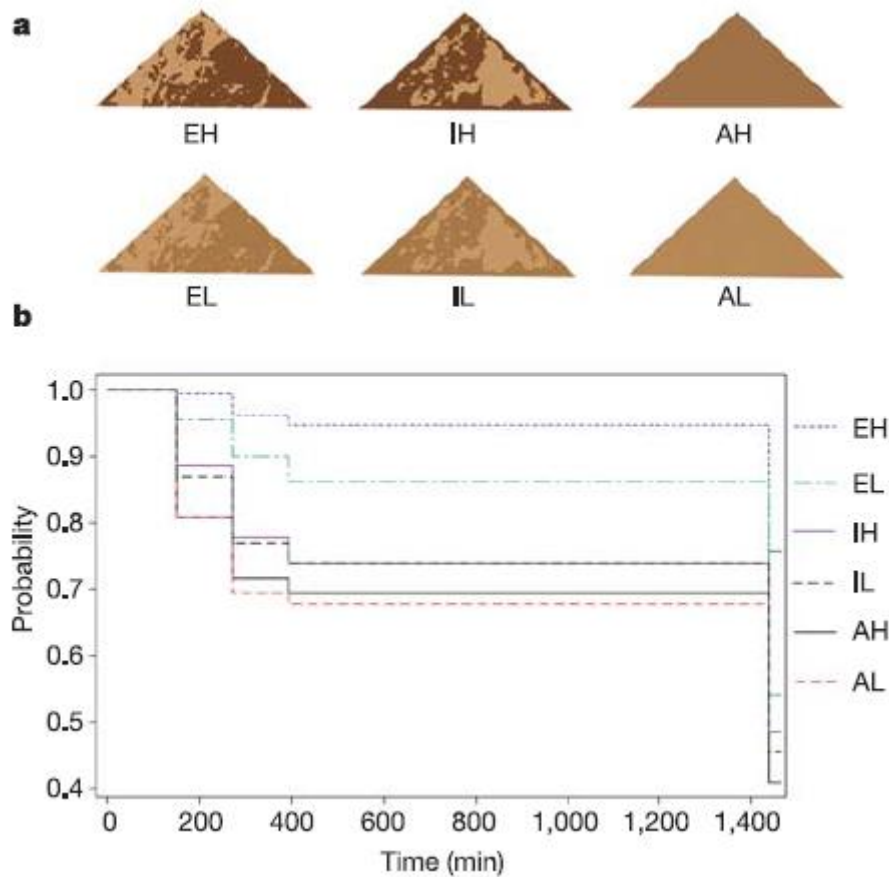


*Figure 2 High-contrast disruptive patterns enhance survival. **a,** Examples of 'moth' targets in experiment 2; **b,** survival curves. The differences between treatments were significant (Wald = 62.26, d.f. = 5, P < 0.001) in the order Edge–high-contrast (EH) > Edge–low-contrast (EL; Wald = 15.31, d.f. = 1, P < 0.001) > Inside–high-contrast (IH) (Wald = 5.20, d.f. = 1, P = 0.023) = Inside–low-contrast (IL) (Wald = 0.00, d.f. = 1, P = 0.952) = Average–low-contrast (AL) (Wald = 1.68, d.f. = 1, P < 0.195) = Average–high-contrast (AH) (Wald = 0.00, d.f. = 1, P = 0.951).*

Experiment 2 had six treatments: the 2 x 2 combination of bicoloured patterns with high or low contrast, placed as in experiment 1's treatment Edge or Inside 2, plus two monochrome treatments that were the average colour of either the high-contrast or the low-contrast colour pairs. As uniquely predicted by the theory of disruptive coloration, the high-contrast-edge treatment survived best (Fig. 2), with high contrast providing minimal benefit in non-disruptive 'Inside' treatments. The results apply to the conditions pertaining in our study (for example winter, and a given habitat type); the extent to which disruptive patterns provide a general advantage over simple crypsis, with different background types (for example

varying spatial and/or chromatic complexity) or different light environments (for example direct or diffuse lighting) therefore awaits further experimentation. Nevertheless, our results provide the strongest support so far for the effectiveness of disruptive patterns against birds, the most commonly invoked visual predators shaping the evolution of protective coloration in insects

## Methods

'Prey' were dead (frozen overnight at -80 °C, then thawed) mealworms (Tenebrio molitor larvae) pinned onto coloured paper triangles 50 mm wide by 25 mm high. These were pinned onto oak trees in the mixed deciduous Leigh Woods National Nature Reserve, North Somerset, UK (28 38.6 0 W, 518 27.8 0 N) and their 'survival' was checked at about 2, 4, 6 and 24 h. Birds took all or most of the mealworm, spiders sucked fluids out, leaving a hollow exoskeleton, and slugs left slime trails; predation in the latter two categories, complete disappearance of a target, or survival to 24 h, were treated as 'censored' values in survival analysis. Both experiments had randomized block designs with ten replicate blocks, run in different areas of the wood on different dates between October 2003 and March 2004. Each block had 75 (experiment 1; 15 per treatment) or 84 (experiment 2; 14 per treatment) targets in a nonlinear transect of about 1.5 km x 20 m (targets on less than 5% of the available trees in each transect). Treatments were randomly allocated to trees, subject to the constraints that no lichen covered the trunk and no young trees with a trunk circumference less than 0.9 m were used. Colour matches of treatments to natural bark were verified by spectrophotometry of stimuli and bark, followed by modelling of predicted photon catches[16] of a typical passerine bird, the blue tit's (Parus caeruleus) single cone photoreceptors[17], with irradiance spectra from overcast skies in the study site. Our acceptance criterion was simply that cone captures for the experimental stimuli fell within the measured range of those for oak bark.

Experiment 1 used black patterns printed onto dark brown card. Patterns were samples of digital photos of the oak trees at 1:1 reproduction, converted using ImageJ[18] to greyscale and thresholded at 50% to binary (black/white) images to provide, when printed onto brown card, bark-like brown/black spatial variation (Fig. 1). Different samples, from different trees, were used for each replicate target.

Experiment 2 used bicoloured targets printed onto waterproof paper (Hewlett Packard Laserjet Tough Paper) with a Hewlett Packard Colour Laserjet 2500 (600 dots per inch) printer, with colour pairs chosen to have either high or low contrast. Colours were chosen from frequency distributions of the eight-bit RGB (red, green, blue) values from digital photographs of the oak trees in the study site, reduced to 16 bins in each colour channel. Photos (about 267 mm x 200 mm; 2,560 pixels x 1,920 pixels) were taken with a Nikon Coolpix 5700 camera, calibrated[19] to linearize the relationship between radiance and the greyscale in each colour channel, and saved as uncompressed TIFF files. Digital photographs lack ultraviolet information that birds can see[20], but lichen-free oak bark reflects negligible ultraviolet[21]. Even a properly calibrated RGB image does not precisely simulate the avian-perceived colour of many natural objects, owing to differences in the spectral sensitivity of bird long-wave, medium-wave and short-wave cones compared with human cones[22]. However, because our treatments varied only in relative colour contrast, any error associated with this method was considered minor, an assumption verified retrospectively by spectrophotometry and colour-space modelling. We chose colour pairs from the eight most frequent RGB triplets in the bark photos as follows: a 'background' colour, then a triplet that was similar to the background (low contrast), and one that differed markedly (high contrast). The major difference between colours was in overall brightness not hue, but we could not systematically vary only one colour dimension

within the available common bark colours. Sample numbers of background and contrasting colours were balanced for which was darker/lighter, and so there were no significant differences between bicoloured treatments in the brightest or darkest colour or average colour (analyses of variance on RGB sums and all possible ratios; P > 0.9). Monochrome treatments were also created as the means of the respective R, G and B values of the two colours in bicoloured high-contrast and low-contrast treatments. Different colour pairs and patterns, from different trees, were used for each replicate target.

Survival analysis was by Cox regression[23,24] with the factors treatment and block. Cox regression assumes that all survival functions have the same shape; this proportional hazards assumption was checked by plotting partial residuals against ranked survival times24. There were significant block effects in both experiments (in experiment 1, Wald = 121.78, d.f. = 9, P < 0.001; in experiment 2, Wald = 271.50, d.f. = 9, P < 0.001), reflecting differences in average predation rates in different parts of the woods on different dates, but this was not relevant to our hypotheses.

# References

1. Endler, J. A. Progressive backcground in moths, and a quantitative measure of crypsis. Biol. J. Linn. Soc.22, 187–231 (1984).

2. Endler, J. A. An overview of the relationships between mimicry and crypsis. Biol. J. Linn. Soc. 16, 25–31 (1981).

3. Thayer, G. H. Concealing Coloration in the Animal Kingdom; An Exposition of the Laws of Disguise through Color and Pattern; Being a Summary of Abbott H. Thayer's Discoveries (Macmillan, New York, 1909).

4. Cott, H. B. Adaptive Coloration in Animals (Methuen, London, 1940).

5. Merilaita, S. Crypsis through disruptive coloration in an isopod. Proc. R. Soc. Lond. B 265, 1059–1064 (1998).

6. Silberglied, R. E., Aiello, A. & Windsor, D. M. Disruptive coloration in butterflies - lack of support in Anartia fatima. Science 209, 617–619 (1980).

7. Behrens, R. R. False Colors: Art, Design and Modern Camouflage (Bobolink, Dysart, Iowa, 2002).

8. Thayer, A. H. The law which underlies protective coloration. Auk 13, 124–129 (1896).

9. Endler, J. A. On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. 41, 315–352 (1990).

10. Endler, J. A. A predator's view of animal color patterns. Evol. Biol. 11, 319–364 (1978).

11. Bennett, A. T. D., Cuthill, I. C. & Norris, K. J. Sexual selection and the mismeasure of color. Am. Nat. 144, 848–860 (1994).

12. Kiltie, R. A. Countershading: universally deceptive or deceptively universal? Trends Ecol. Evol. 3, 21–23 (1988).

13. Ruxton, G. D., Speed, M. P. & Kelly, D. J. What, if anything, is the adaptive function of

countershading? Anim. Behav. 68, 445–451 (2004).

14. Waldbauer, G. P. & Sternburg, J. G. A pitfall in using painted insects in studies of protective coloration. Evolution 37, 1085–1086 (1983).

15. Merilaita, S., Tuomi, J. & Jormalainen, V. Optimization of cryptic coloration in heterogeneous habitats. Biol. J. Linn. Soc. 67, 151–161 (1999).

16. Maddocks, S. A., Church, S. C. & Cuthill, I. C. The effects of the light environment on prey choice by zebra finches. J. Exp. Biol. 204, 2509–2515 (2001).

17. Hart, N. S., Partridge, J. C., Cuthill, I. C. & Bennett, A. T. D. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine: the blue tit (Parus caeruleus L.) and the blackbird (Turdus merula L.). J. Comp. Physiol. [A] 186, 375–387 (2000).

18. Rasband, W. ImageJ v. 1.30 (http://rsb.info.nih.gov/ij/docs/, National Institutes of Health, USA, 2003).

19. Parraga, C. A., Troscianko, T. & Tolhurst, D. J. Spatiochromatic properties of natural images and human vision. Curr. Biol. 12, 483–487 (2002).

20. Cuthill, I. C. et al. Ultraviolet vision in birds. Adv. Stud. Behav. 29, 159–214 (2000).

21. Majerus, M. E. N., Brunton, C. F. A. & Stalker, J. A bird's eye view of the peppered moth. J. Evol. Biol. 13, 155–159 (2000).

22. Cuthill, I. C. et al. Avian colour vision and avian video playback experiments. Acta Ethol. 3, 29–37 (2000).

23. Cox, D. R. Regression models and life-tables. J. R. Stat. Soc. B 34, 187–220 (1972).

24. SPSS for Windows Release 9.0 (SPSS Inc., Chicago, 2003).

## Acknowledgements

## Authors' contributions

I.C.C. designed the experiments and stimuli; M.S., J.S., T.M. and I.C.C. performed the experiments; A.P. wrote the programs for colour analysis and camera calibration; T.S.T. advised on design and colour modelling.

## Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to I.C. (i.cuthill@bristol.ac.uk).