Coincident disruptive coloration

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Even if an animal matches its surroundings perfectly in colour and texture, any mismatch between the spatial phase of its pattern and that of the background, or shadow created by its three-dimensional relief, is potentially revealing. Nevertheless, for camouflage to be fully broken, the shape must be recognizable. Disruptive coloration acts against object recognition by the use of high-contrast internal colour boundaries to break up shape and form. As well as the general outline, characteristic features such as eyes and limbs must also be concealed; this can be achieved by having the colour patterns on different, but adjacent, body parts aligned to match each other (i.e. in phase). Such ‘coincident disruptive coloration’ ensures that there is no phase disjunction where body parts meet, and causes different sections of the body to blend perceptually. We tested this theory using field experiments with predation by wild birds on artificial moth-like targets, whose wings and (edible pastry) bodies had colour patterns that were variously coincident or not. We also carried out an experiment with humans searching for analogous targets on a computer screen. Both experiments show that coincident disruptive coloration is an effective mechanism for concealing an otherwise revealing body form.

Keywords: camouflage; disruptive coloration; crypsis; animal coloration; defensive coloration

1. INTRODUCTION

Most recent tests of the theory of disruptive coloration have focused on the disguise of the body’s outline (e.g. Merilaita 1998; Cuthill *et al.* 2005; Schaefer & Stobbe 2006; Stevens *et al.* 2006b; Fraser *et al.* 2007). When placed at the body’s edge, the high-contrast colour boundaries that are characteristic of disruptive patterning create false contours of higher stimulus intensity than those of the real outline (Stevens & Cuthill 2006; Stevens *et al.* 2006a). In this way, the probability of object recognition through boundary shape is diminished. However, the pioneers of the theory of disruptive coloration Abbott Thayer (1909) and Hugh Cott (1940) also emphasized the importance of concealing other characteristic, and thus potentially revealing, body parts, such as eyes and limbs. Cott (1940, ch. 5) devoted a whole chapter of his influential textbook to this topic, arguing that the successful disguise of such features could be achieved through what he termed ‘coincident disruptive coloration’.

Our study attempts to test the effectiveness of coincident disruptive coloration against avian predators, but first it is important to isolate the mechanism(s) involved. A large part of Cott’s treatment of the topic concerns the disguise of eyes, features that are likely to be difficult to conceal because perfect circles are rare in natural backgrounds. For those species with coloured irises and circular pupils, the resulting concentric circles are likely to be particularly obvious (Cott 1940, p. 82). These features that make eyes intrinsically conspicuous,

and the fact they predict the presence of another animal (e.g. predator or prey), may make them particularly salient features in visual search (cf. the use of ‘eyespot’ in predator deterrence, Stevens 2005; Stevens *et al.* 2007). Cott (1940) therefore argued that the dark eye stripes seen in many taxa act to disguise the outline of the eye. However, in the context of modern accounts of disruptive coloration that emphasize the differences between disruptive coloration and background matching (e.g. Merilaita 1998; Cuthill *et al.* 2005; Stevens 2007), we feel that not all eye stripes fulfil the criteria of Cott’s principle of coincident disruptive coloration. For example, in the plains viscacha (*Lagostomus maximus*) in figure 1a (from Cott 1940, p. 89), the dark eye stripe that surrounds the whole eye creates a matching surround with which the dark eye blends. Here the mechanism is one of reduced conspicuousness of the eye (relative to the head) rather than a disruption of eye shape. This is a principle similar to concealment of a whole animal through background matching, rather than an interference with the correct identification of shape which is characteristic of disruptive coloration (Stevens 2007). Some eye stripes, however, do fulfil Cott’s criteria. For example, if a narrow dark eye stripe bisects the line of the eye (e.g. figure 1b; *Rana sphenoccephala* from Cott 1940, p. 84), and the eye itself has some colours that match the stripe and others that match other colours on the head, then the coincidence of two-tone coloration between eye and head-plus-stripe genuinely disrupts the circular form of the eye. The clearest examples of Cott’s proposed mechanism are seen in his illustrations of frogs (figure 1c and Cott 1940, pp. 69–71), where the (apparently disruptive) patterns on the legs coincide perfectly with patterns on the body when the animal is at rest with its limbs tucked in. In this way, parts of each limb blend with different parts of the animal’s trunk, such that

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Figure 1. Drawings adapted from the artwork by Hugh Cott, illustrating the use of eye stripes to conceal the eyes of (a) a plains viscacha (vizcacha in Cott 1940; *Lagostomus maximus*) and (b) the frog *Rana sphenoccephala*. (c) Coincident colours on the leg and body of the frog *Rana temporaria*, which create false contours running across the two body parts. Modified from Cott (1940, figs. 37, 31 and 21, respectively), by permission of Oxford University Press.

the highest contrast edges are neither at the outline of the limb nor the trunk; the distinctive shapes of both limbs and body are disguised. Because both differential blending and high contrast are involved, and the result is disguise of shape rather than minimizing pattern conspicuousness *per se*, we feel that this example better fits with the term coincident disruptive coloration than some examples of concealment of eyes using eye stripes. (As stated earlier, Cott does provide examples of multi-coloured eyes and eye stripes which do employ disruptive coloration through differential blending, but the point here is simply to emphasize that multiple mechanisms may be at work; so it is our task to isolate and test the effectiveness of each.)

Our test of Cott's principle uses artificial moth-like prey placed on trees (Cuthill *et al.* 2005). Two features that make these potentially detectable to a predator are the triangular outline of the 'wings' and the cylindrical (edible) 'body'. The rationale of our experiment is therefore to create two-tone disruptive patterns on the wings and/or the body that are either coincident with each other, or not. We also employ treatments where the body matches the underlying wings, or not, without having coincident patterns. In this way our aim is to separate the potentially separate benefits of disguising a body part through colouring it to match the rest of the body against which it is viewed (a simple colour-matching benefit, as argued above for the use of monochrome eye stripes to conceal monochrome eyes), from true coincident disruptive coloration, where the benefit lies in breaking up the shape of the body part. We replicate the experiment in the field with bird predators, and in the laboratory with human subjects searching for targets on computer screens. The latter serves two purposes: in the human experiment the task is unambiguously detection, whereas in the field we cannot distinguish a failure to detect the prey from a

rejection of the prey due to the unknown preferences of individual birds as a result of their uncontrolled prior experience. Next, there is the comparative interest in determining whether the same camouflage principles fool predators with different visual systems.

2. MATERIAL AND METHODS

(a) *Experiment 1*

Experiment 1 was conducted in Leigh Woods National Nature Reserve, North Somerset, UK (2°38.6' W, 51°27.8' N) in July and August 2007. The artificial prey were notionally moth like, without any attempt to mimic a particular species. They consisted of triangular wings 50 mm wide by 25 mm high made from waterproof HP Laserjet Tough Paper (Hewlett-Packard, Palo Alto, CA, USA) to which we pinned, on the midline, *ca* 5 mm diameter by 20 mm long cylindrical 'bodies' made from pastry. The pastry was prepared the evening before and, to facilitate handling, left overnight in a freezer at -10°C to harden. All prey had two-tone disruptive patterns on the wings, comprising a darker and a lighter tone, printed at 300 dpi with an HP Colour Laserjet 2500 printer (the electronic supplementary material explains how the patterns were created). Different samples, from different locations on 100 different trees, were used for each replicate target. All image manipulations and colour space calculations (see below) were carried out using MATLAB R2006 (The Mathworks Inc.) incorporating the Image Processing Toolbox and our own programs.

We used two colour variants, designed to match oak bark for experimental blocks carried out under different weather conditions: light brown paired with very dark brown to match the bark ridges and shadowed troughs of oak bark under dry conditions, and mid-brown paired with very dark brown for use in wet conditions, when rain had darkened the bark. The pastry comprised, for any one batch, 30 g of lard and 90 g of plain flour, to which was added, for the very dark brown, 1.5 ml red, 6 ml yellow, 4.5 ml blue and 1.5 black SuperCook food colouring; for the mid-brown, 0.5 ml red, 2 ml yellow, 1.5 ml blue and 10 ml water; and for the light brown, 0.25 ml yellow, 0.25 ml blue, 0.25 black and 15 ml water. The match of wings and pastry colours to each other, and to oak bark, was assessed, as described previously (Cuthill *et al.* 2005; Stevens *et al.* 2006b), using spectrophotometry combined with calculation of the photon catches of the retinal photoreceptors of a typical woodland passerine bird, the blue tit (*Cyanistes caeruleus*), using irradiance spectra collected at our field site (see electronic supplementary material for further details).

There were 10 treatments (figure 2); all had two-tone wings, but the wings differed according to whether the midline (where the body was pinned) was monochrome (dark or light) or was two-tone, with the upper half dark and the lower half light, or vice versa. Pastry bodies were all light, all dark or two-tone. By placing a two-tone body on wings with a two-tone central section, such that the dark portion of the body was coincident with the dark of the wings, and the light portion of the body was coincident with the light of the wings, a two-tone coincident disruptive target was created (TTC). By rotating the body 180 degrees such that the light portion of the body was backed by a dark section of wing coloration, and the dark part of the body on a light section, a target with identical colours on wings and body, but non-coincident in coloration, was formed (two-tone-on-two-tone, non-coincident; TTN). The prediction from Cott's theory is that the coincidence of body and wing colours will conceal the body through differential blending, and so treatment TTC will have a

Figure 2. (a–j) Examples of the targets used in experiment 3 (human visual search) and schematically, with central rectangles replaced by pastry bodies, experiment 1 (avian field experiment): (a) TTC (two-tone body on two-tone wings, coincident), (b) DD (dark body on dark wings), (c) LL (light body on light wings), (d) TD (two-tone body on dark wings), (e) TL (two-tone body on light wings), (f) DT (dark body on two-tone wings), (g) LT (light body on two-tone wings), (h) LD (light body on dark wings), (i) DL (dark body on light wings), (j) TTN (two-tone body on two-tone wings, non-coincident). The treatments without central bodies/rectangles, ZD, ZL and ZT, are not shown. The columns (a–j) are ordered according to predicted decreasing conspicuousness through background matching alone; an additional coincident disruptive effect would predict that TTC should be the least conspicuous of all. The inset photograph, bottom right, shows a two-tone target (dry weather variant) in experiment 2.

survival advantage over TTN. Any survival advantage of treatment TTC over TTN may, however, lie in simple matching of the wing colour (because the wing forms the ‘background’ against which the body is viewed; see §1). Therefore a crucial comparison is between this two-tone coincidentally coloured treatment and treatments where the body matches the wings to a similar degree, but there is no disruption of body shape and no differential blending of different parts of the pastry body with different portions of the wings. These are treatments dark on dark (DD), where a dark body is placed on wings with a dark central region, and light on light (LL), where a light body is placed on wings with a light central region. Figure 2 illustrates our predictions for survival, from the highest on the left to the lowest on the right. If a simple colour match between body and (coincident) wing is all that matters, then all three treatments in the left-hand column should survive best. If disruption of body shape through differential blending of two tones confers an additional benefit, then TTC should survive better than DD and LL (below it in figure 2). These three treatments should survive better than treatments in the figure 2d–g, where the body only partially matched the central region of the wings (two-tone body on light, TL, or dark, TD, wings; dark or light body on two-tone wings: DT and LT, respectively). The lowest survival should be observed in the treatments on the right-hand side of figure 2, where the body did not match the colour of the central portion of the wings (dark on light, DL, or light on dark, LD, or non-coincident two-tone-on-two-tone TTN).

The experiment was run in 10 blocks, 5 of the ‘dry’ colour scheme and 5 of the ‘wet’; these were selected according to the weather at the time, and were haphazardly interspersed and uncorrelated with date. Each block had 100 targets

(10 replicates of each treatment). A single block comprised 100 mature oak trees along a nonlinear transect of 1–2 km in length and *ca* 20 m in width, with less than 5 per cent of the trees along a transect used in each replicate. The low density of targets and the fact that separate blocks were run in different areas of Leigh Woods, on different days, reduced the chances of multiple prey encounters by an individual predator. Similar experiments have been run in these woods before, but the previous experiment, with similarly low densities and sites used only once, had been run in winter and finished 7 months earlier; the target type also differed (different patterns and dead mealworms as the edible component). Although the experiment was conducted by the authors (who were clearly not blind to treatment), unconscious bias was minimized by picking the spot to which a target would be affixed first, then randomly and blindly selecting a target from a thoroughly mixed bag and affixing it to this pre-chosen spot. Selected areas of bark were lichen free, but otherwise of no particular pattern. Targets were pinned at head height (175–190 cm) and facing away from footpaths and tracks, to minimize the possibility of interference by members of the public. The targets were always pinned with the body/midline approximately vertical (‘head up’). After 2, 6, 24 and 48 hours the targets were checked to see whether the edible body had been wholly or partially eaten, and such targets were removed and recorded as predated. Any targets attacked by non-avian predators (principally ants and spiders, plus a few slugs) were removed and scored as censored, as were targets still present at the 48 hours check. Data were analysed using Cox regression, a semi-parametric form of survival analysis (Cox 1972; Klein & Moeschberger 2003) with subsequent pairwise tests controlling for multiple testing using the Dunn-Sidak method (Zar 1999).

(b) Experiment 2

Differences in survival of targets with two-tone bodies compared with monochrome could, in part, be due to differences in acceptability of the prey rather than camouflage. The two-tone pastry did not look warningly coloured to us, but it is conceivable that a brown and close-to-black target is perceived as similar to a typical yellow and black warning pattern. To test this possibility directly, we conducted a field experiment in which the different pastry bodies used in experiment 1 (the light colours of the dry and wet variants, the dark brown colour, and the dry and wet variants of the two-tone treatment) were attached to highly conspicuous wings (figure 2, bottom right). The latter were grey, with a luminance two-standard deviations higher than the mean luminance of oak bark (identical to the non-background-matching treatment of Stevens *et al.* 2006b). In this way, all targets were highly conspicuous to the birds, so predation should reflect acceptability as prey rather than detection.

Fifteen replicates of these five treatments were presented in a random order, in each of five blocks, giving a total sample size of 75 in each treatment. The protocol was similar to experiment 1, but checks were carried out every 1 hour and the trial terminated after 6 hours, because the increased conspicuousness of targets was expected to accelerate predation rate. The entire experiment was replicated twice: in Leigh Woods National Nature Reserve, in areas of wood used in experiment 1, and in Ashton Court Estate, North Somerset (2°38.5′ W, 51°27.1′ N), where no experiments with any type of artificial prey have been conducted by our group, or to the best of our knowledge by anyone else, before. The reason for running two replicates was to test the acceptability of the coloured pastry to the same population

of birds as used in the first experiment (although not necessarily the same individuals), and also in an area where the birds were naive to these prey. The experiment took place in September 2007.

(c) *Experiment 3*

Experiment 3 was a laboratory-based study, conducted at the Department of Experimental Psychology, University of Bristol, in August 2007. Subjects were 10 male and 10 female human volunteers between the ages of 20 and 48 years, with normal or corrected-to-normal vision and naive to the object of the experiment. Consent, protocols and briefing followed the guidelines of the British Psychological Society.

The subjects were sequentially presented with 90 pictures of oak bark from 90 trees, converted to greyscale, within which a camouflaged target could be present (a design copied directly from Fraser *et al.* 2007). Greyscale images were used to focus the search on pattern and form rather than colour. The viewing distance was 1 m and the pictures were displayed on a 19" Sony Trinitron monitor with 1024 by 768 pixel resolution, refresh rate 80 Hz; the pictures themselves were 400 by 400 pixels, with 50 pixel wide, white bands either side of a section of tree-trunk cropped to 300 by 400 pixels (for examples see the electronic supplementary material). Subjects were told that each picture might or might not contain a single target, but with no clue to the frequency of each, then told to press one computer key if they saw a target, and a different key if they did not. They were told to respond quickly and accurately and that, if they did not respond within 10 s, the computer would advance to the next picture. After being given written instructions and shown example pictures, they were allowed six practice trials before the experiment began. The experiment comprised six blocks of 14 pictures each, between which subjects were allowed to take a break; in practice, they never took this opportunity. The software used to display stimuli and record responses was Display Master using DirectX (DMDX for Windows; free software written by Jonathan Forster, University of Arizona, and downloaded from www.u.arizona.edu); the software was calibrated to the computer-specific frame and refresh rates using TIMEDX, by the same author. The time taken to detect the target, to the nearest 10 ms, and search success was recorded.

Each block contained one example from each of 14 treatments, in an order randomized separately for each block and subject. The 14 treatments included analogues of the 10 treatments in experiment 1 (figure 2), plus 3 treatments where there were wings but no body (dark, light or two-tone along the midline), and one treatment of a tree with no target present. The three treatments with wings but no body were included to assess whether the presence of a body did actually increase conspicuousness, a fundamental assumption behind the research. It was impossible to test this in the field (experiment 1) because the assay of detection was consumption of the body. Wings were 38 pixels wide by 19 pixels high, created in the same fashion as the printed wings for experiment 1 (but at far lower resolution). From a large excess, subsets were chosen, which were dark on the midline, light on the midline, or two-tone. For treatments with a body, a 5 by 12 pixel rectangle was superimposed on the midline. For light bodies, the rectangle was coloured 8 per cent lighter or darker (with probability 0.5) than the light shade used on wings; for dark bodies, the rectangle was coloured 8 per cent lighter or darker (with probability 0.5) than the dark shade used on wings. Two-tone bodies were half dark and half light, with dark and light each independently differing from the dark and light wing components as described. The reason for this

small mismatch between wing and body shades was simply because, without a difference, the body would be undetectable (indeed, undefined). In experiment 1, because the body was a three-dimensional cylinder proud of the laminar wings, even matching wings and body were always discriminable to some degree owing to self-shading (the effect that countershading is thought to conceal; Ruxton *et al.* 2004).

The mean time to detect the target, and the proportion of errors (missed targets or, in the case of trees with no targets, false positives), were calculated for each treatment for each subject. When subjects were timed out (failed to respond within 10 s), these were also treated as errors, on the reasoning that failure to detect the target within the given time can be considered a failure at the search task. If one instead treats time-outs as missing values, the only treatment that is substantially affected is that of the trees without a target present (see §3). Here, errors are false positives, so a failure to detect the target within 10 s does not represent a detection failure. Because time and accuracy are, *prima facie*, equally valid measures of search efficiency, and are potentially traded off against each other, we analysed them as joint dependent variables using MANOVA. Time was log-transformed and the proportion of errors was arc-sine-square-root transformed to satisfy uni- and multivariate normality, and homoscedasticity, assumptions; subject was a random effect and treatment a fixed effect. Linear contrasts were used to test pairwise comparisons (Rosenthal *et al.* 2000); although many of our comparisons were planned, some were *post hoc* investigations; so, to be conservative, we indicate significance after controlling for multiple testing using the Dunn-Sidak method (Zar 1999). We present measures of raw effect size, and standard errors, so that interested readers can gauge candidate effects that do not reach statistical significance by these very conservative criteria (Nakagawa & Cuthill 2007). All statistics were carried out using SPSS v. 14 for Windows (SPSS Inc. 2005).

3. RESULTS

(a) *Experiment 1*

Twenty-six per cent of the data were censored: 20 per cent by virtue of survival to the end of the 48 hours trial, 5 per cent through consumption by ants, spiders or slugs, and 1 per cent through complete disappearance of the target including wings and pin (which we cannot unambiguously assign to predation as opposed to a simple failure by the authors to find the target). Neither the colour variant (paler for dry conditions, darker for wet) nor its interaction with treatment had detectable effects (Wald = 1.265, d.f. = 1, $p = 0.261$ and Wald = 12.059, d.f. = 9, $p = 0.210$, respectively). For simplicity of interpretation and more accurate estimate of the effect sizes, we therefore present results from a model without the colour variant term and, instead, treat block as a 10-level factor rather than a five-level factor nested within colour variant. The results are qualitatively unchanged if the treatment effects are estimated from the full model or, indeed, each colour variant is analysed separately.

There were significant effects of block (Wald = 43.223, d.f. = 9, $p < 0.001$) and treatment (Wald = 97.529, d.f. = 9, $p < 0.001$). The treatment with coincident disruptive coloration (TTC) survived significantly better than all other treatments (figure 3). Importantly, the two-tone coincident treatment, TTC, survived significantly better than the otherwise identical, but non-coincident, two-tone treatment (TTN;

Figure 3. Survival curves for the targets in experiment 1. Curves are the probability of surviving bird predation as a function of time, based on Kaplan–Meier estimates to account for censoring due to non-avian predation and survival to the end of the study period. The two long gaps without mortality correspond to overnight periods when targets were not checked. Treatment codes: TTC (two-tone coincident), DD (dark body on dark wings), LL (light body on light wings), DT (dark body on two-tone wings), LT (light body on two-tone wings), TD (two-tone body on dark wings), TTN (two-tone non-coincident), TL (two-tone body on light wings), LD (light body on dark wings), DL (dark body on light wings).

Wald=40.173, d.f.=1, $p<0.001$), and the two treatments where the body matched the single colour of the middle section of the wings on which they were viewed: DD (Wald=9.418, d.f.=1, $p=0.002$) and LL (Wald=22.714, d.f.=1, $p<0.001$). Considering the latter two treatments, DD survived significantly better than all other treatments except the aforementioned TTC and LL (DD versus LL, Wald=3.802, d.f.=1, $p=0.051$), although the difference from two-tone-on-light (TL) was marginal (Wald=3.903, d.f.=1, $p=0.048$). LL had similar survival to the treatments with two-tone bodies on monochrome wings, TD and TL (Wald=0.516, d.f.=1, $p=0.472$ and Wald=0.002, d.f.=1, $p=0.961$ respectively). However, LL survived significantly better than monochrome bodies on two-tone wings (DT, Wald=4.636, d.f.=1, $p=0.031$, and LT, Wald=12.474, d.f.=1, $p<0.001$), and treatments where the bodies and wings mismatched (DL, Wald=31.885, d.f.=1, $p<0.001$, and LD, 57.683, d.f.=1, $p<0.001$). The same is clearly also true for DD, because it survived slightly better than LL (results not shown). The lowest survival rate was seen in LD, which survived significantly less well than all treatments, even the other mismatching treatment, DL, which was the second poorest survivor (LD versus DL, Wald=4.203, d.f.=1, $p=0.040$). In turn, DL survived significantly less well than the partially matching treatments (DL versus LT, Wald=5.125, d.f.=1, $p=0.024$; comparisons with TD, TL and DT, all $p<0.001$). It is notable that the survival of LD and DL was significantly poorer than the two-tone non-coincident treatment TTN, even though the bodies mismatched the wings in all three treatments. TTN survived similarly to the partially matching treatments DT, LT, TD and TL. In summary, two-tone coincident targets survived best, followed by the wing-matching treatments DD and LL, which in turn tended to survive better than the four partially

matching treatments and the two-tone non-coincident targets; treatments where the body did not match the central colour of the wings survived the poorest. Superimposed upon this, and unexpected, dark bodies seemed to survive better than light bodies, when all other factors were held constant.

(b) Experiment 2

In the experiment run in the same site as experiment 1 (Leigh Woods), 6 per cent of cases were censored (1.5% from slug and ant predation, 4.5% through survival for the 6 hours trial). The low frequency of censored data is probably attributable to the faster predation rate of these conspicuous targets. There was no significant effect of block (Wald=6.996, d.f.=4, $p=0.136$) or treatment (Wald=2.719, d.f.=4, $p=0.606$). In terms of trends, the two-tone body from the 'wet variant' colour scheme survived least well and the light body from the 'dry variant' colour scheme survived best (electronic supplementary material, figure S2a).

In the experiment run at the novel field site, 17 per cent of cases were censored (2% from ant predation, 15% through survival for the 6 hours trial). There was no significant effect of block (Wald=1.505, d.f.=4, $p=0.826$) or treatment (Wald=3.661, d.f.=4, $p=0.454$). In terms of trends, the light body from the wet variant colour scheme survived least well and the two-tone body from the wet variant colour scheme survived best (electronic supplementary material, figure S2b). Therefore there was no obvious consistent pattern across the two replicate experiments, and all pastry body colours appeared equally acceptable as prey when presented in a conspicuous context.

(c) Experiment 3

There was a significant effect of treatment on the joint distribution of log-transformed response time and the arc-sine square-root transformed proportion of errors

Figure 4. Experiment 3. Mean proportion of trials (across 20 subjects) in which subjects failed to find the target or were timed out, plotted against their mean response time. Treatment codes: TTC (two-tone coincident; right triangle), DD (dark body on dark wings; left triangle), LL (light body on light wings; down triangle), DT (dark body on two-tone wings; plus), LT (light body on two-tone wings; cross), TD (two-tone body on dark wings; asterisk), TTN (two-tone non-coincident; open square), TL (two-tone body on light wings; open circle), LD (light body on dark wings; open diamond), DL (dark body on light wings; open triangle), ZL (no body, light wings; filled diamond), ZD (no body, dark wings; filled square), ZT (nobody, two-tone wings; filled triangle) and tree (no target present; filled circle). The arrow shows where the tree-only treatment mean shifts if time-outs are ignored and only false positives are counted; other points are little affected, as most errors were due to incorrect assignment as 'target absent' rather than a failure to make a decision within the 10 s time window.

(Wilks $\lambda=0.125$, $F_{26,492}=34.574$, $p<0.01$; univariate results are presented in electronic supplementary material, table S1). The longest response time was for the pictures of trees without a target; discounting errors through reaching the time-out criterion of 10 s, the error (false positive) rate dropped from 37 per cent to 7 per cent (figure 4). Of the treatments with a target present, the two-tone coincident treatment (TTC) had a significantly higher response time and error rate than the target types where the bodies matched the wing background but were not disruptive, LL (Wilks $\lambda=0.271$, $F_{2,18}=24.236$, $p<0.001$) and DD (Wilks $\lambda=0.260$, $F_{2,18}=25.587$, $p<0.001$). TTC was also significantly harder to locate than the two-tone non-disruptive treatment TTN (Wilks $\lambda=0.105$, $F_{2,18}=76.562$, $p<0.001$). The three treatments where the targets were wings only, with no body, had similar response times and errors (ZD versus ZL, Wilks $\lambda=0.955$, $F_{2,18}=0.421$, $p=0.663$; ZD versus ZT, Wilks $\lambda=0.975$, $F_{2,18}=0.230$, $p=0.797$; ZL versus ZT, Wilks $\lambda=0.993$, $F_{2,18}=0.061$, $p=0.941$). Importantly, the presence of a body did make targets easier to locate compared with otherwise identically patterned targets (ZD versus DD, Wilks $\lambda=0.367$, $F_{2,18}=15.539$, $p<0.001$; ZL versus LL, Wilks $\lambda=0.300$, $F_{2,18}=20.960$, $p<0.001$), except where the target had coincident disruptive coloration (ZT versus TTC, Wilks $\lambda=0.768$, $F_{2,18}=2.726$, $p=0.092$).

The treatments where the body mismatched the wings were the easiest to locate, significantly easier than the treatment with the next lowest response times and error rates, dark on two tone (DL versus DT, Wilks $\lambda=0.339$, $F_{2,18}=17.560$, $p<0.001$; LD versus DT, Wilks $\lambda=0.181$, $F_{2,18}=40.778$, $p<0.001$). LD was in fact easier to locate than DL (Wilks $\lambda=0.357$, $F_{2,18}=16.224$, $p<0.001$), exhibiting fewer detection failures even though the response times were similar (figure 4; electronic supplementary material, table S1). All the targets where the body partially matched the wings (LT, DT, TL, LT) and TTN were intermediate in detectability between the fully matching targets (DD, LL, TTC) and the mismatching targets (LD and DL). For example, the two closest in detectability, DD and TD, still showed a significant difference (Wilks $\lambda=0.551$, $F_{2,18}=7.331$, $p=0.005$). It is also notable that the two-tone non-coincident treatment was less detectable than the other treatments where the body completely mismatched the wings (TTN versus DL, Wilks $\lambda=0.226$, $F_{2,18}=30.756$, $p<0.001$; TTN versus LD, Wilks $\lambda=0.100$, $F_{2,18}=81.409$, $p<0.001$).

4. DISCUSSION

Our results support Cott's principle of coincident disruptive coloration. In both experiment 1, in the field with bird predators, and experiment 3, a human visual search task, the two-tone coincident treatment (TTC) fared best. It was less conspicuous than the other two treatments (DD and LL) where the body matched the underlying wing colour, which indicates a benefit of disruption (involving differential blending) above and beyond a benefit of body concealment through matching the colour of the wing against which it is seen. The lower conspicuousness of TTC compared with the two-tone non-coincident treatment (TTN), the only difference being that the body colours in TTN were out-of-phase with their background, also supports the role of differential blending in effective disruptive coloration.

Results of the human visual search experiment (3) broadly mirrored the bird results from experiment 1. This is significant for three reasons. First, the human results are unambiguously the result of detectability differences, so they reinforce the bird experiment, where detectability is only inferred as the cause of differences in survival rates (although experiment 2 provided independent validation of this assumption). Second, although steps were taken to minimize any unconscious bias through differential target placement in experiment 1, the possibility could still have remained; but this possibility was close to zero in experiment 3 because locations were coordinates randomly selected by computer program. Third, the differences between targets with and without a body present on the wings (ZD being less detectable than DD and ZL less than LL) supported a central assumption behind both experiments 1 and 3. If presence of a body had not made targets more conspicuous, there would be no benefit in having coincident disruptive coloration. Interestingly, the coincident disruptive treatment (TTC) survived as well as similarly patterned targets

without a body (ZT), reinforcing the conclusion that it is a highly effective strategy. In passing, we note that the lack of any differences between ZD, ZL and ZT indicate that the higher survival of TTC is not an artefact of having a horizontal colour boundary, as opposed to a single colour, at the midline. Response time appeared to be the more sensitive indicator of differences in prey detectability, with error rates varying less between treatments. However, given that there is likely to be a speed–accuracy trade-off, and subjects had control over whether they made fast and inaccurate or slow and more accurate decisions, we feel that a joint analysis of times and errors through MANOVA is the most appropriate analysis.

The laboratory and field experiments are complementary, and the similarity of the results should not be taken to mean that (easier-to-run) laboratory experiments on humans can substitute for field experiments on non-humans. Although experiment 3 shows that the patterns significantly affect search efficiency under controlled conditions, experiment 1 provides ecological validity. It shows that these differences matter in the field, with non-human predators searching under natural varying illumination and varied backgrounds. The treatment effects observed in both field and laboratory were additive. Matching of body and wing colours improved concealment, but a coincident disruptive boundary across wing and body was better still. Partial matching of body to wings was a significant improvement over no match. There was no obvious difference in conspicuousness of targets with a two-tone body on monochrome wings, or vice versa. The reduced conspicuousness compared with body–wing mismatching targets (DL and LD) can be attributed to either, or both, of the body partially matching the underlying wing background and disruption (creation of a false bounding contour that encompasses the body and the similarly coloured wing patch to which it is adjacent). TTN survived similarly to the partially matching treatments DT, LT, TD and TL, in both the field, under bird predation, and human visual search. This is not because two-tone bodies are less acceptable as prey, because all pastry body colours appeared equally acceptable as prey when presented in a conspicuous context (experiment 2). This suggests a disruptive benefit through breaking up the body with contrasting colours, but without differential blending (here, of parts of the body with parts of the wing or, more generally, parts of an animal with parts of its background). If the differently coloured sections of the animal do not individually have a long enough (true) bounding contour to be recognized as being part of a salient object, and are coloured sufficiently differently that there is no perceptual grouping by similarity of tone, then recognition of the whole may be impaired. It is likely that this would only be effective if the background is highly heterogeneous (Merilaita 2003).

An unexpected result, because dark and light pastry colours were designed, respectively, to match the dark and light wing colours equally well, was a possible survival advantage of dark bodies over light: DD showed a trend towards better survival than LL ($p=0.051$) and DL survived significantly better than LD. No difference in acceptability was found when presented on conspicuous backgrounds (experiment 2), and there was no

difference in detection times in the human search task (although there were more errors for DL than LD). A candidate difference (among many) between the bird and human experiment is that the targets in the latter were two-dimensional rectangles on computer screens, whereas the pastry bodies had three-dimensional relief. As such, they would have exhibited some degree of self-shading and, dependent upon the amount of direct sunlight, cast shadows on the wings. Self-shading is a potent cue to three-dimensional form (Ruxton *et al.* 2004) and it may be that shading is less detectable on a dark body than a light one. This is pure speculation, but deserves to be investigated further, perhaps within the same framework as research on countershading.

In both the bird and human experiments, the bodies in TTC, DD and LL matched their underlying wings equally, but TTC had the advantage of differential blending between body and wing: one portion of its body matched one part of the wing and another part of the body matched a different portion of the wing. By this mechanism, coupled with the high-contrast colour boundary across the body, a (false) contour that is more salient than the true body outline is created through the body and wing together. We feel that the term ‘coincident disruptive coloration’ applies most strongly to this effect (as with Cott’s frogs; figure 1c). Concealment of conspicuous body parts by means of colour matching with the surrounding or adjacent body (as with some eye stripes; figure 1a but not b), without any disruptive contrasting colours or differential blending, has many more similarities to background matching. The principle is exactly that which distinguishes disruptive coloration from background matching by virtue of the perceptual mechanism being fooled (Stevens *et al.* 2006a; Stevens 2007). Disruptive coloration and background matching are (both) maximally effective when the contrasting patterns on the animal’s body are perfectly in phase with those patterns to which they correspond in the background. By this means, there is minimal discontinuity in the background texture that might reveal the presence of the animal (a background matching benefit), but also differential blending is maximized (maximizing the disruptive effect). However, natural textured backgrounds are frequently complex and heterogeneous. Therefore, for the animal to find a sample of background to which it can perfectly align its own coloration, and achieve the necessary orientation through visual feedback, may be difficult. Even cuttlefish (*Sepia officinalis*), which can change their skin colours to match the substrate, do not consistently achieve perfect phase matching with the background texture (Chiao & Hanlon 2001; Chiao *et al.* 2005; Shohet *et al.* 2006; Kelman *et al.* 2007; Mathger *et al.* 2007). However, these constraints do not exist with disguise of body parts through coincident disruptive coloration, where coincidence can be achieved through physiology (control of colour pattern development) or behaviour. The body posture may predate the particular camouflage pattern and be taxon-typical, with the (developmentally) reliable positions of body parts relative to each other allowing the secondary evolution of colours with phase matching across these body parts. There may be other organisms, however, that have

changed their posture in order to bring the patterns into coincidence; here the behaviour would be an adaptation to the pre-existing (and previously phase mismatched) colours on different body parts. It would be interesting to evaluate the frequency of these different evolutionary pathways to coincident disruptive coloration.

Whether by an adaptation of colour pattern development to posture or an adaptation of posture to colour pattern, an animal can achieve phase matching of colour patterns on neighbouring parts of its own body. This will only be important for species where the body parts in question are regularly adjacent when exposed to predation risk (e.g. by developmental necessity, such as an eye within a head, or when the animal has a typical resting pose). This is a comparative prediction that deserves attention. Finally, we would like to highlight the role of coincident disruptive coloration in Cott's (1940) persuasive arguments for the survival value of coloration, and for adaptation in general, at a time when natural selection was far from universally accepted within evolutionary biology. It is this coincidence of pattern, without any developmental necessity, which made (and, regardless of the present results, continue to make) Cott's drawings (figure 1) the most compelling evidence for natural selection enhancing survival through disruptive camouflage.

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