Can't tell the caterpillars from the trees: countershading enhances survival in a woodland

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Perception of the body's outline and three-dimensional shape arises from visual cues such as shading, contour, perspective and texture. When a uniformly coloured prey animal is illuminated from above by sunlight, a shadow may be cast on the body, generating a brightness contrast between the dorsal and ventral surfaces. For animals such as caterpillars, which live among flat leaves, a difference in reflectance over the body surface may degrade the degree of background matching and provide cues to shape from shading. This may make otherwise cryptic prey more conspicuous to visually hunting predators. Cryptically coloured prey are expected to match their substrate in colour, pattern and texture (though disruptive patterning is an exception), but they may also abolish self-shadowing and therefore either reduce shape cues or maintain their degree of background matching through countershading: a gradation of pigment on the body of an animal so that the surface closest to illumination is darker. In this study, we report the results from a series of field experiments where artificial prey resembling lepidopteran larvae were presented on the upper surfaces of beech tree branches so that they could be viewed by free-living birds. We demonstrate that countershading is superior to uniform coloration in terms of reducing attack by free-living predators. This result persisted even when we fixed prey to the underside of branches, simulating the resting position of many tree-living caterpillars. Our experiments provide the first demonstration, in an ecologically valid visual context, that shadowing on bodies (such as lepidopteran larvae) provides cues that visually hunting predators use to detect potential prey species, and that countershading counterbalances shadowing to enhance cryptic protection.

Keywords: countershading; crypsis; predation; animal coloration; defensive coloration

1. INTRODUCTION

There is a strong evolutionary pressure for many prey animals to blend into their environment ('crypsis'; Endler 1981; Merilaita *et al.* 2001) or conceal their body outline (Merilaita 1998; Cuthill *et al.* 2005) in order to avoid detection by predators. However, simple colour resemblance to the substrate may not be sufficient to prevent a predator from detecting an animal (Edmunds 1974); when an animal is illuminated from above by sunlight, a shadow may be cast on its ventral surface, generating a brightness contrast between the dorsal and ventral halves (Thayer 1896; a self shadow effect: Hailman 1977; Kiltie 1988). That is, a uniformly pigmented organism may not provide a good match to a uniform background if different parts of the organism are differentially illuminated. In addition to a loss of background matching, this contrast in shading may provide cues of three-dimensional shape to visually hunting predators, enabling them to better visually separate the prey from a background of matching colour and texture (Ramachandran 1988a). Hence differential shading may be used as a 'giveaway cue' to foraging predators either through a reduction in the degree of background matching or providing three-dimensional cues,

or both (Thayer 1896, 1909; Cott 1940; Tinbergen 1958; Sheppard 1975; Hailman 1977; Ford 1990).

According to Thayer, countershading (darker pigmentation on those surfaces normally orientated towards illumination) counterbalances conspicuous shadows cast on a prey animal's body (self-shadow concealment, SSC; Kiltie 1988), rendering the animal optically flat and harder to detect. Optical flattening of a caterpillar, for example, could conceal it within a background of flat leaves (background matching of volume and colour), alternatively flat objects may be harder to detect than three-dimensional ones. While this hypothesis might be correct, plausible alternative explanations for the concealing functions of countershading exist; reducing or removing a shadow on the lower portion of the body may maintain a good match in colour and luminance to a uniform background, rather than making an animal appear flat. Lightening of the surface farthest from illumination may function to reduce shadowing on the edge of the body when viewed from above, thereby reducing a predator's ability to detect the body outline of the prey animal (H. M. Rowland & I. C. Cuthill 2007, unpublished data). Thayer's contemporaries, such as Wallace (1889), Beddard (1895, p. 115) and Cott (1940), suggested that in contrast to providing protection by cancelling the effects of ventral shadowing, a lighter underside could render the animals

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inconspicuous when the ventral surface is viewed from below against a bright sky and with the dorsum to the water or ground—background matching, as opposed to SSC.

Countershading is an extremely common pattern of coloration in terrestrial and aquatic groups (De Ruiter 1956; Hamilton & Peterman 1971; Korner 1982; Nagaishi *et al.* 1989; Ferguson & Messenger 1991; Chapman *et al.* 1994; Ferguson *et al.* 1994; Braude *et al.* 2001; Stoner *et al.* 2003; Gregorin *et al.* 2006; Gomez & Théry 2007). As it is generally limited to animals that are thought to be cryptic, this has led to the suggestion that countershading causes animals to be more difficult to detect (Ruxton *et al.* 2004b). However, it has also been argued that countershading may result purely from non-predatory selection pressures acting differently on dorsal and ventral surfaces, such as abrasion or the need to protect against the damaging properties of UV light (Hamilton 1973; Kiltie 1988).

Published evidence for the protective effects of countershading is growing (Turner 1961; Edmunds & Dewhirst 1994; Speed *et al.* 2005; Rowland *et al.* 2007). Rowland *et al.* (2007) tested the hypothesis that countershading enhances crypsis in two experiments with artificial prey presented to free living birds. In the first experiment, the authors presented artificial prey to a range of bird species on lawns. In the second experiment, prey were presented on colour-matching green boards to individual blackbirds (*Turdus merula*). In both experiments countershaded prey had significantly lower levels of predation than controls. However, a key criticism of the theory of SSC through countershading as a method of protection from predation remains unresolved; diurnal changes in the angle of the sun's light may render SSC ineffective because for a significant proportion of the day illumination does not come directly from overhead (Hailman 1977; Kiltie 1988; Ruxton *et al.* 2004a). In addition, for countershaded prey that live in woodland habitats, shadow concealment may be unimportant because lighting is often diffuse and non-directional (Heran 1976).

Here we address these issues by presenting artificial prey resembling lepidopteran larvae on the upper surfaces of branches of beech trees (*Fagus sylvatica*) where they would be exposed to predation by free-living avian predators (great tits, *Parus major*; blue tits, *Cyanistes caeruleus*; sparrows, *Passer domesticus*; robins, *Erithacus rubecula*) under a range of illuminations, with the sun's elevation and angle varying across the day. This method represents a naturalistic foraging task, incorporating an ecologically relevant range of viewing angles by free-living predators and varying natural lighting conditions.

We evaluated the survival benefits of countershading by testing specific predictions arising from Thayer's hypothesis. When presented on the upper surface of a branch, prey with paler coloration on their undersides should gain enhanced protection from predation compared with (i) uniformly coloured prey that manifest natural shading (which could degrade the degree of background matching and/or provide cues to shape and projection) and (ii) prey that show darker coloration on their undersides (which would have exaggerated shadowing).

Some tree-living prey hang upside-down on branches, and here the prediction from the theory of SSC is that they should be lightened on their dorsal side, such that the orientation of countershaded coloration is reversed, but

the effect on shadow reduction is the same. In fact, prey that rest upside-down underneath branches do often show lighter dorsal surfaces (Tinbergen 1958), for example, in the privet hawk moth; *Sphinx ligustri* (Tinbergen 1957; Sheppard 1975).

The aim of the present study was to determine whether a gradation in shading significantly decreased detectability of prey to avian predators in the field, compared with other prey designed to be cryptic.

2. MATERIAL AND METHODS

(a) Prey and presentation

All three experiments we present here had a randomized block design, with 12 replicate blocks in experiments 1 and 3, and 14 blocks in experiment 2. Each block was run in a different area of the mixed deciduous woodland at Eastham country park, Merseyside, UK (2°57.2' W, 53°19.6' N) between April and August 2006.

Each block had 48 prey (12 of each prey type, see artificial prey) positioned in a nonlinear transect of approximately 500 m. In experiment 1, one each of the four types of artificial prey was attached (using 2.54 cm metal dress-making pins) next to each other on the same branch of the beech tree (*Fagus sylvatica*) at a standard height of between 1.5 and 1.8 m, in a random order, approximately 3–4 cm apart. The design of this first experiment ensured that the free-living predators had the potential to observe a set of four prey types on a single branch (on one tree) under very similar lighting conditions within a set of prey. However, it could be argued that such grouping of prey on a branch presents an unnatural choice for the birds and encounters may not be independent, since all the prey on a given tree may be seen simultaneously. In experiment 2, the prey were randomly allocated to and pinned singly onto the upper surface of a branch in the north, east, south or west zone of the tree, at a standard distance from the trunk (1–1.5 m). All the four prey types were placed in each orientation for an equal number of times.

In experiment 3, the same four artificial prey types were presented on the underside of a single branch on 168 trees, and we again recorded predation over 66 hours. In all cases, branches that were of a smaller diameter than the pastry prey were chosen, so that backscattering of light from the branch would be minimal.

Each prey item was separated from its neighbour by 3–4 cm on the branch. 'Survival' was checked at 6, 18, 24, 30, 42, 48, 54 and 66 hours. Complete disappearance or beak marks in prey were classified as 'prey killed', with the prey surviving to 66 hours classed as 'censored' values in the analysis (Klein & Moeschberger 2003; Cuthill *et al.* 2005).

(b) Artificial prey

Four types of artificial pastry prey (light, dark, countershaded and reverse countershaded) were produced based on the methods employed in previous studies (Edmunds & Dewhirst 1994; Speed *et al.* 2005; Rowland *et al.* 2007). Pastry was made by mixing plain flour and lard in a 3 : 1 ratio. Light pastry was produced by adding 25 ml of green Supercolor food dye and 50 ml of water to 600 g of pastry. Dark pastry was produced by adding 75 ml of the same dye to a second 600 g batch of pastry. We rolled the pastry into 5 mm diameter cylinders, and then cut these cylinders into 15 mm lengths to make individual prey items. Dark and light prey items were made directly from the rolled pastry. To create reverse and

Figure 1. Artificial pastry prey pinned to the upper surface of a beech tree (*F. sylvatica*) branch. From left to right: dark 75 ml prey, countershaded prey (dark dorsal light ventral), light 25 ml prey and reverse-shaded prey (light dorsal, dark ventral). When illuminated from above ventral shadows are cast onto the body of light, dark and reverse-shaded prey, but countershading counterbalances the effects of dorsal illumination and has reduced shadowing.

countershaded prey, we rolled pastry into 2–3 mm diameter cylinders, cut these to 15 mm lengths and then rolled them together to form two-toned prey of the same diameter as the dark and light prey (see figure 1 for photograph of artificial prey).

(c) Assessing colour matching of the prey to branches and leaves

Subjective assessment indicated that the artificial pastry prey designed with a 75 ml solution were darker than those prey designed with a 25 ml solution. However, we needed to confirm this with respect to avian colour perception, since 'colour' is not a property of any object, but rather is a product of the visual and nervous systems of the animal viewing the object (Endler 1990; Guilford & Dawkins 1991). We required a method to quantify colours independently of human perception, or better still, as probably perceived by an avian predator akin to those involved in this study. Colour vision in birds involves the use of four single cone types, one of which is sensitive to ultraviolet light (reviewed by Cuthill *et al.* 2000), and so birds are potentially tetrachromatic (reviewed by Cuthill 2006). In addition to the single cones, birds also possess an additional type of cone, known as 'double cones'. These have a broad spectral sensitivity and are currently thought to be involved in achromatic (luminance) vision (Osorio *et al.* 1999; Jones & Osorio 2004; Osorio & Vorobyev 2005).

We used reflectance spectra of the pastry prey and backgrounds (branches and leaves) to model the colour of the stimuli in tetrahedral colour space, and the brightness of the stimuli in terms of double cone stimulation. To assess the degree of background matching of the pastry prey colour according to avian vision, we analysed pastry and background reflectance spectra using a model of avian visual perception that is based on the spectral sensitivities and the receptor noise of the four cone types that are assumed to function in avian colour discrimination (Vorobyev & Osorio 1998).

Figure 2. The cumulative survival curve of the four prey types in experiment 1. The four lines are dark (black), light (lightest grey), countershaded (dashed line) and reverse-shaded (medium grey) prey types were presented grouped on the upper surface of a branch and the survival over 66 hours was recorded.

Based on the analytical approximation of cone visual pigments and oil droplet spectra, the model calculates cone excitation values for each colour spectrum (Schaefer *et al.* 2007). The chromatic contrasts between pastry and backgrounds were calculated (see Vorobyev *et al.* (1998) for equations) and describe how much the two spectra are separated in receptor space. The units for chromatic contrasts are just noticeable differences (JNDs). One JND is at the threshold of discrimination, while values less than one JND indicate that two colours are indistinguishable, and as values increase above one JND, objects become easier to discriminate. The model is based on the spectral sensitivities of the blue tit (*C. caeruleus*) with relative cone ratios of UVS = 0.3704; SWS = 0.7111; MWS = 0.9926; and LWS = 1.0 and woodland shade irradiance.

(d) Statistical analyses

As the prey were not presented independently on a branch in experiments 1 and 3, the order of disappearance for the four treatments was ranked, and the ranks were analysed with a Friedman's ANOVA with subsequent Bonferroni corrected Wilcoxon signed-ranks tests. As the assumption of independence was probably met in experiment 2, survival analysis was by Friedman's ANOVA with subsequent Bonferroni corrected Wilcoxon signed-ranks tests and also Cox regression (Cox 1972) with the factors prey type and block.

3. RESULTS

(a) Experiment 1

When the prey were pinned next to one another on the upper surfaces of branches, there was a significant effect of prey type on rank disappearance over the 66 hours ($\chi^2_3 = 20.71$, $p < 0.001$). The prediction that countershaded prey would be more difficult to detect and therefore have lower levels of predation than uniformly shaded prey and reverse-shaded prey was supported (figure 2); Bonferroni corrected Wilcoxon tests (three comparisons, test-wise p -value for significance = 0.016) showed that countershaded prey had significantly better survival than dark ($z = -4.306$, $p < 0.001$), light ($z = -3.298$, $p = 0.001$) and reverse-shaded ones

Figure 3. The cumulative survival curve of the four prey types in experiment 2. The four prey lines are dark (black), light (lightest grey), countershaded (dashed line) and reverse-shaded (medium grey) prey types were presented singly on the upper surface of a branch and the survival over 66 hours was recorded.

($z = -3.141$, $p = 0.002$). This finding supports Thayer's prediction that countershaded prey should be inconspicuous when assuming an orientation in which their pigmentation can offset the effect of natural shadows.

(b) Experiment 2

Systematic randomization of the four prey on separate branches facing either north, south, east or west was used to avoid lack of independence between the prey between the trees. With this arrangement of prey, survival data were analysed with Cox regression (Cox 1972; Cuthill *et al.* 2005). The effect of prey type on survival was significant (Wald = 11.58, d.f. = 3, $p = 0.009$) with countershaded prey surviving significantly longer than dark prey (black line; Wald = 10.41, d.f. = 1, $p = 0.001$), light prey (lightest grey line; Wald = 4.82, d.f. = 1, $p = 0.028$) and reverse-shaded prey (medium grey line; Wald = 7.75, d.f. = 1, $p = 0.005$; figure 3). In order to control for independence within this design, we also analysed the effect of prey type on rank disappearance over the 66 hours and found that there was still a significant difference in disappearance time ($\chi^2_3 = 14.45$, $p = 0.002$). The prediction that countershaded prey would be more difficult to detect and therefore have lower levels of predation than uniformly shaded prey and reverse-shaded prey was supported by Bonferroni corrected Wilcoxon tests (three comparisons, test-wise p -value for significance = 0.016). Countershaded prey had significantly better survival than dark ($z = -3.404$, $p = 0.001$), light ($z = -2.911$, $p = 0.004$) and reverse-shaded prey ($z = -2.424$, $p = 0.015$).

(c) Experiment 3

The order of disappearance for the four treatments was ranked, and the ranked data were analysed with a Friedman's ANOVA. We found that there was a significant effect of prey type on rank disappearance over the 66 hours ($\chi^2_3 = 16.855$, $p = 0.001$). Wilcoxon tests with a Bonferroni correction (criterion $p = 0.016$) showed that reverse-shaded prey had significantly better survival than the dark ($z = -3.784$, $p < 0.0001$), countershaded ($z = -2.687$, $p = 0.004$) and light prey ($z = -2.447$,

Figure 4. The cumulative survival curve of the four prey types in experiment 3. The lines are dark (black), light (lightest grey), countershaded (dashed line) and reverse-shaded (medium grey) prey types were presented grouped on the lower surface of a branch and the survival over 66 hours was recorded.

$p = 0.01$). Hence, reverse-shaded prey had better survival than the dark, light and countershaded prey which had pronounced shadowing (figure 4).

(d) Colour analyses

Results from the colour space and achromatic modelling indicated that the main differences between the prey types and the backgrounds were in terms of the chromatic (colour) signal (figure 5 and table 1). When we calculated the chromatic contrasts, both the light '25 ml' prey and dark '75 ml' prey matched the branch more closely than the leaves, though neither matched well as indicated by the large values for the chromatic contrasts, and so would be detectable in terms of colour. As expected, the light 25 ml prey type had a larger achromatic signal than the dark 75 ml prey type (larger double cone photon catches). The achromatic contrasts showed that there was a close match in luminance between the dark 75 ml prey and the branch. By contrast, the match between the light 25 ml prey type was much higher with respect to the leaves, in fact for luminance, the light 25 ml prey was indistinguishable from the leaves.

4. DISCUSSION

The higher survival of the countershaded prey when presented on the upper surface of tree branches, compared with the uniformly coloured prey, confirms the findings of Rowland *et al.* (2007) that countershading provides a significant survival advantage against avian predators. When prey were presented on the underside of a branch, a reversal of the orientation of countershaded coloration (so that the surface closest to illumination was dark) also enhanced protection from predation. This is consistent with the observation that animals with lighter dorsal coloration are observed to orient up-side down (Tinbergen 1958; Sheppard 1975; Nagaishi *et al.* 1989; Chapman *et al.* 1994). These findings across all the three experiments, when the prey were grouped, and when presented singly on branches, provide definitive evidence that a reduction in pigmentation on the side of an animal farthest from the light source provides a camouflage

Figure 5. Tetrahedral colour space showing the location of the different prey and background types. Each point corresponds to the mean level of cone stimulation (mean for all spectra).

benefit. A variety of mechanisms may account for this finding; predators may be better able to visually distinguish a solid object (such as a caterpillar) from a background that it otherwise matches in colour, luminance or texture, if shadows are manifest on the body, because it may provide three-dimensional shape information (Rittenhouse 1786 cited in Hoffman 1988; Ramachandran 1998b), or a shadow may degrade the degree of background matching (a mismatch between body and background colour/luminance), or make the body outline easier to detect. A decrease in shadowing may reduce visual cues of three-dimensional shape to visually hunting predators, rendering the prey optically flat and harder to detect, either because flat objects are harder to detect within a background of flat objects, or more simply because the prey match the larger background of leaves in terms of volume, colour or luminance. Our results support Thayer's hypothesis that a gradation in shading can enhance survival of prey from predation through obliteration of shadows, whether this is because it renders a countershaded animal optically flat or maintains a good degree of background matching (in this case for luminance), thus making the prey animal difficult to detect, still needs resolving.

A difference between this study and that of Rowland *et al.* (2007) is that the uniformly coloured control prey in the present study did not match the background as closely in terms of the chromatic signal. Both the light and dark pastries were determined to be distinguishable from the leaves and branch backgrounds in the chromatic signal, but matched the branches more closely than leaves. In terms of the achromatic signal, the light prey were indistinguishable from the leaves, and the dark prey more closely matched the branches. While the prey were designed to be cryptic controls, it is clear that they would have been detectable by avian predators in terms of colour disparity between the prey and the background. However, the finding that countershading reduced predation compared to the uniformly pigmented controls shows that a gradation in shading reduced the detectability of the prey, suggesting that the birds were attending to a difference in luminance across the body of the controls (observable in figure 1). The results cannot be explained by the argument that the birds had some specific (and unexpected) aversion

Table 1. Chromatic and achromatic contrasts (JND values) between the mean reflectance of the artificial pastry prey (dark 75 ml, light 25 ml) and backgrounds (leaves or branch) calculated according to the model of avian vision (Vorobyev & Osorio 1998). Italics highlight a JND < 1.

	25 ml versus	75 ml versus	branch versus
<i>colour (chromatic)</i>			
75 ml	4.7025		
branch	7.5284	9.1261	
leaf	16.3999	13.0562	11.9982
<i>luminance (achromatic)</i>			
75 ml	13.9818		
branch	18.5376	5.1454	
leaf	0.0459	14.0256	18.5788

to two-tone green prey, because enhanced survival was only shown in the bi-coloured prey positioned so that the light-coloured area was placed in shadow (a criticism of Edmunds & Dewhurst 1994 study).

A key point to the experiments is that the prey were presented in an ecologically appropriate visual setting for the free-living birds. Cott (1940) highlighted the importance of viewing angle in the interpretation of the protective function of countershading; when viewed from the side Cott (1940) noted that countershaded fish were rendered inconspicuous by counteracting the effects of ventral shadowing. However, when viewed by predators from above, dark dorsal surfaces would blend with the dark colour of the ocean, and when viewed from beneath the light ventral surface would harmonize with the bright sky. This is a distinct mechanism from the shadow obliteration effect discussed in our paper; the fish would benefit from simple background matching, as discussed by Wallace (1889) and Beddard (1895). With our presentation system (Edmunds & Dewhurst 1994; Speed *et al.* 2005; Rowland *et al.* 2007), the prey were probably observed at a range of viewing angles that reduce the chance that the prey were surviving owing to background matching alone by being viewed exclusively from above or beneath, but do not rule out the possibility that countershading improves background matching by reducing shadows, which could otherwise provide give-away cues to the prey's existence. Furthermore, the finding that the

countershaded prey survived significantly longer than dark, light and reverse-shaded prey suggests that the birds were specifically attending to the presence of a shadow in these prey forms to detect an object, and hence paid less attention to the countershaded form.

Furthermore, since the prey were left in position for 66 hours, the suggestion that diurnal variation in the position of the sun may result in countershading failing to compensate for the varied shadows cast by solar illumination (Kiltie 1988) can be refuted. The net effect of countershading was to enhance survival of the prey over the 66 hour presentation period, despite the fact that the lighting regime was rendered relatively diffuse by the woodland setting, which should result in the amount of shadowing being reduced.

This study highlights the importance of the correct attitude of countershaded caterpillars with respect to the direction of illumination. De Ruiter (1956) compared the rate of predation by jays (*Garrulus glandarius*) on various lepidopteran larvae presented in normal and inverted positions and found that countershaded larvae in the 'incorrect' orientation had higher predation than countershaded larvae in the correct orientation. However, to further evaluate the protective role of countershading, we see that an investigation into the proportion of time spent in these various orientations by countershaded caterpillars is still required; whether countershaded prey do in fact consistently orient themselves in a manner that counterbalances the effects of illumination remains unresolved.

As Kiltie (1988) noted, countershading may have plausible alternative explanations other than SSC. Countershading could also result from differential selection pressures on dorsal and ventral surfaces, from the need to protect against the damaging properties of UV light, or abrasion (Ruxton *et al.* 2004a). However, the results presented here strongly suggest that countershading functions as Thayer (1896) and others have proposed, and so may be considerably more important in camouflage than recent critiques might suggest.

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