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The role of body shape and edge characteristics on the concealment afforded by potentially disruptive marking

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Disruptive coloration is a camouflage strategy proposed to function by breaking up an animal's boundary and mask its characteristic shape, thereby impairing its recognition by onlookers. Recent studies on disruptive coloration have consistently shown an association between putative 'disruptive' edge coloration and heightened survivorship, but the underlying mechanism is unclear. If edge markings enhance survivorship through disruption, then the success of this camouflage strategy should depend on the visibility of the animal's boundaries and its shape. Here, we experimentally tested the hypothesis that the disruptive camouflage of a prey improves its survivorship in a manner that is conditional on the visibility of its boundaries and its overall shape. We found that both boundary visibility (solid versus translucent boundary) and boundary shape (straight versus ruffled outlines) affected survivorship of artificial moths in a human computer-foraging task. Furthermore, as expected, the observed survival benefits of edge markings were conditional upon the boundaries' visibility. Surprisingly, however, no such interaction was found between edge markings and body shape on overall survivorship. Therefore, it remains uncertain whether disruptive edge markings affect shape perception per se. Collectively, however, our results add further support to the contention that edge markings provide camouflage by breaking up an animal's boundaries in a manner independent of background matching.

Camouflage reduces the likelihood of an object being visually detected and recognized. These two complementary components of visual search (detection, recognition) are implicated in the evolution of two broad types of camouflage: those that reduce an animal's salience in the environment (i.e. background matching) and those that impair the animal's identification once detected (i.e. masquerade and disruptive coloration). Concealment by background matching is achieved when an individual's coloration resembles the colours and textures of its environment (Cott, 1940; Endler, 1984; Ruxton, Sherratt, & Speed, 2004). Whilst background matching is ubiquitous in nature, it has several disadvantages, notably increased predation risk in heterogeneous habitats (or different visual environments) where a background matching solution performs poorly (Merilaita, Tuomi, & Jormalainen, 1999) and an associated lost opportunity cost of exploiting resources if the animal restricts itself to environments it resembles. Even on backgrounds where high-fidelity colour and texture matching are achieved, discontinuities between an animal's body and its background create conspicuous visual cues. The more a prey's outline is revealed by conspicuous edges, the more likely it will be detected and recognized by its predators. To counter these costs of background matching, disruptive coloration is proposed to impair object recognition by masking edge information (Mathger et al., 2007; Stevens & Cuthill, 2006; Webster, Hassall, Herdman, Godin, & Sherratt, 2013).

When evaluating the evidence for disruptive coloration, it is important to consider the numerous possible confounds and place emphasis on functional predictions. In the pioneering study of Cuthill et al. (2005), artificial moth targets overlaid by mealworm baits were presented in the field and subjected to attack from avian predators. Their results demonstrated a large survival benefit to edge-patterned targets; that is, targets with contrasting colour patches that intersect with their boundaries. Subsequent studies have shown that edge-intersecting colour patches increase prey survivorship (Cuthill et al., 2005; Cuthill, Stevens, Windsor, & Walker, 2006; Fraser, Callahan, Klassen, & Sherratt, 2007; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006; Stevens, Cuthill, Windsor, & Walker, 2006; Stevens, Winney, Cantor, & Graham, 2009). Although these studies demonstrate that targets with edge markings have higher survivorship than those without, it is not entirely clear whether this general finding can be attributed to

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enhanced disruption or, alternatively, to a by-product of background matching. For example, in Cuthill et al.'s (2005) study, targets with the edge markings were the least manipulated of the target types and therefore potentially more representative of their backgrounds. A complementary approach that has helped confirm the importance of disruptive coloration as an independent camouflage mechanism is to show that edge markings are nonrandomly distributed compared to their backgrounds (Merilaita, 1998) and yet still provide concealment (Webster et al., 2013).

Here, we experimentally tested the function of disruptive coloration in a complementary way by asking whether the survivorship value of disruptive markings is conditional upon the visibility of the boundaries they are designed to conceal. Combining object properties (either boundary or shape) and edge markings may either magnify or reduce the advantage of edge disruption in improving concealment. If, for instance, a transparent boundary magnifies the benefit of edge disruption, then this may be because a translucent boundary provides better background matching, which in turn facilitates disruption (Fraser et al., 2007). Alternatively, boundary transparency might reduce the relative benefit of edge disruption, because the translucent boundary already renders a high degree of concealment and the addition of edge markings only minimally contributes to concealment. Both types of interaction would produce a dependency of edge disruption on outline properties, attributable to the relative degree to which edge markings and body boundary visibility contribute to masking edge detection.

We used artificial moth targets displayed on a computer screen as simulated prey and human subjects as visually hunting vertebrate predators to carry out two human computer-foraging experiments testing for a survival benefit of edge markings on prey while concurrently varying the boundary visibility and shape of the prey targets. Both experiments used a factorial design to vary moth target treatments. If edge markings function to disrupt prey recognition, then such markings would be expected to increase prey survivorship through interactions with the visibility of the boundaries (edges) and the shape of their bodies.

In the first experiment, we tested for an effect of the visibility of edge boundaries on a prey's body on its survivorship and investigated how putatively disruptive patterns mediate this relationship. We operationalized boundary visibility by the degree of opacity at the target's boundary. Moth targets with ‘high’ boundary visibility had unmanipulated boundaries, and moth targets with ‘low’ boundary visibility had translucent boundaries. The transparency of an animal facilitates its background matching by allowing light to pass through its body (Ruxton et al., 2004). The more light that an organism reflects and scatters, the less translucent it is, which in turn impedes concealment (Johnsen, 2001; Mcfall-Ngai, 1990); furthermore, the less contrast at a boundary, the more difficult it is to segment an object from its background (Singh & Anderson, 2002a, 2002b). If edge markings and boundary visibility interact to enhance prey survivorship, then this would suggest that edge coloration is disruptive because of its dependency on boundary visibility.

An animal's shape also plays an important and somewhat overlooked role in predation, not only in prey escape behaviour (Dayton, Saenz, Baum, Langerhans, & DeWitt, 2005; Langerhans, 2009; Lundvall, Svanback, Persson, & Bystrom, 1999; Van Buskirk & McCollum, 2000) but also concealment. Considerable evidence has emerged confirming the importance of shape for object recognition (Delvenne & Dent, 2008; Liebe, Fischer, Logothetis, & Rainer, 2009; Soto & Wasserman, 2012) and, specifically, its role in identifying animals (Elder & Velisavljevic, 2009; Lloyd-Jones, Gehrke, & Lauder, 2010; Lloyd-Jones & Luckhurst, 2002). The fields of vision science and psychology suggest that highly curvilinear outlines reduce the salience of edge information and subsequently impair shape processing (Panis & Wagemans, 2009). These relationships are a reflection of the underlying stages of shape perception, namely, (1) edge detection, (2) group the detected edges into a boundary (or contour) and (3) fill in the missing pieces to estimate objects' shape (Palmer, 1999). Appreciating the mechanisms of shape perception leads us to make predictions about the detectability of animal shapes.

Whilst the shape of moth wings affects their aerodynamics (Betts & Wootton, 1988), it is possible that shape might also affect their concealment. In a second experiment, we therefore tested the hypothesis that disruptive coloration distorts shape perception (Cott, 1940; Thayer, 1909). We predicted that computerized moth-like triangular images with ruffled sides, simulating moth species with ruffled-edged wings (Fig. 1), should survive longer than those with straight sides when being visually ‘hunted’ by human predators.

If the survival value of edge markings covaries with shape, then this would suggest that edge markings mask the detection/recognition of shapes (through effecting a common visual mechanism related to shape perception). If edge markings function to disrupt shape, then they should render highly detectable/recognizable shapes less conspicuous by degrading vital edge information used to perceive shapes. Correspondingly, there should be less benefit of disruption for shapes that are already difficult to detect/recognize. This conditional concealment can be detected by testing for a statistical interaction, where the presence of an interaction between body shape and edge markings on prey survivorship would be evidence for edge markings functioning disruptively. If the presence of edge markings increases prey survival independent of body shape, then edge markings would likely be improving concealment independent of shape perception, possibly through background matching (and ruling out shape disruption) or by breaking up boundaries irrespective of shape. Alternatively, if the presence of edge markings interacts with body shape in increasing prey survival, then this would suggest a shape-dependent disruptive function of edge markings (see Supplementary Fig. S1).

METHODS

Experimental Protocol

A Microsoft Visual Basic Express® 2008 (Microsoft Corp., Seattle, WA, U.S.A.) program presented cryptic moth targets superimposed on photographs of trees on a computer screen to volunteer human subjects (Webster, Callahan, Godin, & Sherratt, 2009). All participants were visitors to Carleton University's Maxwell MacOdrum Library, where the testing took place. Computer monitors (1900 × 1200 pixels) were rotated to a portrait orientation to display high-resolution grey-scaled tree images (1600 × 800 pixels) with triangular moth targets (60 high × 100 wide pixels) on them. None of the human subjects was red-green colour blind, but presumably they did vary in their spatial acuity (even when wearing lenses), which is not accounted for here. Monitors were positioned 3 m away from subjects, rendering the subtended visual angle of the target 0.35° high by 0.73° wide. Several training screens were presented to individual subjects, pre-exposing them to each treatment. We then orally explained to each subject, using a consistent script, that he/she was required to click on the moth targets as fast as possible using a mouse and, once a target had been successfully clicked on (or when the subject was satisfied that no target was present), the subject could proceed to the next screen by pressing a button in the top left-hand corner of our graphical user interface (GUI). This allowed for a self-determined break period before continuing with their visual search. Either one moth or no moth was presented per tree background during each search task.