Review

Defining disruptive coloration and distinguishing its functions

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Disruptive coloration breaks up the shape and destroys the outline of an object, hindering detection. The principle was first suggested approximately a century ago, but, although research has significantly increased, the field remains conceptually unstructured and no unambiguous definition exists. This has resulted in variable use of the term, making it difficult to formulate testable hypotheses that are comparable between studies, slowing down advancement in this field. Related to this, a range of studies do not effectively distinguish between disruption and other forms of camouflage. Here, we give a formal definition of disruptive coloration, reorganize a range of sub-principles involved in camouflage and argue that five in particular are specifically related to disruption: differential blending; maximum disruptive contrast; disruption of surface through false edges; disruptive marginal patterns; and coincident disruptive coloration. We discuss how disruptive coloration can be optimized, how it can relate to other forms of camouflage markings and where future work is particularly needed.

Keywords: disruptive coloration; camouflage; crypsis; predation; dazzle coloration; background matching

1. INTRODUCTION

Camouflage is one of the most widespread means of reducing the risk of predation in animals (Stevens & Merilaita 2009). Although background matching may provide a powerful method of reducing the probability of detection (e.g. Wallace 1889; Poulton 1890; Beddard 1895), it appears unlikely to maximize concealment in many situations because, as Thayer (1909) proposed, an animal's outline may still give away its telltale shape and reveal its presence. Thayer (1909) argued that, in addition to background matching, camouflage can be achieved through disruptive coloration (originally termed ruptive and secant patterns by Thayer 1909), where patterns break up the animal's appearance and body outline. The idea, first alluded to by Poulton (1890) with respect to contrasting markings on some caterpillars, was formalized by Cott (1940) who presented a series of ideas regarding the appearance and function of disruptive coloration.

The work of Thayer and Cott laid a foundation for disruptive coloration theory, and in recent years there has been an increasing interest and empirical investigation of their ideas. Disruptive coloration has been suggested in a wide range of animals, including most major taxonomic groups (see Stevens *et al.* 2006*a*). For example, potentially disruptive markings

have been investigated in mammals (e.g. Stoner *et al.* 2003), fishes (e.g. Armbruster & Page 1996; Kelman *et al.* 2006), snakes (Beatson 1976), crustaceans (Merilaita 1998) and in particular cephalopods (e.g. Hanlon & Messenger 1988; Chiao *et al.* 2005; Kelman *et al.* 2007). However, many studies use the term disruptive coloration as a subjective category of appearance, without explicitly testing the arrangement of the markings (but see Merilaita 1998) or their function. Conversely, in the last few years alone there have been numerous studies with artificial prey testing the role of disruptive markings in reducing the risk of predation (e.g. Cuthill *et al.* 2005; Merilaita & Lind 2005; Schaefer & Stobbe 2006; Stevens *et al.* 2006*b*; Fraser *et al.* 2007). However, despite this varied research agenda, there is currently no widely used clear and unambiguous definition of the phenomenon, and so much of the essential conceptual work on disruptive coloration remains to be done; a rapidly progressing field is presently advancing without a clear structure. This is a major problem because it also makes identifying disruptive coloration in animals difficult, and there is currently little consensus on how disruption differs from other camouflage strategies, most notably background matching and distractive (dazzle) markings, or whether it can work with potentially 'conspicuous' markings (such as warning colours). Finally, the principle of disruptive coloration actually consists of a collection of more or less related means that have been suggested to result in disruption; we call these 'sub-principles'. However, it is unclear which sub-principles specifically apply to

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disruption and which do not. An unambiguous definition is therefore of paramount importance for the development of this field. It will prevent misunderstandings by unifying the concept and allow a distinction between disruption and other principles of camouflage. Furthermore, it is necessary for generation of testable hypotheses.

2. PREVIOUSLY SUGGESTED SUB-PRINCIPLES RELATING TO DISRUPTION

In essence, Thayer's (1909) and Cott's (1940) writings describe disruptive coloration as markings that conceal the bearer by breaking up its shape with the help of similarities and differences in colour, luminance or texture: difference (i.e. contrast) disconnects adjacent patches of the body surface, whereas similarity merges some body sections to patches of the background and joins separate body parts. Although further sub-principles may yet be suggested, currently, all the ones known seem to be present in Thayer's and Cott's work. However, these need to be organized and classified, and synthesized with respect to recent studies, which is one of the main aims of this paper. In addition, while Thayer's (1909) and Cott (1940) presented several sub-principles regarding how a disruptive effect can be achieved, their discussions of disruptive coloration also included ideas not directly dealing with breaking up shape by coloration. Furthermore, some of their ideas seem to be coupled with the usage of quite different perceptual processes from others. These two latter aspects are problematic because they result in conceptual ambiguity, and because the principle of disruption is not useful if, for example, from an evolutionary point of view it results in several different and possibly conflicting predictions regarding appearance. Finally, some parts of Thayer's and Cott's discussions are contradictory, specifically with respect to certain sub-principles (see §2a). This has sometimes led to confusion among researchers.

Below, we list all nine historical sub-principles that we have found in the literature. Then, we specify those sub-principles directly relevant to disruptive coloration (see also figure 1) and present a functional definition of disruptive coloration. Finally, we discuss how disruptive coloration differs from other forms of camouflage, the optimization of disruption and where future work is of greatest need.

(a) *Differential blending*

Cott (1940) argued that differential blending arises when some colour patches of a pattern blend into the background, while others stand out 'emphatically' from it. Provided that the animal is seen against a broken background, the patches of the pattern will blend into this, destroying the animal's shape: 'its contour will be 'broken up' against both light and dark—light failing to show against light, dark against dark.' (Thayer 1909). Cott's precise meaning is unclear with respect to whether some markings should mismatch the background. We see three different possible interpretations: (i) only some object colours blend, while others are supposed to always stand out strongly from all the background colours, (ii) all the different colours of
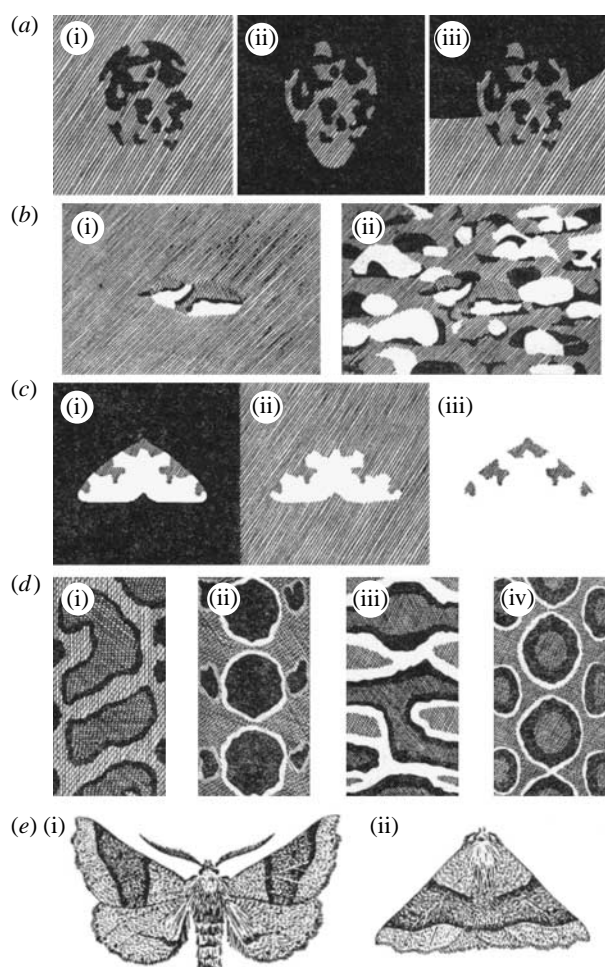
Figure 1. Examples of disruptive coloration (all adapted from Cott 1940), showing the five sub-principles involved. (a) Differential blending, where at least some markings blend into the background ((i),(ii)) or all markings blend into at least some of the background colours ((iii); see main text for details). (b(i),(ii)) Maximum disruptive contrast, where adjacent patterns have high contrast. (c(i)–(iii)) Disruptive marginal patterns, where markings touch the outline of the body. (c(i)) is merely to illustrate the shape of the entire object. (d(i)–(iv)) Disruption of surface, with markings placed away from the body margins creating false edges. (e) Coincident disruptive contrast, where markings cross over and join otherwise revealing body parts, such as wings or legs.

the object blend into different, adjacent colours of the background, or (iii) at any given time at least some of the colours (are likely to) blend into the background. We argue that (iii) sounds similar to the process most likely to work in natural, variable backgrounds, and clearly Thayer did not mean (i).

(b) *Maximum disruptive contrast*

Cott's (1940) second sub-principle, maximum disruptive contrast, predicts that in effective disruptive patterns the adjacent elements should contrast strongly (see also Thayer 1909). Generally, Cott argued that light markings on an otherwise dark object, and dark markings on an otherwise light object will be most effective in creating a disruptive effect. Overall, the main function of high luminance or colour contrast between pattern elements is to break up the outline or the continuity of the surface.

(c) Regularity avoidance

Cott (1940) also discussed the geometric relationship between adjacent elements of the colour pattern. He suggested that the elements should be variable to give an appearance of an aggregate of separate objects, because a simple, invariable shape would be interpreted as a single object. We note that this refers to a type of regularity in the pattern and that there are also other types of regularities, such as pattern symmetry, which may help predators to detect camouflaged prey (Thayer 1909; Cuthill *et al.* 2006*a*,*b*; Merilaita & Lind 2006). Therefore, we name this sub-principle regularity avoidance and suggest that it should cover avoidance of any geometric regularities or repetitions in the pattern that would facilitate detection, including avoidance of symmetric patterns or patterns that easily reveal their symmetry.

(d) Disruptive marginal patterns

This sub-principle relates to the location of markings, such that they intersect the outline of the body (Cott 1940). This does not necessarily mean that they are confined to the body edge, but merely that they touch the outline.

(e) Irregular marginal form

Cott (1940) suggested that irregular marginal form, i.e. morphological/structural complexity of the outline, conceals the shape of an animal. Cott lists a variety of potential examples in his book, of which the comma butterfly, *Polygonia c-album*, with its irregular and complex wing outline is probably the most familiar to European lepidopterists.

(f) Background picturing

Cott (1940) suggested that the disruptive design should closely resemble the particular environment against which it is normally seen. He called this background picturing. This may or may not be synonymous with background matching, depending upon the exact definition used. Thayer (1909) did not consider this as a part of concealment of the contour.

(g) Disguise (disruption) of surface through false edges

In his book, Cott (1940) also considered the process of disrupting the appearance of an animal's surface. Cott's general idea was that breaking up the continuity of the surface through markings that create false outlines and 'holes' on the surface of the animal (i.e. disrupt the surface) would create an appearance of different shape. Cott's use of the term holes is ambiguous, and some elements of his arguments seem to be very similar to background matching, including the actual term 'disguise of surface'. This leaves the interpretation of Cott's writings on this aspect somewhat open. However, it has often been argued that a key element of disruptive coloration is the creation of false internal edges, not corresponding to the true outline, and this may have been what Cott meant. As such, we refer to this sub-principle as 'disruption of surface' henceforth, and argue that it works through the creation of false edges. It seems likely that disruption of surface may be enhanced by maximum disruptive contrast.

(h) Coincident disruptive coloration

This sub-principle describes the continuous patterns that range over different body parts and the outline between them, masking the telltale presence of the otherwise conspicuous appendages or other revealing body parts, such as limbs, antennae or eyes (Cott 1940). This technique could visually join adjacent, discontinuous surfaces separated by a common outline.

(i) Distractive markings

One of Thayer's (1909) theories, alongside ruptive and secant coloration, was the concept of distracting markings. It is clear that Cott (1940) confused this as being the same as or a part of disruptive coloration. However, the term distractive markings typically refers to highly visible markings that may draw the receiver's 'attention' (attention here loosely defined) towards them, and away from the outline of the animal, preventing detection (Thayer 1909). Thayer (1909) believed distractive markings should only be visible in close proximity, when they attract the receiver's gaze away from the body outline. Cott (1940) did not deal with distractive markings as such, but in his account on disruptive coloration he also argued patches of contrasting colours could divert the predator, preventing the determination of form. They need to be used in moderation in relation to the whole area of the body, or will fail in their effect. Finally, distractive markings should be distinguished from motion dazzle markings, both sometimes referred to as dazzle markings, the latter working to make estimates of the bearer's speed and trajectory difficult by viewers (see Stevens 2007; Stevens *et al.* 2008). It is important for future work that researchers carefully distinguish between distraction, motion dazzle and disruptive markings (see below).

3. REORGANIZATION OF THE SUB-PRINCIPLES

Cryptic coloration can be roughly divided into markings that match the background in terms of colour, luminance and marking distribution (background matching) and concealment of body shape or outline (disruptive coloration). These two aims are not independent of each other; a poor match to the background will also expose the shape (see also below). Furthermore, disruptive coloration consists of two main features. The first involves creating the appearance of false edges and boundaries within an object and the second conceals the real object boundary. It is therefore apparent that only those sub-principles of disruption, aiming to change edges and boundaries with the help of coloration (i.e. a patchwork of varying colours or brightness) should be included in disruptive coloration. The sub-principles of regularity avoidance (§2*c*) and background picturing (§2*f*) do not concern concealment of shape. While irregular marginal form (§2*e*) concerns concealment of the outline, it uses the morphological shape of the body outline itself, and not colour patterns. Finally, distractive markings appear mechanistically distinct from disruptive coloration (see also Stevens 2007). This leaves five sub-principles (figure 1): differential blending; maximum disruptive contrast; disruption of surface through false edges; disruptive marginal patterns; and coincident disruptive

coloration, which address the appearance of disruptive coloration from different aspects. Differential blending and maximum disruptive contrast deal with the choice of colour and brightness of the pattern, whereas marginal pattern elements and coincident disruptive coloration deal with the pattern geometry. Disruption of surface through false edges deals with both geometry and coloration. These five sub-principles also represent testable predictions of disruptive theory (see below). Note that even though we suggest the exclusion of the other four from disruptive coloration, this does not mean that they may not be useful for camouflage and may operate in combination with some disruptive patterns.

4. DISRUPTIVE COLORATION: A DEFINITION

We think it of paramount importance that a concise functional definition of disruptive coloration exists. It should draw together the five sub-principles that may account for disruptive coloration, exclude others and be functionally cohesive. Based on the core of the ideas of Thayer and Cott coupled with our reorganization of the sub-principles discussed above, we propose that *disruptive coloration is a set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object's, or part of an object's, true outline and shape*. Thus, disruptive coloration prevents the detection of the real object boundary by extending the continuity between the background features and at least some of the object's markings or between separate body parts, and interrupts the continuity between adjacent areas of the same surface through creation of false edges and boundaries. We define the function as opposed to the appearance of disruptive markings because the former relates to how the markings work (Stevens & Merilaita 2009), whereas appearance is influenced by many factors, including the receiver's vision, the background attributes, the animal's shape and so on. This means that appearance will often vary, making definitions based on this unreliable and oversimplified. Below, we describe how disruption may be optimized, and may relate to other aspects of camouflage and signalling.

5. DISRUPTIVE COLORATION AND MAXIMIZATION OF CRYPSIS

(a) *Optimization of contrast within a disruptive pattern and against the background*

The sub-principles of maximum disruptive contrast and differential blending give only rough directions about the optimal choice of colour and luminance for the patterns used. Cott's (1940) term, maximum disruptive contrast, implies that he thought the contrast within the pattern should be as high as possible, but it is not explicitly clear whether he considered the contrast should be so high that some components do not match the background. Thayer (1909) believed that in variable environments a bold and brilliant disruptive pattern would often result in better concealment than a pattern that matches a single background or an average of many backgrounds, but again was not clear whether this meant that he expected the optimal appearance to involve actually mismatching the environment.

Therefore, two related key issues regarding disruptive coloration are 'does maximal contrast within the pattern actually maximize the disruptive effect' and 'to what level should maximum disruptive contrast be taken to maximize concealment?'

Mechanistically, disruptive patterns may exploit edge detectors in predator's vision by blending the real outline with the background and creating false internal edges, resulting in a failure to segment the true shape of the prey from the background (Osorio & Srinivasan 1991; Stevens & Cuthill 2006). This effect is likely to be more dramatic for high contrasts in luminance or colour between adjacent patches because this will create stronger false internal edges. Indeed, Stevens & Cuthill (2006) found some limited evidence that high-contrasting disruptive patterns were more effective than low-contrast markings at preventing detection by a model of avian visual processing. Such an effect may therefore be maximized by combinations of markings that do not match the background. Hailman (1977) argues that the contrast between the patches on an object should at least equal the contrast between the body patches and the background. Otherwise the contrast between the object and the background will be higher than that between the two body patches. However, this conclusion seems overly simplistic because it ignores differential blending and background matching, and assumes that a patterned object can be cryptic on a uniform background.

Experiments with artificial prey and wild avian predators show that higher internal contrasts between the pattern elements do produce a more effective disruptive effect when all markings match elements of the background (Cuthill *et al.* 2005). Some patterns with a high colour contrast, even with colours not matching the background at all, may also allow for effective disruptive coloration (Schaefer & Stobbe 2006). However, Stevens *et al.* (2006b) have shown that markings with elements exceeding the luminance range of the background yield reduced disruptive camouflage compared with patterns with lower contrast but within the background lightness range. Fraser *et al.* (2007) also found, in experiments where human 'predators' foraged for artificial prey, that highly contrasting disruptive prey with markings not matching the background were detected more quickly than prey with markings matching the background. Most recently, Stobbe & Schaefer (2008) have found that increasing levels of colour contrast of potentially disruptive wing stripes on prey resulted in higher levels of predation from birds in the field. However, the low-contrasting striped prey survived no better than a background matching control, and the negative effect of increasing colour contrast may have been caused by decreasing background matching. Tests of disruptive coloration in real animals are lacking, but in cuttlefish current evidence seems to indicate that the level of contrast within potentially disruptive markings does not greatly exceed the level of contrast of objects in experimental backgrounds (Kelman *et al.* 2007). The above studies suggest that natural selection does not favour the maximization of contrast within a disruptive pattern to lead to non-matching colours, presumably owing to the importance of maintaining concurrent

background matching and because although mismatching markings may maximize the disruptive effect, at some point they would attract predator attention or compromise the level of differential blending.

Clearly, more studies on the topic of optimal contrast are needed. In particular, future work needs to further differentiate between the roles of internal contrast (of the adjacent animal markings) and external contrast (against the background) of the different pattern elements, and how this relates to the background attributes (Endler 2006). For example, while the experiments of Stevens *et al.* (2006*b*) and Stobbe & Schaefer (2008) indicate that excessive contrast is detrimental, both of these involved treatments where the prey with markings of higher contrast were also further from matching the background. Most studies have focused on the optimization of the contrast of the marginal markings, and not distinguished this from that of the internal markings creating false edges. It is not clear whether the level of contrast of the internal markings, to create false edges, should be the same as that of the marginal markings, which break up the true outline. In addition, current experiments investigating disruption have focused on two-coloured patterns only, and so whether two shades are the optimal number of colours for maximal disruptive effect is unknown at present, or what proportions of different colours should be favoured. It is also unknown whether luminance contrast and colour contrast are equally important in creating disruptive effect. Finally, high-contrast patterns may be easier to detect by a predator when the object is moving.

(b) *Spatial attributes of disruptive markings*
Cott (1940) did not apparently make any predictions about the optimal size of the elements of disruptive patterns, and, with the exception of marginal markings, recent research has focused mainly on the optimization of the contrast of disruptive markings rather than their spatial characteristics (e.g. size, shape, density, distribution).

(i) *Marking distribution*
One of the key tenets of disruptive theory is that some markings should be positioned at the edge of the body to break up the outline (Cott 1940). This is now well supported by a range of experiments (e.g. Cuthill *et al.* 2005; Schaefer & Stobbe 2006; Stevens *et al.* 2006*b*; Fraser *et al.* 2007). However, beyond this, little more is known regarding the optimum distribution of pattern elements. Based on breaking up the body outline, it has often been predicted that markings should be found at the edge of the body more often than would be appropriate for simply matching the distribution of markings in the background (e.g. Merilaita 1998; Stevens *et al.* 2006*b*). However, the situation is likely to be affected also by other selection pressures and attributes, such as the size and density of the background markings in relation to body size and shape. For example, very large markings will be more likely to touch the outline of the body by chance alone than would small markings. As such, under some circumstances, disruption may not select for a greater number of peripheral markings than matching the distribution found in the background. An additional factor relates

to the characteristics of the animal itself. Given that any single unmodified body edge could give away the animal's presence, it seems logical that disruptive markings should be distributed to break up each of the animal's body parts or appendages.

Almost all experiments investigating the survival value of disruptive markings have focused on the benefit of breaking up the outline. However, disruptive theory also predicts the importance of creating false internal edges, something which has received almost no experimental investigation. As such, we know little about the distribution of non-marginal markings required to achieve a disruptive effect, and have only indirect clues as to how this sub-principle may function. For example, does the density of markings yielding a maximal disruptive effect deviate from that yielding maximal levels of background matching? How these markings should be distributed also awaits research. In general, it is not even known whether non-marginal elements are advantageous due to an actual disruptive effect, or whether they are only required to maintain effective background matching with respect to distribution of pattern elements (i.e. a patterned outline and a uniform central body region would potentially emphasize the shape of the body).

(ii) *Marking size and shape*
In general, there are not many predictions about the optimal size or shape of the elements of disruptive patterns. Thayer (1909) suggested that the sharply contrasted bold patterns of light and dark should be present in about equal proportions. This is in line with the suggestion that small markings will offer little disruptive benefit, and, conversely, markings that are too large may actually highlight the body edges (Sherratt *et al.* 2005; Stevens 2007). This suggests that the elements of a disruptive pattern may have an optimum size, which may be influenced by the body size of the animal. For instance, the same size markings may be disruptive on a large animal yet highlight the edges of a small animal. No predation experiment has yet investigated the optimal marking size. Merilaita (1998) studied the patterning of the isopod *Idotea baltica* and suggested that it may have been influenced by selection for disruption, because the white spots of the patterning were found to touch the body outline more often than expected by change. Interestingly, the white spots were on average smaller than the white spots found in the background. Assuming that the patterning has a disruptive effect, this result implies that disruption may select for a different optimal marking size than background matching alone.

(iii) *Disruption, dimensionality and body shape*
An object's edge is unambiguous only for two-dimensional shapes, whereas for three-dimensional objects it also depends upon the viewing angle. As such, the optimal distribution of disruptive markings may be more problematic for a three-dimensional animal. Conversely, a background matching marking on a three-dimensional object may, from another angle, function as disruptive marginal patterns. So far, experimental studies on disruptive coloration have focused on flat-bodied prey, partly because marginal

patterns are easy to identify when the animal is flat, or when it is typically viewed from a given angle. Currently, little is known about how disruptive coloration works in three-dimensional animals, and how they should distribute their markings to maximize disruption, compared with the requirements of pure background matching.

Similarly, the experimental backgrounds have so far been flat or nearly flat. However, three-dimensionality of the environment might be important when disruption is considered. For example, search in a three-dimensional environment, such as foliage, requires viewing at varying depths. In such environments, adjacent areas that share an outline are not necessarily next to each other, but may differ in depth, in contrast to a two-dimensional background, where a shared outline is a reliable cue of adjacency. Therefore, detection or recognition of a prey with a disruptive patterning, which breaks its surface into distinct regions, might be more difficult in environments with strong three-dimensional character compared with simpler environments. This could be studied experimentally or with a comparative study between habitats.

(c) Coincident disruptive coloration

Numerous animals, such as amphibians, fishes and moths, have been suggested to use coincident disruptive coloration to conceal their limbs, eyes or other characteristic body parts (e.g. Cott 1940). Barlow (1972) studied obliterative eyelines and their relationship to relative body depth and the slope of the forehead in fishes. He found that vertical eyelines were associated with deep bodies and steep foreheads, whereas horizontal lines were associated with elongate bodies and low foreheads. There are few formal tests investigating either whether coincident markings do indeed serve an anti-predator function, or how they may do so in terms of predator perception. However, recently, Cuthill & Székely (2009) have shown that the survival of artificial prey in the field is significantly enhanced by coincident stripes between the wings and the body not dissimilar to those found in a range of moths. As such, initial work does indicate that such markings are an important method of enhancing concealment, although other potential forms of coincident disruption, such as eyestripes, remain untested. It seems likely that if coincident markings work widely, they may also exploit edge detection mechanisms in visual processing, generating the appearance of markings that run across body regions, but they may also use gestalt principles (a set of descriptive tendencies for visual recognition of features) to unite body regions that appear distinct. Coincident disruptive coloration predicts that in the typical resting position of a prey, similarly coloured elements are more likely to be fused over the edges of different body parts.

(d) The relationship between disruption and other forms of camouflage

(i) Background matching

One of the main challenges faced by researchers studying camouflage is the ability to distinguish between different forms of camouflage in real animals. Further, as discussed by Merilaita & Lind (2005), it may often be difficult to distinguish function from

appearance in camouflage markings; animals may use both disruption and background matching markings simultaneously. As such, on some backgrounds and with certain prey shapes, both disruptive coloration and background matching may select for indistinguishable frequencies of marginally located elements, making it difficult to distinguish whether some aspects of an animal's coloration result from selection for disruption or for background matching. As Merilaita & Lind (2005) pointed out, the shortage of knowledge regarding maximization of background matching may be problematic in experimental studies on disruption, because it can be difficult to tell exactly how background matching should be controlled. Therefore, special care should be taken to prevent or minimize any potential confounding or undesired effects resulting from differential background matching (e.g. Cuthill *et al.* 2005; Fraser *et al.* 2007). Clearly, a better understanding of background matching would also benefit the study of disruptive coloration.

Despite the above caution, there are a range of predictions one can make regarding differences between background matching and disruption. First, because disruption emphasizes the location of markings such that they touch the outline (Cott 1940; Merilaita 1998; Cuthill *et al.* 2005), one may expect that the distribution of markings in disruptive prey should be related to body shape (and size), whereas the distribution of markings should be independent from body shape for background matching (Merilaita & Lind 2005). In essence, background matching is purely about correspondence between the prey markings and the background. While for background matching, the animal markings are expected to match the distribution of the background markings, for disruptive coloration the markings should be distributed to optimally break up the prey outline and generate false edges. This optimum solution will most likely depend on a range of features, including body shape, various attributes of the background markings and also maintaining a sufficient level of background matching.

Finally, it is possible that disruptive coloration will select for different levels of pattern contrasts than that found in the background. We consider it unlikely that these contrasts would lead to strongly non-matching attributes (see above). However, it is possible that disruption could produce a different distribution of contrasts to that found in the background. Wilkinson & Sherratt (2008) make the interesting point that there seems to be an asymmetry in the relationship between background matching and disruptive coloration, such that background matching can be effective without disruptive coloration, but disruption is compromised by ineffective background matching. Further work is needed to clarify whether this is the case for both non-matching coloration and the distribution of colours, luminances and contrasts. In addition, it is widely appreciated that selection pressure can give rise to polymorphisms in background matching within species, but we currently have no clear expectation as to whether this should be the case with disruptive markings (Sherratt *et al.* 2005). However, we may expect polymorphism to arise if there are several ways of being equally disruptive with different markings.

(ii) *Self-shadow concealment*

Given that self-shadow concealment (SSC) through countershading is also seemingly an important way to reduce the risk of detection (Rowland *et al.* 2007; Rowland 2009), it is important to be able to distinguish this from disruption. One of the main functions of SSC is to cancel out differential light intensity, and so SSC should generally select for gradual changes in the coloration of the animal, which should be directly related to the ambient light and the animal's body shape. By contrast, we would expect that disruption should use sharp changes in luminance or colour to create false edges. Many mammals, for example, have a sharp boundary between their darker dorsal surface and lighter underside; it is not clear whether this is to cancel out the illumination from above, to break up the body appearance or for some other function.

(iii) *Distractive markings*

Distractive markings are hypothesized to work by being of such high contrast, both with other patches on the body and with those in the surroundings, so that they may actually stand out from the background (Thayer 1909). This may seem odd, since intuitively one would therefore expect that such markings would attract the attention of any predator to the prey. Regardless, the idea is that, even if the predators do detect such markings, the markings should be meaningless to the predator in the sense that they convey little or no useful information for the detection or recognition of the prey. Instead, the markings are supposed to draw the predator's attention away from more revealing characteristics, such as the body outline. Whether or not this works is still controversial since there has been only one formal experimental test of distractive markings, which failed to support the theory (Stevens *et al.* in press). Regardless, disruptive and distractive colorations have different functions and seem to involve different perceptual mechanisms (Stevens 2007). This also implies that disruptive and distractive effects may be differentially maximized and impose different selection pressures on prey appearance. For example, a marginal location may not be the best for a distractive mark if it attracts the attention of predators to the outline. Unfortunately, there have been few explicit tests of distractive markings, which distinguish them clearly from disruptive coloration. In fact, many studies have often used the principles of disruption and distraction interchangeably. One reason for this is that Cott (1940) placed together these distinct principles of concealment suggested by Thayer (1909). Future studies need to better distinguish between these two forms of coloration.

(e) *Disruptive coloration and signalling*

Finally, because disruptive coloration is widely thought to use high contrasts, it has often been suggested that it can be combined with other, apparently conspicuous types of signal, such as warning colours and motion dazzle patterns. It has frequently been suggested that disruptive markings may be combined with warning colours (Edmunds 1974; Järvi *et al.* 1981; Tullberg *et al.* 2005), for several reasons. First, because spatial resolution decreases with increasing viewing distance, it

is possible that a pattern, which has high internal contrasts or colours not found in the background, blends into one patch that matches the background attributes when viewed from sufficient distance or by a predator with a low spatial acuity (Edmunds 1974; Hailman 1977; Tullberg *et al.* 2005; Stevens 2007; Bohlin *et al.* 2008). This is also an important area of research because warning colour patterns also typically have strong internal contrasts. However, one problem is that many discussions of disruption and warning colours have failed to differentiate between true disruptive coloration and distractive (dazzle) markings. While the former seems to work the best when all colours match the background, distractive markings may be highly effective when possessing non-matching colours. Therefore, it may be possible that warning signals combine a distractive rather than a disruptive function. Finally, because disruptive markings are thought to work best when comprising high-contrast patterns, it is possible that they may also serve a dual function as motion dazzle markings, making it more difficult for predators to capture a moving prey animal (cf. Stevens *et al.* 2008).

6. CONCLUSIONS

The field of disruptive coloration is one of the fastest growing areas in the study of adaptive coloration, but has largely progressed unstructured. Our synthesis suggests that there is still much empirical and theoretical work to be done in this field. An identification of the sub-principles involved, and how they should be optimized, should help to formulate testable hypotheses to further our (currently still limited) knowledge about the optimal appearance and function of disruptive coloration. An important objective for future studies is to determine how widespread disruptive coloration is in nature, and the relative benefits that it may provide in terms of increased survival in real species. Crucially, there is a range of work needed to determine how disruptive coloration should be optimized and how it relates to other forms of coloration.

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