

ANIMAL CAMOUFLAGE: BIOLOGY MEETS PSYCHOLOGY, COMPUTER SCIENCE AND ART

I.C. CUTHILL¹ & T.S. TROSCIANKO²

¹School of Biological Sciences, University of Bristol, UK.

²Department of Experimental Psychology, University of Bristol, UK.

ABSTRACT

Animal camouflage provides some of the most striking examples of the workings of natural selection, whether employed defensively to reduce predation risk, or offensively to minimise alerting prey. While the general benefits of camouflage are obvious, understanding the precise means by which the viewer is fooled represent a challenge to a biologist, because camouflage is an adaptation to the eyes and mind of another animal. Therefore, a full understanding of the mechanisms of camouflage requires an interdisciplinary investigation of the perception and cognition of non-human species, involving the collaboration of biologists, neuroscientists, perceptual psychologists and computer scientists. Modern computational neuroscience grounds the principles of Gestalt psychology, and the intuition of generations of artists, in specific mechanisms that can be tested. We review the various forms of animal camouflage from this perspective, illustrated by the recent upsurge of experimental studies of long-held, but largely untested, theories of defensive colouration.

Keywords: animal colouration, antipredator behaviour, camouflage, colour vision, crypsis, defensive colouration.

1 INTRODUCTION

‘The colours of many animals seem adapted to their purposes of concealing themselves, either to avoid danger, or to spring upon their prey’ Erasmus Darwin, 1794 [1]. One hundred years later, studies of animal camouflage provided some of the earliest support for Erasmus Darwin’s grandson, Charles, and his theory of natural selection [2–4]. But paradoxically, a detailed and comprehensive theory of how camouflage actually works – the mechanisms rather than the broad function – has only recently started to be formulated. With a few notable exceptions [5–7], the concepts have advanced little since the classic work of Abbott Thayer [8, 9] and Hugh Cott [10]. It is not an overstatement to conclude that Cott’s 1940 book, with a strong adaptationist stance typical of behavioural ecology today but unusual for its time, provided a huge leap forward, but inhibited the subsequent study of camouflage for about half a century. Cott seemed to have ‘solved’ camouflage, his razor-sharp insight and the self-evident ‘design’ in the animals featured his illustrations backing up arguments which fused concepts from arts and Gestalt psychology. However, argument from intuition is only the starting point for a properly scientific theory of camouflage, and illustrations, deliberately chosen to illustrate a ‘typical’ situation or selected with a subconscious subjective bias, can be misleading. Furthermore, while Gestalt psychology was the starting point for modern theories of perception, in Cott’s day the theory amounted to a set of unifying principles that made sense of experimental data; the contents of the black box were uncertain. Today, computational neuroscience seeks to expose the mechanisms underlying perception [11]. Only by uniting tightly focussed experiments (in lab and field) with detailed knowledge of the mechanisms underlying vision can a comprehensive theory of camouflage, as evolved by animals or as designed by humans, be developed.

1.1 Camouflage and evolutionary biology

To a biologist, one of the most intriguing, and challenging, features of camouflage is that the major selective force shaping its evolution is the perception of another species. What we see, as human

observers, is irrelevant; what matters in evolutionary terms is the perception and cognition of the animal from which the target species is hiding [12, 13]. This could be a prey concealed from a predator, or a predator concealed from its quarry. What is likely in each case is that, unless that species from which concealment is sought is an Old World primate, the visual system is likely to be very different from that of humans. Human vision has had a trivial role in the evolution of colour patterns in any species other than our own whereas, for example, bird vision has been a major selective force for insect colouration, insects displaying some of the most impressive and diverse camouflage tactics seen in nature. The realisation that other animals see different colour worlds from our own has revolutionised and invigorated the study of signalling [14–17], yet has rarely been applied to camouflage. Both low level perceptual mechanisms and higher cognitive process such as learning have been shown to shape the evolution of signals [18]. Camouflage, where the premium is on concealment rather than conspicuousness, must be similarly influenced, and the ways in which camouflage exploits ‘receiver psychology’ [15] was clearly understood by early writers in both biology [10] and Gestalt psychology [19–21]. A major challenge for biologists is that we still do not have a detailed understanding of which perceptual mechanisms camouflage ‘exploits’, whether the same principles apply to human and non-human animal vision, or which environments and perceptual mechanisms select for which camouflage strategies under different circumstances. The evolutionary biologist interested in explaining camouflage must therefore first understand receptor physiology and the neural processing of the signals emanating from the photoreceptors.

1.2 Camouflage and neuroscience

Theories of vision in psychology [and, to a large extent, artificial intelligence (AI)] are understandably dominated by the human model, but it would be unwise to generalise from such an unusual vertebrate. First, the primate visual cortex is a vastly sophisticated upstream processing unit (if you like, a deluxe Adobe Photoshop™ for image enhancement), whereas most animals do more visual processing nearer the retina. Maybe primates have to do this extensive post-processing, because the retinal array transducing the light information leaves much to be desired? Leaving aside the fact that many vertebrates, including birds, have a fourth retinal cone cell type sensitive to ultraviolet (UV) light [22, 23], Catarrhine primates such as humans have considerable overlap in the spectral sensitivity of their long- and medium-wave (L and M) cones [24]. Most vertebrates have fairly evenly spaced receptor sensitivities, and birds reduce spectral overlap (and decrease bandwidth) further, with pigmented oil droplets that filter the incoming light. This leads to not only a more saturated colour signal in birds [25, 26], but also a greater degree of spatiotemporal noise than primate vision [27, 28]. While the red–green opponent response is much more stable than the blue–yellow response across diurnal changes in illumination for primates, it is less so for birds [27, 28]. This seems to be consistent with the hypothesis [29, 30] that the high degree of overlap in spectral sensitivity of the primate M and L cones represents a trade-off between red–green discrimination and luminance sensitivity, the latter of which in primates is a joint function of M and L cones. This is not the case in birds, in which a distinct cone class, the double cones, seems to subserve luminance-based tasks [31]. Finally, birds’ sensitivity to contrast, at all spatial frequencies, is significantly lower than that of primates [32]. This would appear to be a severe compromise to detecting cryptic prey. Primate and bird visual systems have clearly found different solutions to the trade-offs described above, but the significance of this for detecting prey (or predators) using colour or luminance cues remains to be investigated.

1.3 Camouflage and psychology

To a psychologist, the relevance of camouflage is not so much in the object but in the viewer. How you ‘break’ camouflage revolves around two of the major issues in visual perception, target-background segmentation and object recognition, but under precisely the conditions where this task is most difficult [33]. This is because camouflage patterns have been designed, by natural selection or by humans, to deceive the mechanisms of target-background segmentation and object recognition. Under conditions where targets are designed to be inconspicuous, the ‘binding problem’ (how disparate object features are bound, cognitively, into a whole) is particularly severe. There is little literature on object recognition by humans where the objects are heavily camouflaged, but there is an extensive literature on visual search, including situations in which this is slow and inefficient. This will often be the case with complex natural backgrounds and polymorphic targets, a task which humans and, famously, birds [7, 34–36] readily solve. An understanding of the psychological mechanisms involved in camouflage breaking must deal not only with the figure-ground segmentation issue, but also discrimination between the target and similar objects in the visual field.

There are two traditions in the human visual search literature: the first considers search for a target among ‘distractors’ (Fig. 1a). These are discrete non-target objects, already segmented from the background in early visual processing, that are confusable to differing degrees with the target and each other [37]. The other tradition (of particular concern in the AI approach to vision) focuses on the segmentation process itself: how are objects distinguished from the background in the first place (Fig. 1b)? There is increasing realisation that it is unrealistic to treat segmentation and object recognition (and confusion with distractors) as serial processes with the first completed before the second can occur [38]. This is something we shall return to later with regard to disruptive colouration, where object recognition takes a central role.

1.4 Camouflage and computer science

Researchers in artificial vision must tackle the same issues that challenge psychologists dealing with human visual systems (feature detection, feature binding, target-background segmentation and object recognition). The difference is that they need not be constrained by features specific to human visual systems, either at the receptor level (e.g. spectral sensitivity or spatial distribution) or subsequent processing. Furthermore, because the goal is implementation of algorithms to achieve efficient extraction of the desired information, accounts of vision in computer science must always be rooted in specified mechanisms. For these reasons, approaches developed in computer vision may be particularly useful for understanding animal camouflage. Until recently, most adaptive accounts of camouflage have relied on necessary, but weak, tests showing that a given pattern simply improves concealment (not how) and arguments heavily reliant on introspection: the untested assumption that what fools (or appears to fool) the human observer fools the predator. Consider these quotes from popular biology textbooks (italics added): ‘patterns . . . *detract the eye from the animal’s outline*’, ‘patterns . . . which turn *attention* away from other details and especially from the animal’s outline’. Really? What is the evidence that any of this is going on in the predator’s head? Instead, the way to understand the ‘design features’ of camouflage is to focus on the mechanisms of predator perception and cognition that the colour patterns are designed to fool. Once the putative function (adaptive advantage) of a colour pattern is specified at the level of a neural mechanism in the predator’s nervous system, that function can be tested in precise and powerful ways. In addition, and importantly, taking a computational approach minimises the temptation to impute higher cognitive processes than necessary to explain the phenomenon.

1.5 Camouflage, art and war

It is probably no coincidence that Abbott Thayer (1849–1921) and Hugh Cott (1900–1987), authors of the most influential early texts on the theory of camouflage, were both naturalists and accomplished artists [19, 39]. Long before computational neuroscience started to provide tight mechanistic accounts of visual perception, Thayer and Cott each had an artist's eye for how to use colour and shading to fool the viewer. Furthermore, the persuasiveness of their arguments was undoubtedly aided by the beautiful illustrations in their influential textbooks [9, 10]. Because the focus of this article is animal camouflage, the obvious widespread use of camouflage for military, or recreational hunting, purposes is beyond our scope. However, both Thayer and Cott played important roles in the adoption of camouflage by militarised nations in the Western hemisphere, and it is only in the last few decades that science (in the form of spectral analysis of reflectance spectra and computational analysis of spatial pattern) has begun to replace art and nature as the guiding influence for camouflage design. The artist George de Forest Brush, an acolyte of Thayer, petitioned the United States Navy to adopt Thayer's idea of countershading for battleships from 1899 to 1908 and, with the USA's entry to World War I (WWI), the system was immediately adopted [40]. Several founders of the first US Camouflage Corps were from Thayer and Brush's art circle. Thayer himself travelled to England in 1915 to attempt (unsuccessfully) to persuade the British Navy to use his principles in ship colouration and, later, claimed that the Germans had used ideas from his writings [40]. The noted British zoologist (and, in due course, doctoral supervisor to Hugh Cott), Sir John Kerr, had also appealed to the British Navy to adopt Thayer's countershading on its ships at the outbreak of WWI, as well as 'dazzle' schemes of incongruent geometric patterns designed to interfere with the enemy's optical rangefinders [40–42]. With the dramatic increase in success of U-boat attacks in the latter part of the war, and the advocacy of Lieutenant-Commander Norman Wilkinson, who claimed to

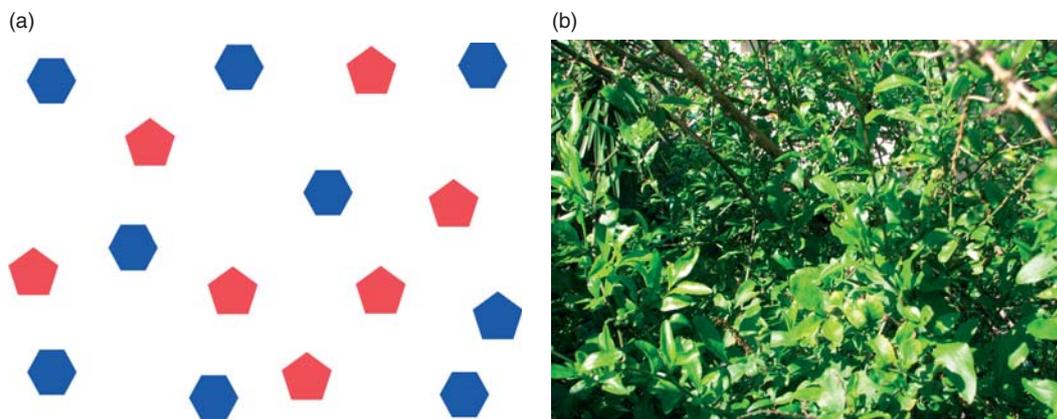


Figure 1: The various perceptual processes required to break camouflage have often been studied separately. In (a) the problem is to distinguish a 'target', here a blue pentagon, from otherwise similar 'distractor' objects, here blue hexagons and red pentagons. In (b) the problem is to distinguish an object of interest, here a chameleon, from a complex background. This is commonly known as 'figure-ground segmentation'. (Clue: look about one third from the right-hand side of the picture, slightly above the middle). Photograph courtesy of, and copyright, Les Underhill, University of Capetown.

have arrived at the concept of distraction camouflage independently of Thayer, the British Admiralty adopted dazzle painting on ships in 1917 [42]. With the advent of alternative ranging devices and sonar, the more bizarre naval camouflage schemes were dropped after WWI and camouflage seems have rapidly ceased to be in vogue, no doubt helped by the cost and complication of applying multiple paint schemes. The University of Glasgow holds a letter from Hugh Cott to Winston Churchill, imploring that the principles of camouflage be taken seriously in military colour schemes, so it seems that by World War II (WWII) the principles of concealment needed to be relearned, and the arguments used by Thayer decades earlier had to be repeated.

At the start of WWII, the Italian army stands out as having a disruptive patterned material (*tela mimetizzata*) used, initially, for tents but subsequently uniforms. Most European armies at the time had drab, monochrome khaki, grey or green uniforms and, during the war, although widespread on vehicles, camouflage uniforms tended to be restricted to elite units or specific theatres of war [42, 43]. Ubiquitous military camouflage is therefore a modern phenomenon and it is interesting to see that the designs are influenced by similar pressures to that imposed by natural selection on animal colouration. Obviously, the perception of the viewer is paramount so, just as insect camouflage needs to extend into the ultraviolet because birds can see UV [23, 44, 45], so must modern military uniforms have a low infra-red signature to fool night-vision equipment [43]. Evolution can only improve on existing designs through mutation and selection from standing genetic variation, so every organism is a weighted combination of phylogenetic history and recent adaptation. For this reason, comparative analyses of adaptation must separate similarities due to phylogeny (evolutionary relatedness) from those due to common selective pressures [46]. Similarly, military camouflage owes much to the history of the nation and army concerned, and not just what is best for a particular background; otherwise, one might imagine that all armies in a particular theatre of war would have similar colour schemes. National conservatism in camouflage design is evident: the brush strokes in the original WWII paratrooper's Denison smock are still apparent in the current British army 'disruptive pattern material', a fondness for pointillism is seen in German camouflage from WWI to WWII to the 'Flecktarn' of the modern German army, while the modern French army uses blocky patterns similar to those employed by Cubist artists on French military equipment in WWI [19, 42]. Part of the diversity of camouflage designs is also due to the conflicting pressure of the need to distinguish friend from foe (in WWII the US Marines abandoned their 'frogskin' camouflage pattern soon after the Normandy landings because of similarity to Waffen SS schemes; in the first Gulf War, the British army swapped from a four-colour to a two-colour desert scheme, because it had previously sold the old design to the Iraqi army [42, 43]). In addition, it is tempting to think that, just as sexual selection can favour animal signals more elaborate than that needed for efficient transfer of information [47], so too some military camouflage designs do more than simply conceal the subject whilst being identifiable as 'friend'. The pixellated patterns of modern digital designs, such as the Canadian Army CADPAT or US Marine MARPAT, clearly cannot have a function in camouflage; natural backgrounds are not pixellated, so the success of the camouflage relies on being seen at sufficient distance for the individual colour blocks to be invisible. Thus, these pixellated patterns seem to have a signalling component: a digital design tells the enemy (and probably, even more importantly, the soldiers wearing it) that this army has the latest and best technology available to it.

2 TYPES OF CAMOUFLAGE

Historical and contemporary accounts classify camouflage in different ways, the most popular breakdown being background matching, disruptive colouration and masquerade. The ability to change colours rapidly to match one's surroundings, dynamic camouflage, is sometimes treated as a separate category. However, we do not do so here because the goal of this article is to explore how

different types of camouflage exploit different aspects of the viewer's perception, rather than the speed of change or mechanisms of colour production. Dynamic camouflage is forever associated in the public's eye with the chameleon (Fig. 1b), and assimilated into our language as synonymous with blending to match the current situation. In fact, chameleons appear to mainly use colour change in signalling to conspecifics [48] and the true masters of dynamic camouflage are the cephalopods, most notably some species of octopus and cuttlefish [49, 50]. Such abilities would seem to be highly advantageous, but are seen in relatively few organisms. Some are undoubtedly constrained by the nature of the epidermal covering (e.g. feathers and fur have their pigment content fixed at the time of growth) or the lack of specialised pigment cells or the nervous control necessary to effect fast changes. Even if not an absolute constraint (i.e. physiologically or genetically impossible), the (untested) assumption is that many animals have a lifestyle and/or environment where rapid change is not sufficiently advantageous for natural selection to have overcome such constraints.

2.1 Masquerade

Cott (1940) distinguished between resemblance to a specific background object and a generalised resemblance to the background. The former is now commonly referred to as masquerade, the latter as background matching or crypsis [51]. It might seem like an entirely semantic point whether, say, a leaf-like body form constitutes resemblance to a specific object (a.k.a. masquerade) or represents background matching. However, in principle, the two types of concealment are interfering with predator perception in different ways. Masquerade, mimicry of a specific background object (e.g. a leaf or bird's dropping), depends on incorrect object recognition rather a failure to segment an object from the background. As such, the necessary perceptual models for understanding masquerade are those relevant to target-distractor discrimination rather than with those related to target segmentation from a complex textured background. An animal adopting masquerade would, if placed on a highly contrasting background, still be ignored by the viewer because, it has not been recognised as being a significant object (e.g. for a predator, suitable prey). Conversely, an animal reliant on background matching would, if similarly treated, be revealed and cease to be protected. This thought experiment, to our knowledge, has never been performed and, in practice, a masquerade-type camouflage would often benefit from a failure of segmentation and detection, in common with background matching. Indeed, particular backgrounds can sometimes be classified as a set of distractor objects or as a homogeneous texture (Fig. 2), and human, and animal, brains are liable to switch between different percepts.

2.2 Background matching

Intuitively the simplest form of camouflage to understand, background matching or crypsis [51–53] succeeds when the viewer does not discriminate the object from its background: a failure of target-ground (or figure-ground) segmentation. Lack of object recognition is not implied; the viewer does not even detect that an object is there, because it *blends into the background*. Many classic examples of natural selection in the wild have been attributed to background matching under predation risk, most famously, or infamously [54, 55], the peppered moth *Biston betularia*. What is less clear, and highlighted in recent reviews [56], is just what aspects of the background need to be matched, and how well?

Whether an object matches the background depends on (at least) two things. First, how the viewer's nervous system filters the incoming information, both spectrally (from a continuous spectrum of light to, in humans during daylight, three photoreceptor outputs) and spatially (dependent upon the

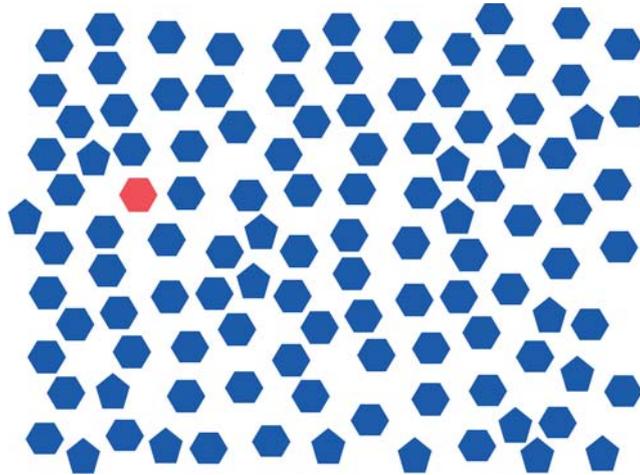


Figure 2: Although one could treat finding the red hexagon as a target-distractor discrimination problem, one can just as easily view this as a figure-ground segmentation task, with the blue hexagons and pentagons treated as a single, slightly heterogeneous, texture.

extent and sensitivity to contrast of the receptive fields of the post-receptor neurones). Second, the local distribution statistics of this spatiochromatically filtered data. From this perspective, it is clear that what is effective camouflage will differ according to the nature and degree of 'data reduction' effected by the viewer's nervous system and, because it affects the signal:noise ratio, the heterogeneity of the immediate background. Successful camouflage will be that which matches the statistics of the neurally filtered visual scene: the same distribution of luminance, colour, textures, edges and, where salient to the viewer, derived features such as shapes. Thayer [9] was probably the first to think of the animal's colours comprising a sample of the background, and he meant this quite literally; he used to view and paint habitats through stencils shaped like the animals he studied. Endler [5, 51] introduced a more formal treatment of how background-matching camouflage should relate to the statistics of the background; he defined cryptic colouration as that which represents a random sample of the background (at the time and place of greatest predation risk). This highly specific definition of crypsis, as opposed to the word being synonymous with camouflage in general, is considered by some as too restrictive [57, 58]. However, Endler's aim was to provide an operational definition that allowed the extent to which an animal matches the colours, textures and patterns in the background to be quantified.

The 'random sample' definition of crypsis has created some controversy [59, 60], mainly centred around a debate about whether all random samples of the background are equally cryptic. The first point to emphasise is that, to be effective, the sampling must be at the spatial scale appropriate to the object being concealed. If an animal matches a common colour in the background, but the animal is larger than any thus-coloured patches in the background, it will be conspicuous (Fig. 3). Second, it is clear that if a random sample, in cutting through portions of background patches, creates new shapes that are themselves rare in the background, then it will be less than perfectly concealed (Fig. 3). More subtly, even if these two problems are avoided, it will still be the case that, all other factors being equal, not all samples from the background will be equally well hidden. This has been shown empirically, with birds hunting for artificial patterned targets against complex backgrounds in

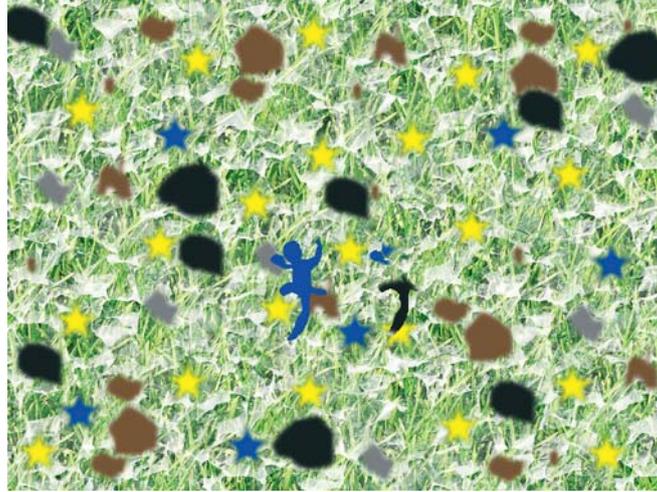


Figure 3: Random sampling of colours from the background does not always maximise concealment. Two lizard-like creatures are detectable near the middle of this complex background. The left-hand one is conspicuous because, although blue is a common background colour, it is a different spatial scale (and shape) from the colour patches which have been sampled. The right-hand lizard, although far better concealed, is still detectable because the sampling creates new shapes (the black tail and blue limb) that are themselves not found in the background.

the lab [59], and a simple thought experiment shows why this should be the case. Imagine a mosaic background of coloured patches, each patch larger than the animal seeking concealment, with shades drawn from a normal (Gaussian) distribution. An animal coloured according to the mean background colour will, if it settles at random, often find itself on a patch close to its own colour. An animal that is a rare background colour will more often find itself mismatching its background. Formally, for any arbitrary distribution of background colours (or, more generally, features) the best concealed animal, on average, will be that which adopts the most likely value in the background distribution ('most likely' in the statistical sense of maximum likelihood). The earlier caveat 'all other factors being equal' is important. First, if the animal can select its background, then all random samples from the background distribution can, in fact, be equally cryptic, although an animal that deviates from the most likely colour will pay a higher search, or opportunity, cost in finding or restricting itself to particular background patches. Second, if the predator can adjust its search behaviour, through learning or natural selection over evolutionary time, then 'maximum likelihood crypsis' will cease to be optimal. If the prey is the most common colour in the background, then the predator could learn (or evolve) to search intensively only those patches that are the common colour. Such predator behaviour selects for polymorphism in prey, something demonstrated experimentally in elegant experiments, where artificial prey on computer screens were allowed to evolve under predation by Blue Jays *Cyanocitta cristata* [7, 34]. The evolutionarily stable outcome is likely to be a distribution of prey colours that matches those in the background. In other words, under conditions of optimal predator behaviour, the optimal colouration for crypsis is that which matches the sampling distribution of background attributes, close to Endler's [5] 'random sample' definition.

Whilst the requirements for optimal background pattern matching can thus be stated simply, none of the published models applied to animal colouration allow one to perform the necessary calculations of ‘match’. Successful receptor-based models of colour discrimination [61] and statistical methods for comparing sets of colour patches [62] do not address spatial pattern, and methods for comparing the distribution of colour patch types and sizes [5] do not capture the attributes of patch shape or relative position. Physiologically based (as opposed to AI) models incorporating both spatial and chromatic attributes of visual scenes are relative new [63]. Based on low-level properties of the retinal cone cells and post-receptor processing, measured psychophysically, such models allow one to quantify the luminance, colour and textural differences that a would-be camouflage breaker must exploit. Spatiochromatic models have yet to be tested in the context of camouflage breaking, but offer promise for application to non-human animals because the models are based only on low-level properties of vision, properties that can be readily measured.

2.2.1 Multiple backgrounds and compromise crypsis

While Thayer [9] noted that a habitat generalist could not be perfectly camouflaged against all backgrounds, it was Merilaita who first formalised the conditions under which compromise camouflage could have higher fitness than a specialist strategy of matching one background type [6, 64]. Although compromise camouflage can be seen as an alternative to Endler’s ‘random sample’ definition of optimal crypsis, Endler himself had earlier clearly considered how compromise crypsis could sometimes be favoured: ‘Species that are not as specific for background habitats show a lower mean crypsis than specialists because their patterns must be some sort of average of all backgrounds against which they rest, and cannot be very cryptic on any single background. The semi-generalists show a higher mean crypsis than the generalists, probably because it is easier to resemble two habitats than many’ [5]. As captured by Merilaita *et al.*’s [6] model and similar approaches that allow for changes in predator behaviour [65], in the event of a likely trade-off between the effectiveness of a given camouflage in two habitats, a compromise strategy is favoured when the trade-off is convex (improved camouflage in one habitat does not decrease concealment in the other by a proportionate amount). Ruxton *et al.* [56] reason that this is more likely for habitats that are visually more similar, and we can use a toy model to see why (Fig. 4). However, implementation and testing of more rigorous perceptual models, where one can predict the shape of the trade-off function from visual attributes of the background, has not been attempted.

2.2.2 Countershading and concealment

Many animals are darker on their backs than their bellies. Another of Abbott Thayer’s early insights was that this dorso-ventral pattern could represent camouflage in the face of illumination from above [8]. Thayer realised that a uniformly coloured object, even if it matched the background colour perfectly, would receive greater irradiance on its upper surface and its underside would be in shadow. Just as an artist would use a dorso-ventral shading to create the illusion of solidity in a 2D drawing, so a real object could be revealed by its differential illumination and self-shading (Fig. 5). Thayer [8] proposed that a countershaded pattern, inverting the gradient of illumination, would counterbalance the differential shading and so disguise 3D form. At one level, this could be considered a form of background matching because there is a better match to the reflected radiance of the background when viewed from above or, in aquatic environments, where the veiling light represents a background, the side. At another level, and one which Thayer himself emphasised, the disguising of 3D form itself – the ‘flattening’ of the object – could interfere with object recognition [56, 66, 67]. As such, it could be classed as a separate type of camouflage, with certain commonalities to both background matching and disruptive colouration.

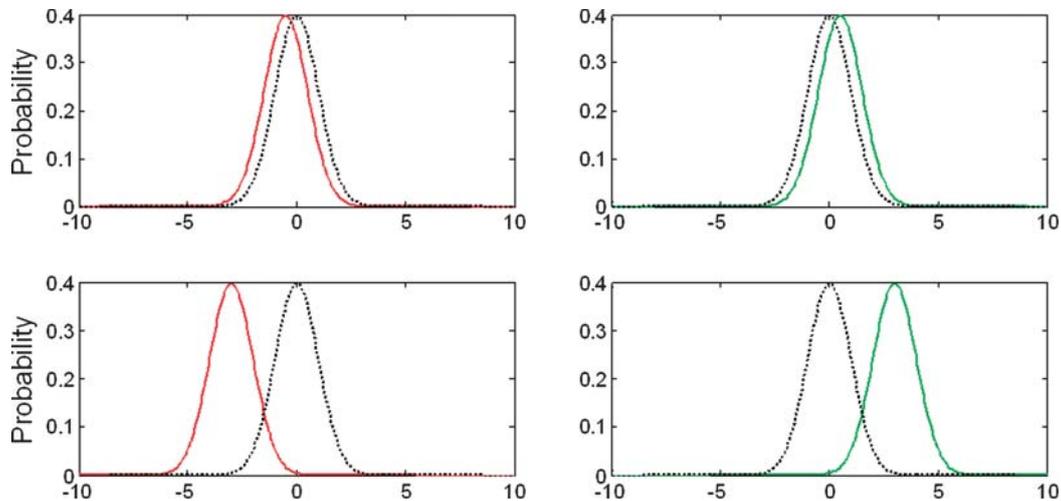


Figure 4: Conditions under which compromise camouflage may, or may not, be advantageous across multiple backgrounds. Plotted are the subjective probabilities of some object attribute along a perceptual dimension (N.B.: the perceived value as opposed to a measured attribute; in the case of light intensity, for example, perceived differences are likely to relate to the logarithm of the intensity). The Gaussian curves could represent real variation or subjective error around a single value. In the top panels, the animal with compromise camouflage (dotted curve with mean zero) is found in two sub-habitats (left and right panels) with very similar background values of the attribute (red with mean -0.5 , green with mean $+0.5$); it is well matched to each type of background so compromise camouflage may be advantageous. In the bottom panels, the animal with compromise camouflage is found in two sub-habitats with markedly different background values of the attribute (red with mean -3 , green with mean $+3$); it is poorly matched to either background, so compromise camouflage is likely to be maladaptive. In practice, it is the relationship between detectability and fitness (e.g. probability of being eaten) that will determine the success of compromise camouflage in any one situation.

For many decades, Thayer's theory that a countershaded body colouration represents camouflage through concealment of 3D shape was universally accepted. However, as more recent authors have emphasised, the near-ubiquity of the pattern of colouration does not mean that there is the same universal explanation. There are other, perfectly sound, reasons for a countershaded body colouration [56, 66, 68]. If predator threat comes mainly from above (e.g. raptors), then a background matching camouflage is only required on the dorsal surface. Likewise, pigmentation as protection from damaging UV rays is only required on the surfaces exposed to sunlight. In either case, on the reasonable assumption that pigment production has some cost, it makes economic sense to have reduced pigmentation on body parts not seen from above or regularly exposed to strong sunlight. Direct experimental evidence that a countershaded colouration actually is effective as camouflage is relatively rare [69, 70]. Nevertheless, when tightly controlled experiments have been performed, they support Thayer's theory [71, 72].

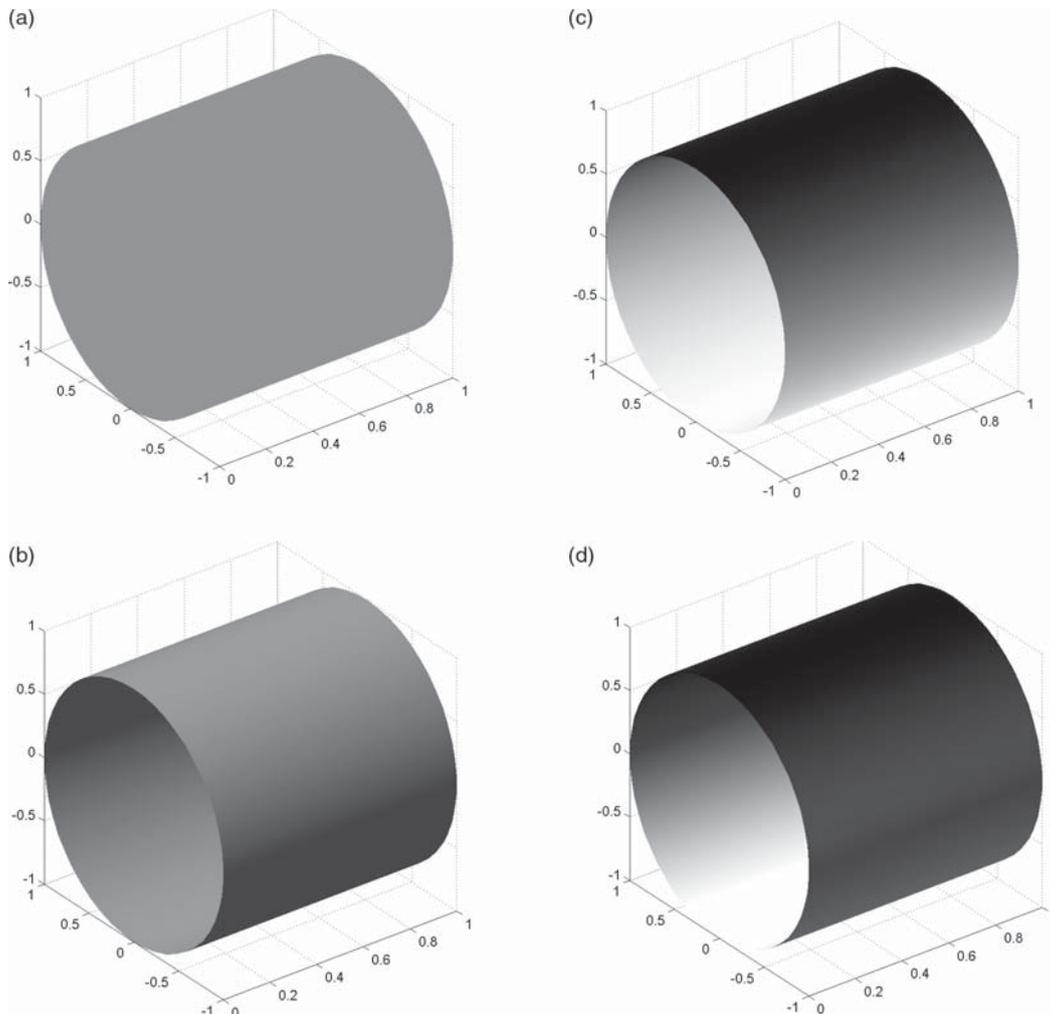


Figure 5: The homogeneous grey cylinder (a), when lit from above (b), is revealed by the gradient in reflected light created by self-shadowing. The countershaded cylinder (c), which is darker on top in a gradient that counterbalances the potential illumination, when lit from above (d) has fewer clues to its 3D form.

2.3 Disruptive colouration

The US Army Field Manual on Camouflage, Concealment and Decoys (FM-3, Department of the Army, Washington, DC, 30 August, 1999) defines disruption as ‘altering or eliminating regular patterns and target characteristics’. Whilst disruptive colouration may work in tandem with background matching [73, 74], the key distinction is that it functions through interference with object or feature *recognition* rather than detection per se [58, 75]. In fact, several phenomena are grouped under the heading ‘disruptive’ colouration (clear from the fact that the aforementioned FM-3 includes use of

pyrotechnics and flares under this heading, and Thayer frequently used the term ‘dazzle colouration’), and these probably exploit different perceptual mechanisms.

2.3.1 Outline disguise

The most familiar role of disruptive patterns, in military or animal camouflage, is to break up the outline of the body, the latter (on account of mismatches in the spatial phase of patterns, or shadows) potentially revealing an animal even if it perfectly matches the background [8, 9]. Merilaita [76] analysed the distribution of white patches on a marine isopod (*Idotea baltica*) and showed that they intercepted the edge of the animal’s body more than expected by chance. Thus, although the colour of the animal suggests simply crypsis (it is brown with white spots on a brown alga which has white spots due to epizoids living on its surface), the distribution of colours suggests an additional use of disruptive colouration. That placement of contrasting colour patches at a body’s periphery enhances concealment above and beyond similarly background-matching colours placed non-peripherally, was tested by Cuthill *et al.* [73]. They used small triangular notionally moth-like targets, baited with dead mealworms, pinned to oak trees throughout natural woodlands; they then tracked the disappearance of the mealworms over time. The higher ‘survival’ of targets with edge-disrupting patterns compared to targets without peripheral patterns, and of oak-like patterned targets compared to monochrome brown or black, illustrates the benefits of both disruptive colouration and background matching (Fig. 6).

Through computational modelling, Stevens and Cuthill [75] have shown how high contrast boundaries between disruptive pattern elements at a body’s outline interfere with detection of the (weaker) true edge. Disruptive colouration can be said to exploit edge-detection mechanisms to create false bounding contours, and so interfere with object recognition by outline. Their model, parameterised for bird vision, successfully predicted the survival of artificial prey under avian predation in the field (Fig. 6). Cuthill *et al.* [73] also showed that shades that contrasted more strongly with each other were more effective than lower-contrast shades, just as Thayer [9] and Cott [10] had proposed. Cott went further and, in what he termed the principles of differential blending combined with maximum disruptive contrast, he proposed that some colours on an animal should blend with the background, whereas others should stand out (maximally). That is, disruptive patterns may be more effective in inhibiting object recognition if some colour patches are highly conspicuous. Whether this is so remains unclear, there being evidence both for [77] and against the proposition [74, 78]. We call this the Friesian Cow Paradox (on a suggestion from Daniel Osorio): on the strong theory of disruptive colouration, a black-and-white Friesian cow should be better concealed on a black-and-grey rocky background than would a black-and-grey cow, because, while the black blends with the background, white creates the maximum disruptive contrast with black. This seems paradoxical because our intuition suggests that the conspicuousness of the white would override any benefits of disrupted object recognition; at the very least we might expect the conspicuous but unrecognised white objects to provoke closer inspection, at which point the cow is revealed. However, maybe other animals have less sophisticated object recognition algorithms, or are more wary and less curious, than humans. With only three experiments that have ever addressed this issue [74, 77, 78], and opposite conclusions drawn, this issue demands rigorous investigation [79].

Another issue that remains to be examined is the relative efficacy of chromatic vs. luminance contrast between disruptive colour patches. Schaefer and Stobbe [77], based on analysis of the contrasts present in their artificial prey, concluded that chromatic contrast was probably more important. If colour is a more reliable cue to surface properties than luminance (because of variable illumination; [80]), then an animal with homogeneous colour may be more detectable than one of homogeneous luminance. On this argument, chromatic disruptive patterns may be particularly effective. Yet luminance

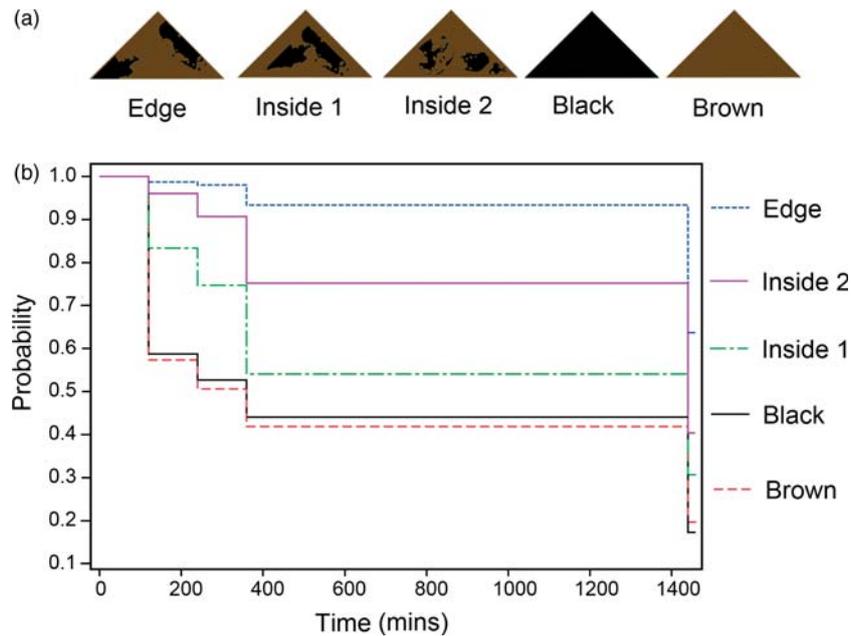


Figure 6: The benefits of disruptive coloration for concealment of outline. (a) Cuthill *et al.* [73] used artificial ‘moths’ of five different types: background-matching patterns of brown and black placed at the edge, two variants also with background-matching patterns, but placed inside the boundary of the triangle, and monochrome brown and monochrome black. (b) The ‘survival’ of the artificial prey under bird predation, when placed on oak trees in the field. The targets with patterns placed so as to disrupt the edge of the ‘wings’ disappeared at a slower rate than otherwise similar background matching targets with patterns placed inside the margins. The latter in turn survived better than the two monochrome targets. Reproduced with permission from Cuthill *et al.* (2005) *Nature* 434, 72–74 (Nature Publishing Group).

contrast present in high spatial frequencies at the body’s edge will often be the primary cue available to edge detector mechanisms, particularly in otherwise background-matching prey. Indeed, in our modelling of our own experimental prey [75], luminance edges were more readily detected than chromatic edges. We expect that the luminance/colour issue depends on spatial scale, given different receptive field sizes in the two domains. Thus, the issue needs to be addressed empirically through separation of luminance and chromatic information in factorial experimental designs, combined with computational models of object detection.

Many animals are bilaterally symmetrical and, because symmetry is a potent cue in visual search, symmetrical patterning is likely to reduce the effectiveness of crypsis [81–84]. However, not all symmetrical patterns are equally conspicuous [83], and one might predict that symmetry in patterns exhibiting high contrast disruptive patterns might be especially costly. Symmetry in the high contrast patches might be expected to be more conspicuous and the symmetry might perceptually ‘bind’ the colour patches that the disruptive patterns are designed to render separate. In an experiment on birds searching for artificial prey, we [82] found that effects of symmetry and disruptive patterning were additive, so there was no disproportionate cost of symmetry in disruptive vs. cryptic prey. However,

we used disruptive patterns in which all colour elements blended with (different) components of the background, and so the effect of symmetry on patterns with maximum disruptive contrast (as defined above) remain untested. Furthermore, all previous experiments (op. cit. [81–83]) have only compared perfectly symmetrical with completely asymmetrical prey. Crucially, it is unknown whether low levels of asymmetry in camouflage reduce detection chances, or are even detectable [85], so maybe, from a starting point of high symmetry, the strength of selection for asymmetrical cryptic colouration is negligible.

2.3.2 Disguising salient body parts

Although a body's outline is the most obvious cue to the presence of a camouflaged object, Thayer [9] and Cott [10] both emphasised the importance of disguising salient body parts such as eyes and limbs. Whilst black eye stripes are cited as examples, some eye stripes may be better described as a form of background matching: the dark stripe creates a local background against which the, otherwise conspicuous, dark circle of the eye blends. Conversely, Cott's beautiful illustrations of congruent colour patches on the legs and body of frogs (Fig. 7) exploit exactly the same mechanisms of false boundary creation as when the whole body's outline is disguised (see above). Whether this works in practice has recently been tested by using dyed pastry tubes as the 'bodies' of artificial moths, with colour patterns overlapping, or not, between 'wing' and 'body' [86]. Coincident disruptive patterns across wings and body reduced predation risk, the distinctive shape of the body being disguised through blending with disruptive patterns on the triangular wings.

2.3.3 Surface disruption, crowding effects and lateral inhibition

'Crowding' refers to an interference between closely-spaced scene elements which decreases the visibility of individual elements, and which is enhanced in developmental disorders of vision such as amblyopia [87]. Recent work on crowding [88] suggests that it shares similarities to failures of feature binding in identification tasks and that the features which are 'bound' are sampled over a surprisingly large region of visual space. Thus, high contrast elements near an edge could disrupt the perception of the (lower contrast) edge. Lateral inhibition enhances contrast locally, thus increasing the salience and potential disruptive influence of a pattern near the body's edge. Stevens *et al.* [89], using artificial targets under bird predation in the field, showed that high contrast patches interior to, but near, the edge of the targets reduced detectability. This is consistent with a lateral inhibition effect.

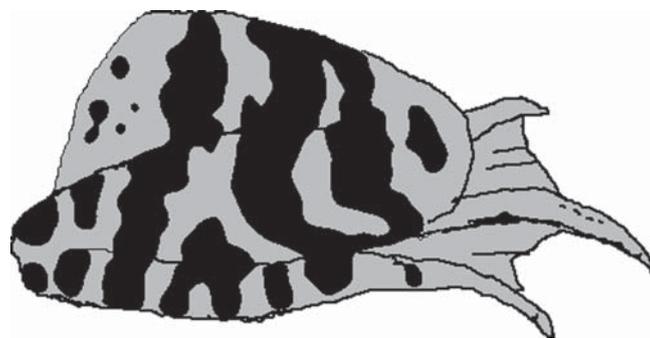


Figure 7: Coincident colours on the leg of the frog *Rana temporaria* that create false contours running across the two body parts. Source: Redrawn from Cott (1940; Figure 21).

2.3.4 Distraction of attention

While placing contrasting colour patches at the body's edge or on prominent features are the most obvious uses of disruptive colouration, other phenomena are discussed under the same banner. For example, Thayer [9] also used the term 'dazzle colouration' [19, 39, 41] and Endler [79], like many before, considered that 'conspicuous elements distract the predator's attention'. The explanations we discussed under 'outline disguise', namely, the exploitation of edge-detection mechanisms, are liable to be pre-attentive. However, colours that act via distraction of attention might be effective even if they did not occur on the body edge. Therefore, like other recent authors [57, 89], we feel that there are disruptive effects that potentially exploit different mechanisms from those reliant on edge detectors. One is the use of high contrast repetitive patterns placed at irregular angles to interfere with motion perception and target tracking [90], as in the WWI warships discussed earlier. However, 'dazzle' marks could work in static camouflage via (at least) two mechanisms.

Scenes are not analysed in a single process, but rather are inspected by an attentional mechanism which filters information at any one time and scene location. Attention is required for most object recognition tasks, and its deployment in humans is usually studied by measuring eye movements. Such eye movements are task-relevant and lead to little memory for previously-inspected information [91, 92]. The effects of camouflage on eye movements has only recently received attention [93], but we posit that, when an object is effectively camouflaged, eye movements to detect it will be more widely distributed, and more numerous. Thus (for human observers), eye tracking can provide a rich description of the visual demands of an object localisation and recognition task. If high contrast colour patches aid camouflage because they distract attention from the features of objects that aid recognition (e.g. boundaries, eyes), then we predict eye movements would be drawn to the former and, crucially, attend to boundaries, eyes, etc. less than in the absence of the distraction features. Importantly, object recognition must be impaired or the theory fails. This specific hypothesis on the mechanism involved is yet to be tested, but in fact the evidence that any natural camouflage marks act through distraction of attention is surprisingly sparse. Dimitrova *et al.* [94], in aviary experiments on blue tits (*Cyanistes caeruleus*) hunting for artificial prey, have shown that search times for prey with high contrast marks on them were longer than for similar prey that actually matched the background better. This could be a distraction effect, but the conspicuousness needed to distract attention would itself seem to be costly if it draws a predator to investigate a location that it otherwise might ignore. Indeed, Stevens *et al.* [95] found that conspicuous markings applied to otherwise cryptic artificial prey, in the field, reduced their survival. More generally, if conspicuous markings constitute a reliable predictor of the presence of a prey item, it would seem plausible that predators would learn this and any distraction effect would become irrelevant. Perhaps distraction marks could be effective if similar colours and shapes occur in the background, or on non-prey objects, at sufficient frequency that predators do not learn that they predict prey presence.

3 CONCLUSIONS AND WIDER SIGNIFICANCE

Bringing computational and psychological approaches to bear on an age-old biological question, the adaptive role of colouration in concealment, has clear benefits, but the flow of ideas is not one-way. Because visual systems have evolved to solve real-world problems, of which camouflage breaking is one, then many design features of human vision should be explicable with reference to the ecology of humans and other primates. The evolution of trichromacy as an adaptation to frugivory or folivory is a clear example [24]; the attempt to relate vision to the statistics of natural scenes is another [96–98]. An evolutionary perspective can also explain features of visual systems that are not obvious solutions to immediate problems, but instead phylogenetic constraints (or rather, legacies of ancestral solutions to different problems). Some of the (many) differences between human and, for

example, bird colour vision may be legacies of our dichromatic, largely nocturnal, mammalian past, where visual pigments, retinal oil droplets and photoreceptor specialisation for luminance and chromatic vision were lost [22]. Just as we seek to modernise the biological study of colouration through infusion of the theory and technology of computational neuroscience, so we wish to free the latter of the (usually unrecognised) constraints of modelling the world through human eyes.

ACKNOWLEDGEMENTS

We would like to thank the Biotechnology and Biological Sciences Research Council, UK, for funding our research and colleagues, particularly Neill Campbell, Martin Stevens, John Endler and Sami Merilaita, for discussions on many of the ideas we have written about.

REFERENCES

- [1] Darwin, E., *Zoonomia*, J. Johnson: London, 1794 (reprinted by Project Gutenberg www.gutenberg.org).
- [2] Wallace, A.R., *Darwinism. An Exposition of the Theory of Natural Selection with Some of its Applications*, Macmillan & Co: London, 1889.
- [3] Poulton, E.B., *The Colours of Animals: Their Meaning and Use. Especially Considered in the Case of Insects*, 2nd edn, The International Scientific Series, vol. LXVIII, Kegan Paul, Trench Trübner & Co. Ltd.: London, 1890.
- [4] Beddard, F.E., *Animal Coloration; An Account of the Principle Facts and Theories Relating to the Colours and Markings of Animals*, 2nd edn, Swan Sonnenschein: London, 1895.
- [5] Endler, J.A., Progressive background matching in moths, and a quantitative measure of crypsis. *Biological Journal of the Linnean Society*, 22(3), pp. 187–231, 1984. [doi:10.1111/j.1095-8312.1984.tb01677.x](https://doi.org/10.1111/j.1095-8312.1984.tb01677.x)
- [6] Merilaita, S., Tuomi, J. & Jormalainen, V., Optimization of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society*, 67(2), pp. 151–161, 1999. [doi:10.1111/j.1095-8312.1999.tb01858.x](https://doi.org/10.1111/j.1095-8312.1999.tb01858.x)
- [7] Bond, A.B. & Kamil, A.C., Visual predators select for crypticity and polymorphism in virtual prey. *Nature*, 415, pp. 609–613, 2002. [doi:10.1038/415609a](https://doi.org/10.1038/415609a)
- [8] Thayer, A.H., The law which underlies protective coloration. *The Auk*, 13, pp. 477–482, 1896.
- [9] Thayer, G.H., *Concealing-Coloration in the Animal Kingdom: An Exposition of the Laws of Disguise Through Color and Pattern: Being a Summary of Abbott H. Thayer's Discoveries*, Macmillan: New York, 1909.
- [10] Cott, H.B., *Adaptive Coloration in Animals*, Methuen & Co. Ltd.: London, 1940.
- [11] Rolls, E.T. & Deco, G., *Computational Neuroscience of Vision*, Oxford University Press: Oxford, 2002.
- [12] Bennett, A.T.D., Cuthill, I.C. & Norris, K.J., Sexual selection and the mismeasure of color. *American Naturalist*, 144(5), pp. 848–860, 1994. [doi:10.1086/285711](https://doi.org/10.1086/285711)
- [13] Endler, J.A., On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society*, 41(4), pp. 315–352, 1990. [doi:10.1111/j.1095-8312.1990.tb00839.x](https://doi.org/10.1111/j.1095-8312.1990.tb00839.x)
- [14] Endler, J.A., Signals, signal conditions, and the direction of evolution. *American Naturalist*, 139(Suppl.), pp. S125–S153, 1992. [doi:10.1086/285308](https://doi.org/10.1086/285308)
- [15] Guilford, T. & Dawkins, M.S., Receiver psychology and the evolution of animal signals. *Animal Behaviour*, 42, pp. 1–14, 1991. [doi:10.1016/S0003-3472\(05\)80600-1](https://doi.org/10.1016/S0003-3472(05)80600-1)
- [16] Ryan, M.J. & Keddy-Hector, A., Directional patterns of female mate choice and the role of sensory biases. *American Naturalist*, 139, pp. S4–S35, 1992. [doi:10.1086/285303](https://doi.org/10.1086/285303)

- [17] Endler, J.A. & Basolo, A.L., Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, **13**(10), pp. 415–420, 1998. [doi:10.1016/S0169-5347\(98\)01471-2](https://doi.org/10.1016/S0169-5347(98)01471-2)
- [18] ten Cate, C. & Rowe, C., Biases in signal evolution: learning makes a difference. *Trends in Ecology and Evolution*, **22**(7), pp. 380–387, 2007. [doi:10.1016/j.tree.2007.03.006](https://doi.org/10.1016/j.tree.2007.03.006)
- [19] Behrens, R.R., *False Colors: Art, Design and Modern Camouflage*, Bobolink Books: Dysart, Iowa, 2002.
- [20] Behrens, R.R., Camouflage, art and Gestalt. *North American Review*, **265**(4), pp. 8–18, 1980.
- [21] Behrens, R.R., Visual art and camouflage. *Leonardo*, **11**(3), pp. 203–204, 1978. [doi:10.2307/1574143](https://doi.org/10.2307/1574143)
- [22] Cuthill, I.C., Color Perception, in: *Bird Coloration. Mechanisms and Measurement*, eds G.E. Hill & K.J. McGraw, vol. 1, Harvard University Press: Cambridge MA, pp. 3–40, 2006.
- [23] Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S. & Hunt, S., Ultraviolet vision in birds. *Advances in the Study of Behaviour*, **29**, pp. 159–214, 2000. [doi:10.1016/S0065-3454\(08\)60105-9](https://doi.org/10.1016/S0065-3454(08)60105-9)
- [24] Surridge, A.K., Osorio, D. & Mundy, N.I., Evolution and selection of trichromatic vision in primates. *Trends in Ecology & Evolution*, **18**(4), pp. 198–205, 2003. [doi:10.1016/S0169-5347-\(03\)00012-0](https://doi.org/10.1016/S0169-5347-(03)00012-0)
- [25] Vorobyev, M., Coloured oil droplets enhance colour discrimination. *Proceedings of the Royal Society of London B*, **270**(1521), pp. 1255–1261, 2003. [doi:10.1098/rspb.2003.2381](https://doi.org/10.1098/rspb.2003.2381)
- [26] Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C., Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A*, **183**, pp. 621–633, 1998. [doi:10.1007/s003590050286](https://doi.org/10.1007/s003590050286)
- [27] Lovell, P.G., Tolhurst, D.J., Parraga, C.A., Baddeley, R., Leonards, U. & Troscianko, J., Stability of the color-opponent signals under changes of illuminant in natural scenes. *Journal of the Optical Society of America A*, **22**(10), pp. 2060–2071, 2005. [doi:10.1364/JOSAA.22.002060](https://doi.org/10.1364/JOSAA.22.002060)
- [28] Lovell, P.G., Tolhurst, D.J., Parraga, C.A., Baddeley, R.J., Leonards, U., Troscianko, J. & Troscianko, T., Opponent channel responses to changes in the illuminant of natural scenes for primates and birds. *Perception*, **34**, pp. 59, 2005.
- [29] Osorio, D., Ruderman, D.L. & Cronin, T.W., Estimation of errors in luminance signals encoded by primate retina resulting from sampling of natural images with red and green cones. *Journal of the Optical Society of America A*, **15**(1), pp. 16–22, 1998. [doi:10.1364/JOSAA.15.000016](https://doi.org/10.1364/JOSAA.15.000016)
- [30] Osorio, D. & Vorobyev, M., Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society of London B, Biological Sciences*, **263**, pp. 593–599, 1996. [doi:10.1098/rspb.1996.0089](https://doi.org/10.1098/rspb.1996.0089)
- [31] Jones, C.D. & Osorio, D., Discrimination of orientated visual textures by poultry chicks. *Vision Research*, **44**, pp. 83–89, 2004. [doi:10.1016/j.visres.2003.08.014](https://doi.org/10.1016/j.visres.2003.08.014)
- [32] Ghim, M.M. & Hodos, W., Spatial contrast sensitivity of birds. *Journal of Comparative Physiology A*, **192**(5), pp. 523–534, 2006. [doi:10.1007/s00359-005-0090-5](https://doi.org/10.1007/s00359-005-0090-5)
- [33] Troscianko, T., Benton, C.P., Lovell, P.G., Tolhurst, D.J. & Pizlo, Z., Camouflage and visual perception. *Philosophical Transactions of the Royal Society of London B*, **364**(1516), pp. 449–461, 2009. [doi:10.1098/rstb.2008.0218](https://doi.org/10.1098/rstb.2008.0218)
- [34] Bond, A.B. & Kamil, A.C., Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, pp. 3214–3219, 2006. [doi:10.1073/pnas.0509963103](https://doi.org/10.1073/pnas.0509963103)
- [35] Pietrewicz, A.T. & Kamil, A.C., Visual detection of cryptic prey by blue jays (*Cyanocitta cristata*). *Science*, **195**, pp. 580–582, 1977. [doi:10.1126/science.195.4278.580](https://doi.org/10.1126/science.195.4278.580)
- [36] Pietrewicz, A.T. & Kamil, A.C., Search image formation in the Blue Jay (*Cyanocitta cristata*). *Science*, **204**, pp. 1332–1333, 1979. [doi:10.1126/science.204.4399.1332](https://doi.org/10.1126/science.204.4399.1332)

- [37] Duncan, J. & Humphreys, G.W., Visual search and stimulus similarity. *Psychological Review*, **96**(3), pp. 433–458, 1989. [doi:10.1037/0033-295X.96.3.433](https://doi.org/10.1037/0033-295X.96.3.433)
- [38] Brady, M.J. & Kersten, D., Bootstrapped learning of novel objects. *Journal of Vision*, **3**(6), pp. 413–422, 2003. [doi:10.1167/3.6.2](https://doi.org/10.1167/3.6.2)
- [39] Behrens, R.R., The theories of Abbott H. Thayer: father of camouflage. *Leonardo*, **21**, pp. 291–296, 1988. [doi:10.2307/1578658](https://doi.org/10.2307/1578658)
- [40] Behrens, R.R., *Art & Camouflage*, North American Review: Cedar Falls, Iowa, 1981.
- [41] Behrens, R.R., The role of artists in ship camouflage during World War I. *Leonardo*, **32**, pp. 53–59, 1999. [doi:10.1162/002409499553000](https://doi.org/10.1162/002409499553000)
- [42] Newark, T., Newark, Q. & Borsarello, J.F., *Brassey's Book of Camouflage*, Brassey's (UK) Ltd.: Littlehampton, 1996.
- [43] Newark, T. & Miller, J., *Camouflage*, Thames & Hudson: London, 2007.
- [44] Church, S.C., Bennett, A.T.D., Cuthill, I.C. & Partridge, J.C., Avian ultraviolet vision and its implications for insect protective coloration, in: eds H.V. Emden & M. Rothschild, *Insect and Bird Interactions*, Intercept Press: Andover, pp. 165–184, 2004.
- [45] Church, S.C., Bennett, A.T.D., Cuthill, I.C. & Partridge, J.C., Ultraviolet cues affect the foraging behaviour of blue tits. *Proceedings of the Royal Society of London B*, **265**, pp. 1509–1514, 1998. [doi:10.1098/rspb.1998.0465](https://doi.org/10.1098/rspb.1998.0465)
- [46] Harvey, P.H. & Pagel, M.D., *The Comparative Method in Evolutionary Biology*, Oxford University Press: Oxford, 1991.
- [47] Andersson, M., *Sexual Selection*, Princeton University Press: Princeton, NJ, 1994.
- [48] Stuart-Fox, D. & Moussalli, A., Selection for social signalling drives the evolution of chameleon colour change. *PLoS Biology*, **6**(1), pp. e25, 2008. [doi:10.1371/journal.pbio.0060025](https://doi.org/10.1371/journal.pbio.0060025)
- [49] Hanlon, R., Cephalopod dynamic camouflage. *Current Biology*, **17**(11), pp. R400–R404, 2007. [doi:10.1016/j.cub.2007.03.034](https://doi.org/10.1016/j.cub.2007.03.034)
- [50] Hanlon, R.T., Forsythe, J.W. & Joneschild, D.E., Crypsis, conspicuous, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biological Journal of the Linnean Society*, **66**, pp. 1–22, 1999. [doi:10.1111/j.1095-8312.1999.tb01914.x](https://doi.org/10.1111/j.1095-8312.1999.tb01914.x)
- [51] Endler, J.A., An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society*, **16**(1), pp. 25–31, 1981. [doi:10.1111/j.1095-8312.1981.tb01840.x](https://doi.org/10.1111/j.1095-8312.1981.tb01840.x)
- [52] Endler, J.A., Interactions between predators and prey, in: eds J.R. Krebs & N.B. Davis, *Behavioural Ecology: an Evolutionary Approach*, 3rd edn, Blackwell: Oxford, pp. 169–196, 1991.
- [53] Endler, J.A., Frequency-dependent predation, crypsis and aposematic coloration. *Philosophical Transactions of the Royal Society of London B*, **319**(1196), pp. 505–523, 1988. [doi:10.1098/rstb.1988.0062](https://doi.org/10.1098/rstb.1988.0062)
- [54] Cook, L.M., Changing views on melanic moths. *Biological Journal of the Linnean Society*, **69**(3), pp. 431–441, 2000. [doi:10.1111/j.1095-8312.2000.tb01215.x](https://doi.org/10.1111/j.1095-8312.2000.tb01215.x)
- [55] Coyne, J.A., Of moths and men: intrigue, tragedy and the peppered moth. *Nature*, **418**(6893), pp. 19–20, 2002. [doi:10.1038/418019a](https://doi.org/10.1038/418019a)
- [56] Ruxton, G.D., Sherratt, T.N. & Speed, M.P., *Avoiding Attack*, Oxford University Press: Oxford, 2004. [doi:10.1093/acprof:oso/9780198528609.001.0001](https://doi.org/10.1093/acprof:oso/9780198528609.001.0001)
- [57] Stevens, M. & Merilaita, S., Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society of London B*, **364**, pp. 423–427, 2009. [doi:10.1098/rstb.2008.0217](https://doi.org/10.1098/rstb.2008.0217)

- [58] Stevens, M. & Merilaita, S., Defining disruptive coloration and distinguishing its functions. *Philosophical Transactions of the Royal Society of London B*, **364(1516)**, pp. 481–488, 2009. [doi:10.1098/rstb.2008.0216](https://doi.org/10.1098/rstb.2008.0216)
- [59] Merilaita, S. & Lind, J., Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proceedings of the Royal Society B*, **272**, pp. 665–670, 2005. [doi:10.1098/rspb.2004.3000](https://doi.org/10.1098/rspb.2004.3000)
- [60] Stevens, M., Cuthill, I.C., Párraga, C.A. & Troscianko, T., The effectiveness of disruptive coloration as a concealment strategy, in: eds J.-M. Alonso, *et al.*, *Visual Perception (Part 2): Progress in Brain Research*, vol. 155, Elsevier: Amsterdam, pp. 49–65, 2006.
- [61] Vorobyev, M. & Osorio, D., Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London B*, **265**, pp. 351–358, 1998. [doi:10.1098/rspb.1998.0302](https://doi.org/10.1098/rspb.1998.0302)
- [62] Endler, J.A. & Meilke, P.W.J., Comparing color patterns as birds see them. *Biological Journal of the Linnean Society*, **86**, pp. 405–431, 2005. [doi:10.1111/j.1095-8312.2005.00540.x](https://doi.org/10.1111/j.1095-8312.2005.00540.x)
- [63] Lovell, P.G., Párraga, C.A., Troscianko, T., Ripamonti, C. & Tolhurst, D., Evaluation of a multi-scale color model for visual difference prediction. *ACM Transactions on Applied Perception*, **3**, pp. 155–178, 2006. [doi:10.1145/1166087.1166089](https://doi.org/10.1145/1166087.1166089)
- [64] Merilaita, S., Lyytinen, A. & Mappes, J., Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B*, **268(1479)**, pp. 1925–1929, 2001. [doi:10.1098/rspb.2001.1747](https://doi.org/10.1098/rspb.2001.1747)
- [65] Houston, A.I., Stevens, M. & Cuthill, I.C., Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behavioral Ecology*, **18**, pp. 769–775, 2007. [doi:10.1093/beheco/arm039](https://doi.org/10.1093/beheco/arm039)
- [66] Ruxton, G.D., Speed, M.P. & Kelly, D.J., What, if anything, is the adaptive function of countershading? *Animal Behaviour*, **68**, pp. 445–451, 2004. [doi:10.1016/j.anbehav.2003.12.009](https://doi.org/10.1016/j.anbehav.2003.12.009)
- [67] Rowland, H.M., From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philosophical Transactions of the Royal Society of London B*, **364(1516)**, pp. 519–527, 2009.
- [68] Kiltie, R.A., Countershading: universally deceptive or deceptively universal. *Trends in Ecology & Evolution*, **3(1)**, pp. 21–23, 1988.
- [69] Speed, M.P., Kelly, D.J., Davidson, A.M. & Ruxton, G.D., Countershading enhances crypsis with some bird species but not others. *Behavioral Ecology*, **16**, pp. 327–334, 2004.
- [70] Edmunds, M. & Dewhirst, R.A., The survival value of countershading with wild birds as predators. *Biological Journal of the Linnean Society*, **51(4)**, pp. 447–452, 1994.
- [71] Rowland, H.M., Cuthill, I.C., Harvey, I.F., Speed, M.P. & Ruxton, G.D., Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. *Proceedings of the Royal Society B*, **275(1651)**, pp. 2539–2545, 2008.
- [72] Rowland, H.M., Speed, M.P., Ruxton, G.D., Edmunds, M., Stevens, M. & Harvey, I.F., Countershading enhances cryptic protection: an experiment with wild birds and artificial prey. *Animal Behaviour*, **74**, pp. 1249–1258, 2007.
- [73] Cuthill, I.C., Stevens, M., Sheppard, J., Maddocks, T., Párraga, C.A. & Troscianko, T.S., Disruptive coloration and background pattern matching. *Nature*, **434**, pp. 72–74, 2005.
- [74] Stevens, M., Cuthill, I.C., Windsor, A.M.M. & Walker, H.J., Disruptive contrast in animal camouflage. *Proceedings of The Royal Society B*, **273(1600)**, pp. 2433–2438, 2006.
- [75] Stevens, M. & Cuthill, I.C., Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings of the Royal Society B*, **273(1598)**, pp. 2141–2147, 2006.
- [76] Merilaita, S., Crypsis through disruptive coloration in an isopod. *Proceedings of the Royal Society B*, **265(1401)**, pp. 1059–1064, 1998.

- [77] Schaefer, H.M. & Stobbe, N., Disruptive coloration provides camouflage independent of background matching. *Proceedings of the Royal Society B*, **273(1600)**, pp. 2427–2432, 2006.
- [78] Fraser, S., Callahan, A., Klassen, D. & Sherratt, T.N., Empirical tests of the role of disruptive coloration in reducing detectability. *Proceedings of the Royal Society B*, **274(1615)**, pp. 1325–1331, 2007.
- [79] Endler, J.A., Disruptive and cryptic coloration. *Proceedings of the Royal Society B*, **273**, pp. 2425–2426, 2006.
- [80] Osorio, D. & Vorobyev, M., Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proceedings of the Royal Society of London B*, **272**, pp. 1745–1752, 2005.
- [81] Cuthill, I.C., Hiby, E. & Lloyd, E., The predation costs of symmetrical cryptic coloration. *Proceedings of the Royal Society B*, **273**, pp. 1267–1271, 2006.
- [82] Cuthill, I.C., Stevens, M., Windsor, A.M.M. & Walker, H.J., The effects of pattern symmetry on detection of disruptive and background-matching coloration. *Behavioral Ecology*, **17(5)**, pp. 828–832, 2006.
- [83] Merilaita, S. & Lind, J., Great tits (*Parus major*) searching for artificial prey: implications for cryptic coloration and symmetry. *Behavioral Ecology*, **17**, pp. 84–87, 2006.
- [84] Osorio, D., Symmetry versus crypsis. *Trends in Ecology and Evolution*, **9(9)**, pp. 346–346, 1994.
- [85] Swaddle, J.P., Limits to length asymmetry detection in starlings: implications for biological signalling. *Proceedings of the Royal Society of London B*, **266(1426)**, pp. 1299–1303, 1999.
- [86] Cuthill, I.C. & Székely, A., Coincident disruptive coloration. *Philosophical Transactions of the Royal Society of London B*, **364**, pp. 489–496, 2009.
- [87] Levi, D.M. & Klein, S.A., Vernier acuity, crowding, and amblyopia. *Vision Research*, **25**, pp. 979–991, 1985.
- [88] Pelli, D.G., Palomares, M. & Majaj, N.J., Crowding is unlike ordinary masking: distinguishing feature integration from detection. *Journal of Vision*, **4**, pp. 1136–1169, 2004.
- [89] Stevens, M.S., Winney, I.S., Cantor, A. & Graham, J., Outline and surface disruption in animal camouflage. *Proceedings of the Royal Society B*, **276**, pp. 781–786, 2009.
- [90] Stevens, M., Yule, D.H. & Ruxton, G.D., Dazzle coloration and prey movement. *Proceedings of the Royal Society B*, **275**, pp. 2639–2643, 2008.
- [91] Irwin, D.E. & Zelinsky, G.J., Eye movements and scene perception: memory for things observed. *Perception & Psychophysics*, **64(6)**, pp. 882–895, 2002.
- [92] Tatler, B.W., Gilchrist, I.D. & Land, M.F., Visual memory for objects in natural scenes: from fixations to object files. *Quarterly Journal of Experimental Psychology A*, **58(5)**, pp. 931–960, 2005.
- [93] Neider, M.B. & Zelinsky, G.J., Searching for camouflaged targets: effects of target-background similarity on visual search. *Vision Research*, **46(14)**, pp. 2217–2235, 2006.
- [94] Dimitrova, M., Stobbe, N., Schaefer, H.M. & Merilaita, S., Concealed by conspicuousness: distractive prey markings and backgrounds. *Proceedings of the Royal Society B*, in press, 276, pp. 1905–1910, 2009.
- [95] Stevens, M., Graham, J., Winney, I.S. & Cantor, A., Testing Thayer’s hypothesis: can camouflage work by distraction? *Biology Letters*, **4**, pp. 648–650, 2008.
- [96] Wachtler, T., Lee, T.W. & Sejnowski, T.J., Chromatic structure of natural scenes. *Journal of the Optical Society of America A*, **18(1)**, pp. 65–77, 2001.
- [97] Sekuler, A.B. & Bennett, P.J., Visual neuroscience: resonating to natural images. *Current Biology*, **11(18)**, pp. R733–R736, 2001.
- [98] Tolhurst, D.J. & Tadmor, Y., Discrimination of spectrally blended natural images: optimisation of the human visual system for encoding natural images. *Perception*, **29(9)**, pp. 1087–1100, 2000.