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Introduction

Animal camouflage: current issues and new perspectives

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1. THE IMPORTANCE AND HISTORY OF CAMOUFLAGE RESEARCH

The study of camouflage has a long history in biology, and the numerous ways of concealment and disguise found in the animal kingdom provided Darwin and Wallace with important examples for illustrating and defending their ideas of natural selection and adaptation. Thus, various forms of camouflage have become classical examples of evolution. In a broader sense, camouflage has been adopted by humans, most notably by the military and hunters, but it has also influenced other parts of society, for example, arts, popular culture and design.

Animals use camouflage to make detection or recognition more difficult, with most examples associated with visual camouflage involving body coloration. However, in addition to coloration, camouflage may make use of morphological structures or material found in the environment, and may even act against senses other than vision (Ruxton 2009). In nature, some of the most striking examples of adaptation can be found with respect to avoiding being detected or recognized, with the strategies employed diverse, and sometimes extraordinary. Such strategies can include using markings to match the colour and pattern of the background, as in various moths (e.g. Kettlewell 1955), and to break up the appearance of the body, as in some marine isopods (Merilaita 1998). Camouflage is a technique especially useful if the animal can change colour to match the background on which it is found, such as can some cephalopods (Hanlon & Messenger 1988) and chameleons (Stuart-Fox *et al.* 2008). Further remarkable examples include insects bearing an uncanny resemblance to bird droppings (Hebert 1974) or fish resembling fallen leaves on a stream bed (Sazima *et al.* 2006), to even making the body effectively transparent, as occurs in a range of, in particular, aquatic species (Johnsen 2001; Carvalho *et al.* 2006). Examples such as

leaf mimicry in butterflies helped convince Wallace (1889), for example, of the power of natural selection. Other strategies may even stretch to the use of bioluminescence to hide shadows generated in aquatic environments (Johnsen *et al.* 2004), and include 'decorating' the body with items from the general environment, such as do some crabs (Hultgren & Stachowicz 2008). This diversity of camouflage strategies is a testament to the importance of avoiding predation, as this is surely one of the most important selection pressures an organism can face. Concealment represents one of the principal ways to do so.

Camouflage research has for a significant length of time linked biology, art and the military, stemming from the work and influence of Abbott Thayer and Hugh Cott. Indeed, Thayer's (1896, 1909) and Cott's (1940) works are still hugely influential and contain a range of untested ideas. However, in spite of its long history and widespread occurrence, research on natural camouflage has not progressed as rapidly as many other areas of adaptive coloration, especially in the last 60–70 years. There are several reasons for this, including that human perceptions have often been used to subjectively assess a range of protective markings, rather than working from the perspective of the correct receiver. In general, the mechanisms of camouflage have often been erroneously regarded as intuitively obvious. Furthermore, many researchers may have found more showy types of animal coloration, for example, aposematism, mimicry and sexual ornamentation, more exciting than the often (but not always) duller colours and patterns used for camouflage. Thus, until recently, the study of natural camouflage has progressed slowly; little had changed in our understanding of how camouflage works since the landmark book of Hugh Cott in 1940. Therefore, many of the striking examples of camouflage, such as those discussed above, have not been formally tested, and the benefit that these different types of concealment bring to animals has rarely been quantified in survival terms and how they specifically work. However, gradually an appreciation of rigorous and objective experimental and analytical methods has increased over descriptive, often subjective, methods in the study of camouflage. Norris & Lowe's (1964)

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Table 1. Terms and definitions relevant to visual camouflage.

camouflage, meaning all strategies involved in concealment, including prevention of detection and recognition

crypsis (initially preventing detection):

(*a*) *background matching*, where the appearance generally matches the colour, lightness and pattern of one (specialist) or several (compromise) background types

(*b*) *self-shadow concealment*, where directional light, which would lead to the creation of shadows, is cancelled out by countershading

(*c*) *obliterative shading*, where countershading leads to the obliteration of three-dimensional form

(*d*) *disruptive coloration*, being 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

(*e*) *flicker-fusion camouflage*, where markings such as stripes blur during motion to match the colour/lightness of the general background, preventing detection of the animal when in motion

(*f*) *distractive markings*, which direct the 'attention' or gaze of the receiver from traits that would give away the animal (such as the outline)

masquerade, where recognition is prevented by resembling an uninteresting object, such as a leaf or a stick

motion dazzle, where markings make estimates of speed and trajectory difficult by the receiver

motion camouflage, movement in a fashion that decreases the probability of movement detection

first objective quantification of coloration was important, and in particular, the work by Endler (1978, 1984) pioneered and promoted the rigorous study of animal coloration and had a broader influence outside of the field of camouflage.

In the last few years, there has been an explosion of camouflage studies. The renewed interest in concealment has partly arisen following a growing body of research into warning coloration and mimicry, and with increased knowledge of visual perception and computer science. In addition, trying to understand the proximate mechanisms involved in different forms of camouflage includes the need for integrating psychological and ecological factors. This can enable an understanding of the natural selection and constraints imposed on camouflage, which both influence the optimization and evolution of the camouflage strategies. Currently, there are a growing number of researchers interested in camouflage, producing more interdisciplinary links between biology, visual psychology, computer science and art. It is an exciting time to study camouflage, and the contributions to this theme represent this growing interdisciplinary effort.

2. DEFINING CAMOUFLAGE STRATEGIES

During the many years naturalists have been interested in camouflage, a number of different terms have been used to describe the various suggested ways of concealment. This diverse terminology means that, for some phenomena, there are several synonymous names, and that some terms have been used differently by different authors and over time. It is important for clarity to use coherent and consistent terminology, and one aim of this theme issue is to try to clarify this

somewhat confusing use of terms. Above, we suggest a list of terms and definitions (table 1). In defining different forms of camouflage, we use the term 'function' to describe broadly what the adaptation may do (e.g. breaking up form, distracting attention), and the term 'mechanism' to refer to specific perceptual processes (e.g. exploiting edge detection mechanisms, lateral inhibition). Ideally, camouflage strategies should be defined by how they use or exploit specific mechanistic processes. However, one current problem in defining different forms of camouflage is that we do not know enough about the perceptual mechanisms involved. This is clearly a huge area of work for the future.

With respect to visual camouflage, some authors have argued that defining camouflage types based primarily on appearance is useful. We do not doubt that categorisation of appearances has merits in some circumstances, such as for comparative studies (e.g. Stoner *et al.* 2003). However, others advocate far more extensive uses of descriptive terms. For example, Hanlon (2007) argues that animal camouflage patterns can effectively be defined by three basic pattern classes, 'uniform', 'mottle' and 'disruptive', and that while initially based on appearances in cephalopods, which can adjust their patterning, the grouping seems to apply to other animals as well. We feel this approach is counterproductive and will lead to confusion, particularly because such an approach does not aid the understanding of how different forms of camouflage function or the different visual mechanisms involved and how these, in turn, impose selection on animal coloration. Instead, definitions should be based on what camouflage does (even if the specific visual processes are uncertain). This is crucial because similar pattern types may have entirely different functions in different animals and circumstances. Stripes, for instance, which Hanlon (2007) groups as disruptive could equally well function in background matching, distraction, as warning signals, or with making estimates of speed and trajectory difficult (motion dazzle), depending on the context. In addition, differences in visual perception across animal groups render these subjective categories ineffective because, for example, a pattern may appear mottled to a predator with good visual acuity, or in close proximity, but may appear uniform if an animal is unable to resolve the markings. Camouflage colorations are also more likely to be a continuum and mixture of features, varying much more and along several dimensions than suggested by the three proposed, discrete 'types' alone. Finally, defining camouflage based on appearance alone risks confounding camouflage functions with developmental limitations. Instead, aiming to understand functions (and eventually mechanisms) gives much greater insight into the selection imposed on the optimization of anti-predator coloration and how they interrelate and differ.

(a) *Definitions*

Below, and in table 1, we define the main forms of concealment, and how they work. We use the term *camouflage* to describe all forms of concealment, including those strategies preventing detection

(crypsis) and recognition (e.g. masquerade). We use 'cryptic coloration' and related words to refer to coloration which in the first place prevents detection. In this, we include the terms *cryptic* (meaning hard to detect/concealed), *crypsis* and *cryptic coloration* (e.g. the use of colours and patterns to prevent detection; cf. crypsis versus aposematism). We include several forms of camouflage under crypsis, including countershading, background matching and disruptive coloration. We do not discuss all of these below, but rather outline some of the main disagreements at present.

(b) *What is 'crypsis'?*

The use of the term crypsis has caused disagreement over the last few years, but we argue that it comprises all traits that reduce an animal's risk of becoming detected when it is potentially perceivable to an observer. In terms of vision, the term crypsis includes features of physical appearance (e.g. coloration), but also behavioural traits, or both, to prevent detection. To distinguish crypsis from hiding (such as simply being hidden behind an object in the environment), we argue that the features of the animal should reduce the risk of detection when the animal is in plain sight, if those traits are to be considered crypsis. Hiding behind an object, for example, does not constitute crypsis (see also Edmunds 1974), because there is no chance of the receiver detecting the animal. We opt for this usage for several reasons. First, this is broadly consistent with the literal and historical terminology; (albeit briefly) Poulton (1890) used the term to describe colours whose 'object is to effect concealment'; Cott (1940) uses cryptic appearance to 'encompass modifications of structure, colour, pattern and habit'; and Edmunds (1974) defines the terms crypsis and cryptic, in terms of predators failing to detect prey. By contrast, some researchers have defined crypsis as synonymous with background matching, largely because they rapidly adopted Endler's (1978, 1984) definition of crypsis, where an animal should maximize camouflage by matching a random sample of the background at the time and location where the risk of predation is the greatest. However, in recent years, it has become clear that the above definition is wrong on a number of grounds. First, matching a random sample of the background does not necessarily minimize the risk of detection when an animal is found on several backgrounds (cf. 'compromise camouflage'; Merilaita *et al.* 1999, 2001; Houston *et al.* 2007; Sherratt *et al.* 2007). Second, the risk of detection can be decreased by disruptive markings, where the emphasis is on specifically breaking up tell-tale features of the animal. Similar points can be made for other camouflage strategies, such as self-shadow concealment (SSC). Finally, matching a random sample on even one background does not guarantee a high level of background matching or crypsis (Merilaita & Lind 2005). This idea of random sample is problematic even on simple backgrounds, because the animal may still be visible due to spatial or phase 'mismatch' with important background features, such as edges (Kelman *et al.* 2007). For these reasons, we simply refer to crypsis as including colours and patterns that prevent detection (but not necessarily recognition).

Despite the above, it is a subject of some debate as to which other forms of camouflage also prevent detection and should therefore be included under crypsis along with background matching (see below). One of the main arguments surrounding what should be included under crypsis regards disruptive coloration, and whether this prevents recognition or detection. While some researchers (e.g. Stobbe & Schaefer 2008) assert that disruption prevents recognition of the animal, we argue that disruptive coloration initially prevents detection by breaking up form (which in turn may also influence recognition) and is therefore a type of crypsis. For instance, disruptive coloration seemingly works by breaking up edge information, so that a predator may not detect a prey item because the salient outlines that may give away its presence have been destroyed.

In countershading, an animal possesses a darker surface on the side that typically faces light and a lighter opposite side. Most researchers seem to now agree that the term refers to the appearance of the coloration and not the function, especially as countershading may be involved with several functions. These include compensation of own shadow (SSC), simultaneously matching two different backgrounds in two different directions (background matching), changing the three-dimensional appearance of the animal, protection from UV light and others (Ruxton *et al.* 2004). For the purposes of this theme issue, the two most relevant functions are SSC, where the creation of shadows is cancelled out by countershading, and 'obliterative shading', where the shadow/light cues for three-dimensional form of the animal are destroyed (Thayer 1896). We argue that SSC prevents detection by removing conspicuous shadows, and obliterative shading prevents detection by removing salient three-dimensional information, so group both these under crypsis.

In principle, some of the issues of defining types of camouflage may be cleared up by specifically defining detection. However, at present, there are few good ways of fully defining camouflage object properties correctly with respect to the relevant viewer's perception. Understandably, there is a real issue that distinguishing between detection and recognition in experimental situations is very difficult, and it follows that preventing detection may also lead to a prevention of recognition, e.g. the receiver does not recognize the form of the animal because it does not detect its edges. What matters is what the colour patterning or other camouflage features primarily do. As such, masquerade need not prevent detection but it does prevent recognition, whereas disruptive coloration and SSC, along with background matching, primarily prevent detection.

An additional form of camouflage, distractive markings, is also included under crypsis because they seemingly prevent detection. Although the distractive markings should be detected, the outline of the body or other revealing characteristics, and thus the main part of the animal, is not. However, we note that little work has specifically investigated distractive markings, and that one could also argue that if part of the object is

detected, then recognition of the prey is also prevented. Clearly, there is much more work to be done.

(c) Other forms of camouflage

We make a distinction between dazzle or distractive markings and disruptive coloration (cf. Stevens 2007) in contrast to Cott (1940), who fused these different concepts in his description of the function of disruptive coloration. Our use of dazzle coloration is also different from 'flicker-fusion camouflage' and startle displays (which involve the sudden appearance of markings, such as spots and bright colours; table 1). Although the term masquerade has sometimes been used synonymously with background matching, generally, it seems uncontroversial that masquerade acts against recognition and is therefore a different form of concealment. Motion camouflage is a term for something quite different, where an animal appears not to be moving at all by 'tricking' the receiver's visual system by moving in a certain way.

3. CONTRIBUTIONS TO THE THEME ISSUE

In this issue there are a range of contributions from researchers spanning multiple disciplines, from behavioural ecology, experimental psychology and computer science, to art history. Hanlon et al. (2009) review and discuss the main camouflage in cephalopods, which have a remarkable ability for rapid colour change. Zylinski et al. (2009) present experiments and discussion about how different forms of camouflage in cuttlefish are produced by features such as edges in the background, and what this can tell us about visual perception in cuttlefish and other animals. Troscianko et al. (2009) apply principles from visual psychology and physiology to discuss various methods involved in visual perception, and how they are important in producing effective camouflage and camouflage breaking. A range of other animals are also capable of colour change, and Stuart-Fox & Moussalli (2009) discuss what these animals, in particular chameleons, can reveal about the proximate and ultimate factors underlying camouflage, signalling strategies and thermoregulation. Théry & Casas (2009) discuss the various functions of spider coloration, webs and decorations, including colour change and concealment. Stevens & Merilaita (2009) synthesize and discuss the principles involved in disruptive coloration, and how disruption relates to other forms of camouflage. One aspect of disruptive coloration is coincident disruption, used to conceal salient body parts such as legs and wings, and Cuthill & Székely (2009) present the first experimental support for this theory with field experiments presenting artificial prey to wild avian predators. Behrens (2009) discusses how art, the military and nature influenced the ideas of Abbott Thayer in producing his theories of camouflage, and how Thayer in turn influenced these fields. Webster et al. (2009) investigate the camouflage and resting orientation of wild moths, using detection experiments with human 'predators', showing that the coloration and resting position of the moths produces effective camouflage. Stobbe et al. (2009) present the findings of laboratory predation experiments with avian predators

and artificial prey, to investigate the relative importance of colour and luminance in effective camouflage. Rowland (2009) reviews previous work and presents new data to investigate the function of countershading in producing camouflage, with Tankus & Yeshurun (2009) adopting a computer vision approach to illustrate how detection of cylindrical objects may work in predators, and how the countershading of prey animals may inhibit this detection process. Caro (2009) presents a comparative study of black and white coloration in mammals and the various forms of camouflage that may stem from these coloration types. Finally, Ruxton (2009) discusses where and how the principles derived from visual camouflage can be applied to other sensory modalities, and reviews the evidence for non-visual camouflage.

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