1 Animal camouflage

Function and mechanisms

Martin Stevens and Sami Merilaita

1.1 Introduction

One cannot help being impressed by the near-perfect camouflage of a moth matching the colour and pattern of the tree on which it rests, or of the many examples in nature of animals resembling other objects in order to be hidden (Figure 1.1). The Nobel Prize winning ethologist Niko Tinbergen referred to such moths as ‘bark with wings’ (Tinbergen 1974), such was the impressiveness of their camouflage. On a basic level, camouflage can be thought of as the property of an object that renders it difficult to detect or recognise by virtue of its similarity to its environment (Stevens & Merilaita 2009a). The advantage of being concealed from predators (or sometimes from prey) is easy to understand, and camouflage has long been used as a classical example of natural selection. Perhaps for this reason, until recently, camouflage was subject to little rigorous experimentation – its function and value seemed obvious. However, like any theory, the possible advantages of camouflage, and how it works, need rigorous scientific testing. Furthermore, as we shall see below and in this book in general, the concept of concealment is much richer, more complex and interesting than scientists originally thought.

The natural world is full of amazing examples of camouflage, with the strategies employed diverse and sometimes extraordinary (Figure 1.2). These include using markings to match the colour and pattern of the background, as do various moths (e.g. Kettlewell 1955; Webster *et al.* 2009; Chapter 7), and to break up the appearance or shape of the body, as do some marine isopods (Merilaita 1998). While we often think of camouflage as a property of a prey animal, predators also regularly have markings for concealment to remain undetected/unrecognised by their prey, including many spiders, which possess striking camouflage to be hidden from both predators and prey (Chapter 14; Figure 1.2). Mammals are also an interesting group that have camouflage for both defensive and aggressive purposes (Chapter 16). Camouflage is a technique especially useful if the animal can change colour to match the background on which it is found, as can some cephalopods (Hanlon & Messenger 1988; Chapters 9 and 10) and chameleons (Stuart-Fox *et al.* 2008; Chapter 13). Further remarkable examples include insects that are strikingly similar to bird droppings (Hebert 1974) or fish that resemble

Animal Camouflage, ed. M. Stevens and S. Merilaita, published by Cambridge University Press.

Cambridge University Press
978-0-521-15257-0 - Animal Camouflage: Mechanisms and Function
Edited by Martin Stevens and Sami Merilaita
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Figure 1.1 Left: A frogmouth bird, often assumed to be camouflaged by remaining motionless and resembling tree trunks or large branches; an example of masquerade. Right: A camouflaged moth (unknown species) against a tree trunk in Cambridgeshire, UK. (Photographs: M. Stevens.) See plate section for colour version.

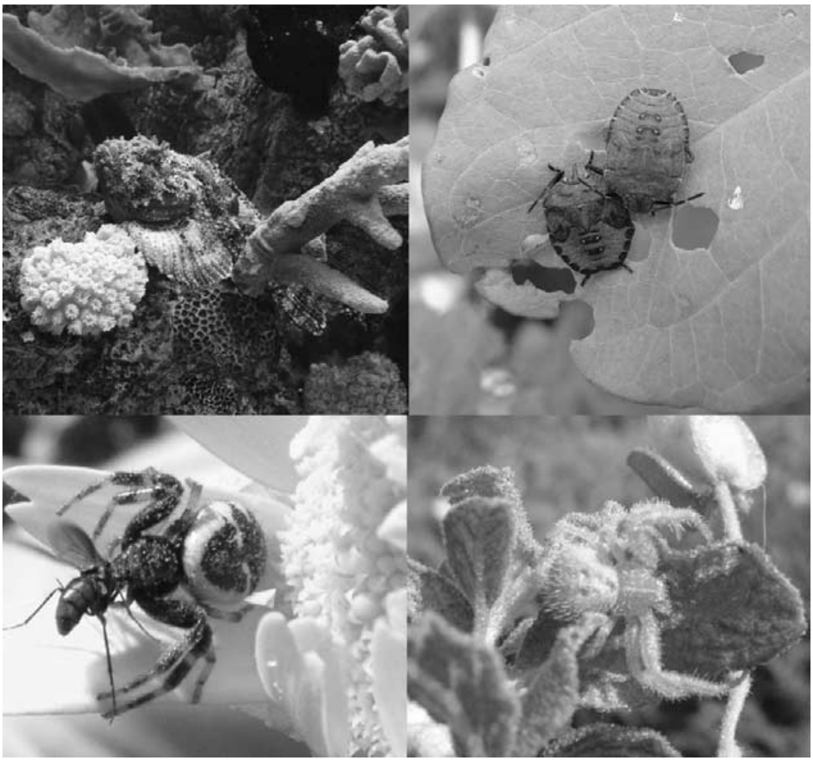

Figure 1.2 Top left: A rock fish (unknown species) camouflaged against the substrate. Top right: Two green shieldbug nymphs *Palomena prasina* matching the colour of the leaf background. Bottom left and right: Two crab spiders, *Synema globosum* and *Heriaeus mellotei*, that resemble their general background to be concealed from predators and their prey. (Photographs: M. Stevens.) See plate section for colour version.

fallen leaves on a stream bed (Sazima *et al.* 2006), and various animals that even have a transparent body (Johnsen 2001; Carvalho *et al.* 2006). Examples like those above helped convince Wallace (1889) and his contemporaries of the importance of avoiding predators and the overall power of natural selection (Caro *et al.* 2008). Other strategies may even stretch to the use of bioluminescence to hide shadows generated in aquatic environments (Johnsen *et al.* 2004; Claes & Mallefet 2010), as well as 'decorating' the body with items from the general environment, such as in some crabs (Hultgren & Stachowicz 2008; Chapter 12) and snails (Yanes *et al.* 2010). Animals must also possess appropriate behaviours to go with their camouflage markings, including resting at the most appropriate orientations to maximise their concealment (Chapter 7). This diversity of camouflage strategies is a testament to the importance of avoiding predation (or catching a meal), as these are surely among the most important selection pressures faced by any animal. Much empirical work on camouflage has been undertaken in terrestrial systems, yet as Chapter 11 illustrates, marine environments are full of camouflaged organisms and these will also make a valuable area of research in the future.

1.2 Camouflage: a history of the idea

The importance of camouflage has been realised for at least 200 years. Indeed, Charles Darwin's evolutionist grandfather Erasmus Darwin commented over 200 years ago: "The colours of many animals seem adapted to their purposes of concealing themselves, either to avoid danger, or to spring upon their prey" (Darwin 1794). Charles Darwin himself commented on the value of camouflage in *On the Origin of Species* (Darwin 1859), yet generally only in passing, perhaps because he thought the presence of camouflage needed little explanation. Instead, Darwin left discussions of concealment to his contemporaries, in particular Wallace (see Caro *et al.* 2008 for a discussion of Wallace's role in the development of camouflage theory), Beddard (1895) and Poulton (1890). Generally, these and other nineteenth-century naturalists concentrated on describing how animals could match the general colour of the environment in which they were found, or imitate inanimate objects found in their habitats. However, around the end of the nineteenth century the American artist Abbott Thayer (1896, 1909), and to a lesser extent Poulton, discussed for the first time that other forms of camouflage also existed. These included most notably obliterative shading (see countershading below) and ruptive (disruptive) coloration. Thayer in particular went to great lengths in expounding the importance of camouflage (Chapter 6), with his over-exuberance about camouflage often coming at the expense of acknowledging other functions of coloration (e.g. sexual signals, warning colours), and even landing him in some infamous debates with the then US president T. Roosevelt (Roosevelt 1911; Kingsland 1978; Behrens 1988, 2009; Nemerov 1997). Thayer's perspective on natural camouflage came largely from his profession as an artist, yet camouflage research has for a significant length of time also linked biology and the military, stemming both from the influence of Thayer, and later the British zoologist Hugh Cott (1940, who was also a keen pioneer of the use of photography to study animal coloration (Cott 1956)). Both Thayer and Cott had also roles in influencing the US and British governments to adopt camouflage uniforms and 'dazzle' camouflage

Cambridge University Press
978-0-521-15257-0 - Animal Camouflage: Mechanisms and Function
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on ships based on their studies of art and natural history (Behrens 1999, 2002, 2009). Overall, Thayer (1896, 1909) and Cott's (1940) works are still hugely influential and contain a range of crucial ideas; in recent years, much research has been generated from investigating some of these previously untested theories.

However, in spite of its long history and widespread importance, research on natural camouflage had not progressed as rapidly as many other areas of adaptive coloration, especially in the last 60–70 years. Furthermore, when it was researched, human perspectives were generally used to assess subjectively the colours and markings, rather than analysing the perceptions of the correct receiver. This is despite the fact that sensory and cognitive systems differ greatly between animals. This latter point has been known for some time (Allen 1879; Lubbock 1882; Wallace 1891), and is important because it is the viewer's perception, not our own, that has created the selection pressure on the animal's coloration. Perhaps most of all, though, the mechanisms of camouflage were often erroneously regarded as intuitively obvious, and many researchers focussed on (generally) more showy types of animal coloration, for example aposematism, mimicry and sexual ornamentation. Thus, until recently the study of natural camouflage has progressed slowly, and little had changed in our understanding since Cott's landmark book in 1940. However, gradually an appreciation of rigorous and objective methods has increased over more descriptive and subjective approaches in the study of camouflage. Norris & Lowe's (1964) first objective quantification of coloration was important, and in particular, work by Endler (1978, 1984) pioneered and promoted the rigorous study of animal coloration, with a broader influence outside of the field of camouflage. Recently, there has been an explosion of studies of camouflage with researchers from biology, visual psychology, computer science and art involved (Stevens & Merilaita 2009a). The resurgent interest in concealment stems partly from a growing effort to study both the proximate mechanisms involved, as well as the functional advantage of different forms of camouflage, and a greater appreciation in considering the visual and cognitive systems of the receiver (Stevens 2007). In general, one of the aims of this book is to promote the rigorous study of animal coloration, incorporating information on the perception of the relevant receivers. In the last few years, much work on camouflage has been undertaken with these points in mind, and the subject has become a good example of how scientists studying animal coloration can do so in a rigorous and objective way, with theories and techniques from a range of scientific disciplines. The chapters in this book represent various examples of this. Other areas of protective coloration, such as studies of warning signals and mimicry have, in contrast to camouflage research, been relatively slow to adopt such approaches and frequently still rely on human assessment or fail to consider, for example, the vision of the receiver (but see for example; Siddiqi *et al.* 2004; Darst *et al.* 2006, and some other studies).

1.3 The different types of camouflage

Unsurprisingly, in a subject that has been studied and discussed for around 150 years, a number of different terms have been used to describe the various types of camouflage.

Table 1.1 Terms and definitions relevant to visual camouflage.
Here, 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 those preventing recognition (e.g. masquerade). We use 'cryptic coloration' and related words to refer to coloration that, in the first instance, prevents detection. We include several forms of camouflage under crypsis, including countershading, background matching and disruptive coloration.

Crypsis: a range of strategies that prevent 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).
  (g) **Transparency**, where part of an animal's body is transparent, reducing the likelihood that it will be detected.
  (h) **Silvering**, common in aquatic environments and where an animal's body is highly reflective (like a mirror) making it difficult to detect when light incidence is non-directional (such as due to strong scattering by water-borne particles).
Masquerade: prevents recognition by resembling an uninteresting object, such as a leaf or a stick.
Motion dazzle: markings that make estimates of speed and trajectory difficult by the receiver.
Motion camouflage: movement in a fashion that decreases the probability of movement detection.

This diverse terminology means that some phenomena have several synonymous names, whereas other specific terms have been used differently over time. Clearly, it is important for clarity to use coherent and consistent terminology, and this was our aim in a recent paper (Stevens & Merilaita 2009a). Below, we list the terms and definitions that we recently discussed, with some further additions to that list (Table 1.1). In defining different forms of camouflage we use the term 'function' to describe broadly what the camouflage type may do (e.g. breaking up form, distracting attention, and so on), and 'mechanism' to refer to specific perceptual processes (e.g. exploiting edge detection mechanisms, lateral inhibition, and so forth). Ideally, camouflage strategies should be defined by how they utilise 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 (but see Troscianko *et al.* 2009; Chapters 8 and 10). 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; Caro 2009). However, others advocate far more extensive use of descriptive terms. For example, Hanlon (2007) recently argued that animal camouflage patterns can effectively be defined by three basic pattern classes: 'uniform', 'mottle' and

Cambridge University Press
978-0-521-15257-0 - Animal Camouflage: Mechanisms and Function
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'disruptive'. As stated previously (Stevens and Merilaita 2009a), we feel this approach is counter-productive and will lead to confusion, particularly because such an approach does not aid the understanding of how different forms of camouflage evolved and function, and the visual mechanisms involved. Instead, definitions should be based on what camouflage does (even if the specific visual processes are uncertain). This is crucial because similar pattern types (e.g. blotches, stripes) may have entirely different functions in different animals and circumstances, ranging from camouflage to warning and sexual signals. 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. Such patterns are also more likely to be a continuum and mixture of features, varying much more and along several dimensions than by a limited number of discrete 'types' alone. Instead, aiming to understand functions (and eventually mechanisms) gives greater insight into the selection imposed on the optimisation of anti-predator coloration and how such functions interrelate and differ (Stevens 2007; Stevens & Merilaita 2009a).

In the last few decades, the term 'crypsis' has been used by various researchers as broadly synonymous with camouflage. Other researchers have defined the term much more specifically. After the 1970s, many researchers directly equated crypsis with background matching (see below), largely because they rapidly adopted Endler's (1978, 1984) definition of crypsis, where an animal should maximise camouflage by matching a random sample of the background at the time and location where the risk of predation is greatest. However, we argue that crypsis comprises all traits that reduce an animal's risk of becoming detected when it is potentially perceivable to an observer (Stevens & Merilaita 2009a). In terms of vision, 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 (Stevens & Merilaita 2009a). 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 because it is broadly consistent with the literal and historical terminology (see Stevens & Merilaita 2009a). While Endler's (1978, 1984) definition was useful for promoting the rigorous investigation of how camouflage works, the definition appears flawed on a number of grounds. First, matching a random sample of the background does not necessarily minimise 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; Chapter 2). Second, the risk of detection can be decreased by disruptive markings, which break up the outline of the animal (Stevens & Merilaita 2009b), or by self-shadow concealment (Rowland 2009). Finally, Endler's definition implicitly assumes that all random samples of the background will be equally cryptic, but studies have shown that this need not be the case (Merilaita & Lind 2005), and even on simple backgrounds an animal representing a random sample may still be visible due to spatial or phase 'mismatch' with important background features, such as edges

Cambridge University Press
978-0-521-15257-0 - Animal Camouflage: Mechanisms and Function
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(Kelman *et al.* 2007). For these reasons we simply refer to crypsis as including colours and patterns that prevent detection (but not necessarily recognition) (see Table 1.1). Readers should also note that much of our discussion here is based on ideas that stem from visual camouflage, as this has been most extensively studied. However, many of the principles of visual camouflage may also be applied to non-visual senses, and that is the subject of Chapter 17. Finally, most research has considered that animals over evolution more closely match static backgrounds, but this may not always be the case, and backgrounds themselves may change appearance over the course of evolution in response to predator and prey appearances and strategies; see Chapter 15.

1.3.1 Background matching

Background matching involves the appearance of an object generally resembling the colour, lightness and/or pattern of either one background (a specialist strategy) or of several backgrounds (a compromise strategy; Stevens & Merilaita 2009a; Chapter 2). Early discussions of camouflage were almost exclusively along the lines of background matching (or ‘general protective resemblance’; Wallace 1889; Poulton 1890; Beddard 1895; Pycraft 1925). Some of the earliest experiments to test the idea of crypsis showed that green and brown morphs of the European mantid *Mantis religiosa* survived predation most effectively on the background colour that they best resembled (di Cesnola 1904). However, the most famous textbook example of how predation pressure can lead to camouflage is that of industrial melanism in the peppered moth *Biston betularia*, which has become one of the most famous examples of evolution observed in nature, cited in textbooks worldwide (reviewed by Majerus 1998; Cook 2000, 2003; Ruxton *et al.* 2004). Different morphs of the peppered moth survive differentially against avian predators in polluted and unpolluted woodland. The typical form (pale with black specks) is camouflaged from birds in unpolluted woodland against lichen-covered trees, whereas the melanic (dark) form, *carbonaria*, is concealed in polluted woodland, where epiphytic lichen has been killed and soot has darkened tree bark. Consequently, there was a rise of the melanic form in polluted regions of Britain during the industrial revolution, and a subsequent decline following anti-pollution legislation in the 1950s (Cook *et al.* 1986). These patterns were paralleled in continental Europe and North America (Grant *et al.* 1996). Kettlewell (1955, 1956; reviewed by Majerus 1998) showed experimentally that the typical form survives better in unpolluted woodland, whereas the melanic form survives best in polluted woodland. Furthermore, each form was more difficult to locate by humans in the habitats where they survived best. However, recently, the story has come under attack, including the unsupported criticism by Hooper (2002), that Kettlewell committed fraud (see for example Coyne 2002 and Grant 2002 for a refutation of the book’s claims). Other more appropriate criticisms are that camouflage assessment relied on human judgement, even though avian vision differs from human, and that the moths may rest in the tree canopy on the undersides of branches, and only infrequently on trunks, unlike as previously thought (Majerus 1998). This latter criticism, however, seems at least partly incorrect as peppered moths have frequently been found resting on trees after more rigorous surveying (M. Majerus unpublished data). Overall, although

Kettlewell's experiments would not meet the rigour of scientific studies today, there is no doubt that the general findings of his experiments and the example in general is still valid (Majerus 1998; Ruxton *et al.* 2004).

Later experiments have used image-processing techniques inspired by visual processing to understand if and how some animals, with patterns like stripes and spots, may be camouflaged (Godfrey *et al.* 1987). Other experiments have also analysed the coloration of camouflaged prey, such as insect larvae, in the context of the predator's vision (Church *et al.* 1998). Several ingenious experiments with blue jays *Cyanocitta cristata* foraging for moths in photographic slides showed that *Catocala* moths were most difficult for the jays to detect when placed upon the appropriate background (i.e. when a birch-tree-resting moth was placed upon a birch background). Furthermore, when moths were placed on the appropriate background, the orientation of the moths became important in optimising camouflage (Pietrewicz & Kamil 1977). Later experiments following on from this, involving jays and computer-generated prey, have investigated the role of predator cognition and background heterogeneity in leading to different camouflage patterns (Bond & Kamil 2002, 2006). However, despite these and a few other examples, until recently, there were few empirical tests of the theory that both quantify background matching as perceived by the predator, and measure its efficacy in terms of survival value (Ruxton *et al.* 2004). In recent years, this has changed, and there has been a range of studies into the value and optimisation of background matching (see Chapter 2 for a full discussion).

1.3.2 Disruptive coloration

In addition to background matching, one of the oldest theories of camouflage is disruptive coloration. Disruptive coloration is a set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object's, or part of an object's, true outline and shape (Stevens & Merilaita 2009b). A typical example is a body coloration that consists of high-contrast markings that tend to break up the appearance of an animal. Like background matching, we argue that disruptive coloration initially prevents detection of the animal's body shape or form and is therefore a type of crypsis (Stevens & Merilaita 2009a). The original idea was proposed by Thayer (1909; and to a lesser extent Poulton 1890), and then more extensively discussed by Cott (1940), and it quickly became a classic textbook example of camouflage. Furthermore, since then numerous researchers have claimed that various animals have disruptive camouflage, though usually without presenting objective evidence supporting these claims (see Stevens *et al.* 2006a). To date, few studies or study systems have properly tested disruptive coloration in real animals as opposed to other forms of camouflage (but see Merilaita 1998). In contrast, various recent experiments in artificial systems have demonstrated its efficacy and tested the different predictions of disruptive coloration. These have used artificial prey in field, aviary experiments and humans foraging trials for computer targets. These have tested the relative advantage of disruptive coloration compared to background matching, the level of contrast the markings should have and the visual mechanisms that underlie its effectiveness (e.g. Cuthill *et al.* 2005, 2006;

Cambridge University Press
978-0-521-15257-0 - Animal Camouflage: Mechanisms and Function
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Merilaita & Lind 2005; Schaefer & Stobbe 2006; Stevens & Cuthill 2006; Stevens *et al.* 2006b, 2009; Fraser *et al.* 2007; Dimitrova & Merilaita 2010). These studies have also investigated some of the 'sub-principles' (Stevens & Merilaita 2009b) of disruptive coloration, including the idea that coincident disruptive markings can conceal tell-tale features of the body, such as appendages (see Chapter 3). In parallel, studies done on cuttlefish have tested the expression of different types of camouflage, including disruption, over a range of background types (Kelman *et al.* 2007; Hanlon *et al.* 2009; Zylinski *et al.* 2009; Chapters 9 and 10). Disruptive coloration has repeatedly been shown to provide a strong survival advantage in concealment, and the subject now has a very strong theoretical underpinning, and various experiments testing its survival value and function. The main challenge for researchers now is to unambiguously demonstrate the presence and value of disruptive coloration in a range of real animals.

1.3.3 Countershading (obliterative shading and self-shadow concealment)

A countershaded animal possesses a darker surface on the side that typically faces greater light intensity and a lighter opposite side (Rowland 2009; Chapter 4). Most researchers agree that the term refers to the appearance of the coloration and not the function, and countershading appears to be involved with several functions. These include the compensation of the animal's own shadow ('self-shadow concealment'; SSC), simultaneously matching two different backgrounds in two different directions (background matching), changing the three-dimensional appearance of the animal (obliterative shading), protection from ultraviolet (UV) light, and others (Rowland 2009). For camouflage, 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 the three-dimensional form of the animal are destroyed (Poulton 1890; 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' (Stevens & Merilaita 2009a). Like disruptive coloration, countershading is a historical and textbook example of camouflage that until recently had also received little experimental investigation. As with disruptive coloration, countershading has rarely been rigorously studied in real animals. Instead, most studies of countershading have presented artificial pastry prey to birds in the field, either placed on boards or in trees (Speed *et al.* 2004; Rowland *et al.* 2007, 2008). In addition, some work in computer science has aimed to understand how countershading works using machine vision and the detection of concealed three-dimensional objects (Tankus & Yeshurun 2009; Chapter 5).

1.3.4 Masquerade

Masquerade involves preventing recognition of an animal by resembling an uninteresting or inanimate object in the environment, such as a leaf or a stick (Figure 1.1). Defining masquerade has proved difficult in the past, because it bears resemblance to both background matching and mimicry, yet it is distinct from both (see Skelhorn *et al.* 2010b). While masquerade in some respects may be thought of as similar to Batesian mimicry

Cambridge University Press
978-0-521-15257-0 - Animal Camouflage: Mechanisms and Function
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(where a harmless mimic resembles a toxic or unprofitable model so that predators avoid the mimic), masquerade does not require that the model is toxic, but just that the model is not of interest to the receiver. Furthermore, although the term masquerade has sometimes been used synonymously with background matching, generally, it seems uncontroversial that masquerade acts against recognition rather than detection and is therefore a different form of concealment. This also means that masquerade is expected to be less dependent on the appearance of the background against which it is viewed. Although there have been various descriptions of masquerading animals, there have been few tests of how masquerade works and its value. The fundamental problem has been in showing that an animal has been detected but not recognised by a predator (masquerade), as opposed to simply not being detected (background matching). However, recently, experimental support for masquerade has been found in aviary trials with insect larvae (Skelhorn & Ruxton 2010; Skelhorn *et al.* 2010a). In the first study, Skelhorn *et al.* (2010a) presented domestic chicks *Gallus gallus domesticus* with twig-resembling caterpillars (one of two species used) and analysed the time to attack. They found that birds with prior experience of unmodified hawthorn branches, which the caterpillars resembled, took longer to attack the caterpillars than birds with either no previous experience of branches, or experience of branches that had been bound with purple thread to change the appearance, but not shape or odour. Thus, they showed that the birds likely misclassified the caterpillars as the twigs. In a similar follow-up experiment, Skelhorn & Ruxton (2010) showed that caterpillars were less likely to be recognised correctly by chicks when they were presented in isolation from their branch models, presumably because the predators were unable to directly compare the prey to the model. In the future, it will be valuable to investigate how masquerade exploits both the sensory and the cognitive aspects of predator perception.

1.3.5 Motion dazzle

Animals are not just at risk from attack when motionless, but in fact are often easiest to detect when moving. It is therefore not surprising that it has often been suggested that animals may utilise markings that make estimates of speed and trajectory difficult by the receiver: motion dazzle (Stevens 2007; Stevens *et al.* 2008b). Here, unlike Cott (1940) we distinguish motion dazzle from distractive markings, disruptive coloration and flicker-fusion camouflage (Stevens 2007; Stevens & Merilaita 2009a). Few experiments have been conducted on this subject, but there is some support for the idea that motion dazzle markings can prevent accurate judgement of movement from studies with artificial systems (Stevens *et al.* 2008b) and cuttlefish (Zylinski *et al.* 2010). Motion dazzle markings are often thought to include high-contrast markings like bands and stripes, and the elaborate paintings of some World War II ships may have made it difficult for enemy targeters to follow the movements of vessels (Behrens 1999).

1.3.6 Distractive markings

Distractive markings are those that direct the ‘attention’ or gaze of the receiver from traits that would otherwise give away the animal’s presence (such as its outline) (Thayer