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Insect Colours and Visual Appearance in the Eyes of Their Predators

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1 Both authors contributed equally
1 Introduction

Insects exhibit a stunning diversity of colours: consider the splendid spotted butterflies or ladybirds, iridescent odonats or beetles, yellow-and-black striped wasps or flies, brown or green walking sticks or mantids. The previous chapters of this volume have reviewed in great detail the mechanisms of production and development of colouration in insects. It is now time to study insect colours from a more functional and evolutionary perspective and to provide answers to the question ‘why is there such a diversity in insect colouration?’. The vast majority of insect colours and colour patterns is thought to have evolved in relation to the needs of communication with conspecifics, prey and predators. On the one hand, different camouflage strategies are selected to decrease detection probability by non-intentional receivers such as predators or prey. On the other hand, intentional receivers such as conspecifics or predators—in the case of warning colouration—select for more conspicuous colours because they are easier to detect and interpret.

Predators are essential in the evolution of insect colouration. Nearly all animal taxonomic groups comprise insectivorous species and these predators almost all rely, at least partially, on vision for hunting. Spatial vision—the ability to exploit the spatial visual information provided by the environment—appeared more than 500 million years ago (Land and Nilsson, 2002). The advantages that vision provided for orientation, navigation, foraging or reproduction explained its rapid and large evolutionary success, as attested by traces of visual structures in a highly diverse array of fossil records (Land and Nilsson, 2002). Insects, which appeared approximately 100 million years afterwards, had to face visually guided predators from their early evolution. All animals endowed with vision are able to exploit brightness (lightness or luminance) information of their environment. However, some animal species have developed colour vision, that is the ability to distinguish objects differing only by the spectral distribution of the radiant energy (see Kelber et al., 2003 for discussion; Skorupski and Chittka, 2009), to exploit wavelength (chromatic) information independent of brightness. Insect predators add to their taxonomic diversity a diversity in visual performance which results in a manifold pressure on all components of insect colouration, both achromatic (brightness) and chromatic components. In this chapter, we will include all these aspects of colours shown by insects, and we will consider white, grey and black as being colours, to encompass the highest possible number of relevant studies.

It is important to consider all visual features that influence predators’ perception of their insect prey. Not only insect colour and colour pattern (i.e. the spatial organization of colour patches on the insect body) are important for perception, but insect size, shape and texture, as many spatial frames in which colouration is expressed, are also important contributors to visual perception (Troscianko et al., 2009). Moreover, insect visual appearance is subject to important temporal and spatial changes due to background and ambient
light variability and more importantly to the movements of animals in their environment. Although the central target of this chapter will be colouration and colour pattern, we will also consider the other aforementioned aspects to provide a more complete picture of how predators view insects.

Numerous studies have tackled some issues concerning the appearance of insects to predators, either from a correlative, experimental or from a theoretical modelling approach. Most of them have focused on a few signalers or receivers (e.g. Eisner et al., 1967; Schlee, 1986; Exnerova et al., 2006; Jackson and Pollard, 2007; Ioannou and Krause, 2009). They have explored a variety of colour signals, except iridescent signals, the functional significance of which in relation to predators remains unstudied (Doucet and Meadows, 2009). They rarely considered a comparative approach at a large interspecific scale from the signaler side (but see Robbins, 1981; Williams, 2007; Song and Wenzel, 2008). It is thus interesting to generate a more synthetic view and to consider the strategies evolved by both predators and insects. We will first detail predators’ visual performance and their use of vision in prey capture. This will provide the basis for a methodological and conceptual discussion on how to investigate insect colouration viewed by predators. We will then review the strategies evolved by insects to decrease predation risk—namely camouflage and warning colouration—and the impact of the visual interplay between insects and predators on insect population dynamics in the particular case of insect colour polymorphism. We deliberately excluded the evolution of insect Müllerian and Batesian mimicry from this chapter for two reasons. First, the same perceptual principles explain how mimetic and non-mimetic insects are viewed by predators. Second, mimicry itself—origin and maintenance throughout evolution—goes far beyond our initial scope. Similarly, we did not consider in detail cognitive aspects such as learning or memory in predator perception.

2 Predator vision

2.1 Predator visual performance

2.1.1 Visual equipment of insect predators

Insects are preyed upon by a large array of organisms. All vertebrate classes (amphibians, reptiles, birds, mammals and fish) and major invertebrate classes (insects and chelicerates) contain a large number of insectivorous predators. For more information, the reader can consult extensive reviews specific of insects (Briscoe and Chittka, 2001), birds (Hart, 2001b; Ödeen and Hästad, 2003), mammals (Jacobs, 1993), other animal groups (Kelber et al., 2003; Warrant and Nilsson, 2006) or more up-to-date studies on groups like marsupials or bats (Cowling et al., 2008; Müller et al., 2009). We present here a selection of examples of predator species (Table 1). Species have been chosen for their
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<td>Mouse-eared bat (<em>Myotis</em> sp.)</td>
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<td>Siberian dwarf hamster <em>Phodopus sungorus</em></td>
<td>~360, 506, rod ~ 500</td>
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<tr>
<td></td>
<td>Mouse lemur (<em>Microcebus murinus</em>)</td>
<td>~430, ~560, rod ~ 500</td>
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* Mantises likely have one photoreceptor type in their compound eyes and two in their ocelli.

* Robberflies are dipteran, thus closely related to hover flies (which are insectivorous as larvae); grasshopper mice are rodents, thus closely related to the hamster. For maximal sensitivity peaks, all values separated by commas represent peaks for distinct photoreceptor classes. Values within brackets are possible alleles for the LWS cone in primates. ~ represents approximate values when precise values are not determined. – separates the upper and lower values of the range within which the peak is likely located. The abbreviation dc stands for double cones: these cones are responsible for brightness detection and equipped with LWS photopigments.
insectivorous diet or for their phylogenetic proximity to insectivorous species. To a certain extent, they represent what is known to date about the variability in visual equipment of their group. For instance, the majority of diurnal birds have five different types of cones, four types of single cones and one type of double cones. They separate into two types of vision, a sensitivity shifted towards UV represented by the blue tit and the sensitivity shifted towards violet wavelengths represented by the domestic chicken (Hart, 2001b; Ödeen and Hästad, 2003). Conversely, dragonflies show a high variability in photopigments, with a number of photopigments ranging from two to five (Table 1). Although old studies have underestimated the number of photopigments due to incomplete sampling, a large part of the variation may be relevant.

Overall, Table 1 shows that predators’ variation in visual equipment likely translates into substantial differences in visual performance. In addition, most species, even nocturnal, are sensitive to ultraviolet radiation, a wavelength range likely involved in prey detection. These observations lead to interesting conclusions. First, it is crucial to consider predators’ vision and not a falsely convenient human perspective when studying colouration. Although implemented long ago in insect–plant communication studies, this recommendation needed to be re-activated (Bennett et al., 1994; Cuthill et al., 1999) to be followed in studies focused on animal communication. For example, investigation of both predator reaction and insect colouration should use UV radiation, an aspect that can shed a new light on apparently closed cases (Majerus et al., 2000). Predator species listed fulfil the minimal requirements for colour vision ability since they possess at least two different types of photoreceptors. Although this possession is by no means a proof of the ability of colour vision (Kelber et al., 2003; Skorupski and Chittka, 2009), it underlines the importance of considering not only brightness but also the chromatic aspects of insect colouration when studying predators’ behaviour. Major work done on the evolution of colour polymorphism in insects has excluded (for technical reasons) the chromatic aspects of colouration (Bond and Kamil, 1998, 2002, 2006), thereby giving at least a partial view of the explored issue. Including both chromatic and achromatic components of colouration is highly desirable and has been actually done in recent studies (e.g. Stobbe and Schaefer, 2008; Stobbe et al., 2009).

2.1.2 Variation in visual equipment and its relation to insect capture efficiency

One of the best documented examples relating to visual performance and behaviour concerns the effect of visual phenotype on foraging efficiency in primates. In primates, the gene coding for S opsin is on an autosome while the gene coding for L opsin is on the X chromosome. In Old World monkeys like humans, the L gene has undergone a duplication leading to a generalized trichromacy in all individuals. In New World monkeys, the L gene presents several alleles resulting in dichromacy for males and homozygote females and
trichromacy in heterozygote females (e.g. Capuchin monkey, Table 1). Variation in visual equipment translates into variation in ability to detect insects (e.g. Melin et al., 2007). Studies on both human (Morgan et al., 1992) and nonhuman primates (Saito et al., 2005) have shown that dichromacy may be beneficial for breaking colour camouflage. Morgan et al. (1992) explained that colour camouflage exists when the organization of chromatic signals does not coincide, interferes with that of other characteristics like shape or texture distinctive elements. Chromatic signals mask luminance (brightness) signals; they are distractive, preventing rapid recognition of important elements. While all vision phenotypes perform equally well in bright light, dichromat white-faced capuchins make more insect capture attempts than trichromats in restricted illumination (Melin et al., 2007). Dichromats are better at detecting surface-dwelling cryptic insects while trichromats are better at detecting embedded insects (Melin et al., 2007). Osorio et al. (2004) explain why the difference of foraging ability is particularly salient in low light conditions. The yellow-blue colour channel (the only channel available in dichromatic monkeys) fails at low light intensities. While in bright light, the improved chromatic vision of dichromatic monkeys impairs their ability to find cryptic insects, they are left colour-blind in low light intensity, which improves their ability to detect cryptic prey. Caine and Mundy (2000) tested foraging efficiency in marmosets (Callithrix geoffroyi) by presenting them with artificially coloured green (unripe) and orange (ripe) fruit balls. They revealed that trichromats are more efficient than dichromats at detecting orange targets, but only at a long distance and not at a short distance, where both types of visual system had similar performance.

Differences in performance can be seen not only between animals differing in their number of visual pigments, but also between animals with the same number of visual pigments. Birds are a good example. Despite their diversity in ecology and species, birds have two main types of photoreceptor sets: most passerines (e.g., blue tit) and parrots have a sensitivity shifted towards UV while other species (e.g. quails or chickens) have a sensitivity shifted towards violet wavelengths (Ödeen and Hästad, 2003). Whether this differential in UV sensitivity translates into significant differences in performance at detecting objects in the environment is still controversial (Hästad et al., 2005; Schaefer et al., 2007). The increased sensitivity to UV may be offset by the rarity of the photoreceptors and the noise associated to their response to light (Vorobyev et al., 1998).

2.1.3 Retinal organization and neural processing influence predators’ ability to detect prey

Apart from the equipment in photoreceptors, the anatomical structure of the eye is crucial for visual performance. In insects, visual acuity, defined as the finest grating that can be resolved by the eye, is inversely proportional to the angle between two adjacent ommatidia, that is, compound eye units (Land, 1997).
The smaller the inter-ommatidial angle, the better the acuity and the greater the distance at which environmental structures can be used for visual guidance. Yet, packing ommatidia on a retina limited in size comes at a cost: ommatidia with smaller diameter have a lower capture rate, which reduces contrast resolution and degrades image quality. Most insects with the lowest inter-ommatidial angle (<1°) are predators: dragonflies, mantids and sphucid wasps (Land, 1997).

In these predatory insect species, the highest acuity is obtained from an area involved in prey tacking, a dorsal band called ‘fovea’ in which ommatidia are much larger, with ommatidia axes nearly parallel and small inter-ommatidial angle (Olberg et al., 2007). This area with maximal spatial resolution also has a high temporal resolution, which facilitates motion detection (Kral and Prete, 2004). Predatory insects such as dragonflies adjust their position relative to their prey to keep them in the fovea (Olberg et al., 2007), a behaviour that optimizes prey detection. Such a fovea is also present in mantids and robberflies (Land, 1997), but not in mantispids, which have similar prey hunting tactics as mantids (Kral et al., 2000). Despite similar capture behaviour, mantispids are less efficient than mantids at capturing prey (Kral et al., 2000), which is likely due to their lack of fovea.

Another example of retinal structure can be seen in jumping spiders. These insectivorous species have single-lens camera-type eyes. The three pairs of secondary eyes are monochromatic, specialized in motion detection and have a poor spatial acuity. Conversely, the pair of principal eyes (frontal antero-median eyes) have a higher visual performance and colour vision (Blest et al., 1981). Principal eyes contain an everse retina with the rhabdoms—the light absorbing parts of the ommatidia—projecting towards the lens and no reflecting tapetum behind the retina (Blest, 1985; Norgaard et al., 2008). Some species, namely Salticoidae and a few Spartaeines like Portia, have evolved principal eyes with high spatial acuity that exceeds by tenfold that of the best seeing insects of similar size (Harland and Jackson, 2004). Such visual acuity has evolved twice independently within the Salticidae (Su et al., 2007). Photoreceptors in the salticid antero-median eyes are organized in four successive layers along the light path. To reach the rearmost layer, light must pass through layers IV, III and II. Only layer I has a fine, regular mosaic of receptors necessary for detailed vision. Salticoidae and a few Spartaeines like Portia present a highly ordered foveal retinal layer I that contains regularly packed light guiding rhabdomeres, where light beams are compartmented more efficiently (Harland and Jackson, 2004; Su et al., 2007). As a consequence, these species can distinguish between conspecifics and prey at larger distance than Lyssomaninae and most Spartaeinae species which have a less ordered foveal layer I in the retina of their principal eyes (Harland et al., 1999).

Not only invertebrates but also vertebrates, like birds and mammals, present a retinal area of maximal resolution. In mammals, for instance, this region accounts for less than 1% of the retinal area; it is structurally and functionally specialized for high resolution and stereoscopic vision, a property stemming
from a high number of ganglion cells and a corresponding large brain area dedicated to processing information coming from this area (Rapaport and Stone, 1984). These animals adapt their movement to maintain their prey in this area of highest resolution.

Beyond the anatomical organization of receptive cells, there often exists a functional regionalization in the retina. The different types of photopigments are not evenly or randomly distributed on the retina, creating distinct regions differing by their composition in photopigments. This regionalization in photopigment composition, which is common in insects (Briscoe and Chittka, 2001) as well as in other groups such as birds (Hart, 2001a) or mammals (Szél et al., 1996), is related to animal ecology and helps to make an optimal link between the visual organization of natural scenes and the organization of light receptors. In birds, while the relative proportions of the different photoreceptor classes reflect bird phylogeny, their distribution on the retina is associated to diet, feeding behaviour and habitat (Hart, 2001a). This distribution of photoreceptors may also be complemented by a variation in oil droplet pigmentation. Oil droplets are light filters associated to cones in birds; by narrowing cone spectral absorption domain, they enhance colour discrimination (Vorobyev, 2003) at the expenses of absolute sensitivity. Areas with reduced oil droplet concentration are likely associated with prey detection, as suggested for the sacred kingfisher (Todiramphus sanctus; Hart, 2001a). In dragonflies, the fovea is dominated by UV and blue photoreceptors (Olberg et al., 2007). Be they perchers or hawksers, dragonflies approach their prey from below. They thus usually have to detect their prey against the sky. Incorporating receptors maximally sensitive to the wavelengths dominant in the blue sky is thus an efficient strategy to extract maximal visual information from the visual environment in which prey are usually seen. This regionalization is also rendered more efficient by appropriate hunting behaviours. When perching, dragonflies orientate away from the sun, with their fovea directed to the sky, a position that optimizes prey detection (Prete, 1999; Sauseng et al., 2003). When pursuing their prey, they tend to maintain a constant angle between the prey and the horizon on the retina by moving their head in order to keep their target in the fovea (Olberg et al., 2007).

Finally, neural processing of photoreceptor outputs is crucial to determine the level of visual performance. In dragonflies, the complex retinal structure is complemented by neural pathways that efficiently integrate the visual information provided by photoreceptors. Two types of neurons are dedicated to recognition of small moving features in the environment; their response is related to the brightness contrast between these features and the background (O’Carroll, 1993): moving bar detectors are orientation but not direction selective neurons which respond more strongly to isolated bars than to several bars. Small target moving detectors are orientation selective neurons which respond to targets subtending visual angles equivalent to just one or two facets of a compound eye. These insects are endowed with a visual acuity of approximately 1° (between 1° and 2° in Land, 1997; 0.8° in Nordström and O’Carroll, 2006), which is remarkable
for insects. As a consequence, they do not react to background motion itself; in case they do, it is in a random way, as if they were responding to small features of the background itself. They keep responding even when the background is moving at the same velocity as the target (Nordström et al., 2006). These neurons help to detect moving prey in a visual clutter and are built to compensate for predators’ self-motion while hunting the prey.

2.1.4 *Weighing the role of vision relative to other sensory channels*

While some predators rely heavily on vision to detect and capture their prey, other predators use more intensively different sensory modalities like olfaction and may exert little influence on the evolution of the colouration of their prey. Even if the importance of visual information can be predicted from the visual equipment of the taxonomic group to which it belongs, different species of the same group may strongly differ in the relative importance they give to different sensory modalities. For example, some predatory heteropterans (Nabidae and Reduviidae) have been experimentally shown to depend more on olfaction than on vision to locate prey patches and orientate to prey at close range (Freund and Olmstead, 2000). Other predatory heteropterans (Reduviidae) have been suggested to depend more on the visual stimuli (colour and movement) than on the scent provided by their prey (Parker, 1969a,b). Similarly, experiments performed on closely related coccinellid species revealed that *Coleomegilla maculata* shows the same predation rate in dark and light environment and no preference for any prey colouration while *Coccinella septempunctata* prey on the most conspicuous prey and more in light than in dark environment (Harmon et al., 1998). While visual cues are not important for the former, they appear essential to guide predator attack in the latter species. Lizards use mainly visual cues at large distance and a combination of visual and olfactory cues at short distance (Hasegawa and Taniguchi, 1994).

Most insectivorous bats maintain a good visual sensitivity under nocturnal illumination (Ellins and Masterson, 1974). A growing body of evidence shows that not only echolocation but also vision plays a role in prey detection and capture, with a trade-off between visual equipment and hearing performance (Zhao et al., 2009). Some lineages (e.g. vespertilionids) have a moderate hearing and two different types of cones—one sensitive to UV and the other to green—and a potential colour vision. Other lineages (e.g. rhinolophids) developed a more sophisticated echolocation and showed a concurrent loss of UV sensitivity, with a vision only sensitive to light intensity (Zhao et al., 2009). Bats also differ in their use of vision. The gleaning bat (*Macrotus californicus*) locates prey on the ground by vision (Bell, 1985). Aerial-hawking bats have been suggested to use the bright sky at dusk to backlight their prey (Pettigrew, 1980). Experiments show that they use visual cues to locate stationary insect prey above the vegetation. Gleaning bats that forage on the ground cannot use the sky to create a brightness contrast and enhance prey conspicuousness.
However, they seem to use vision to locate their prey (Bell, 1985) and prefer visual to sonar cues to locate them (Eklof and Jones, 2003). For all the bats studied to date, visual cues seem to facilitate the initial prey detection but may not be involved in the terminal attack (Eklof et al., 2002; Eklof and Jones, 2003). However, little is known about the exact visual cues bats could use for prey detection (Eklof et al., 2002). Prey colouration may not play an important role as suggested by the absence of preference for dark or light targets (Eklof et al., 2002) or morphs in the peppered moth Biston betularia (but see Whittle et al., 1976; Majerus, 2008). However, function and mechanisms of vision in bats and its importance relative to other sensory modalities have aroused research interest only recently (Müller et al., 2009) and should benefit from future studies both in behaviour and physiology.

2.2 ROLE OF VISUAL SIGNALS IN INSECT PREDATION

2.2.1 Visual cues useful for prey detection and recognition

Predation is characterized by different steps, namely, detection, identification, attack, capture and consumption. The mechanisms of prey detection and capture have been studied in detail for a few insectivorous predators, mainly in mantids and mantispids, dragonflies, spiders, tiger beetles and toads. Experimental for their large majority, these studies have identified some of the visual features—shape, colour, movement, texture—that influence prey detection and recognition and evaluated the importance of vision in capture mechanisms. In a recent review, Troscianko et al. (2009) detail the relationship between object visual features and receiver cognitive processes. Although visual mechanisms are mainly known from studies of mammalian vision, they also explain how animals with different vision perceive objects like camouflaged prey in the environment, suggesting that visual mechanisms are likely similar from a functional point of view.

Prey contour and shape are fundamental cues for detection and recognition. While colour, texture or size do not uniquely identify an animal, shape is what best identifies an animal (Troscianko et al., 2009). Prey contour can be inferred from the detection of animal boundaries, that is the detection of sudden changes in light intensity and spectral content. Local edge segments are detected and then assembled in objects, the shape of which is then reconstructed by the brain (Troscianko et al., 2009). Animal shape is recognized for the potential target to be considered a valid prey. Insect predators often prefer elongated (worm-like silhouette) targets [mantis (Yamawaki, 1998); toad (Ewert, 2004)]. From a series of experiments conducted in the praying mantis (Mantis religiosa), the importance of edge in prey detection and probability of attack were determined. Praying mantis presented with objects at close distance preferentially strike at edges (Poteser and Kral, 1995) and direct more attacks at squares than discs or triangles of equal surface (higher edge to area ratio in squares compared to discs Hyden and Kral, 2005).
Prey size is also crucial for detection. Larger objects are generally more detectable than smaller objects. This increased detectability can translate directly in a higher predation risk. For instance, this is the case for birds that attack larger larvae more often than small ones, as shown by Remmel and Tammaru (2009) with field experiments involving birds preying on artificial prey items. For these large predators, larger prey are not only more detectable but also more valuable in terms of energetic content.

Prey colouration is important for detection. Without entering into too much detail, we want to underline the importance of both chromatic and achromatic components of colouration in prey detection. Detection of small (subtending a small angle on the retina, small in size and/or at long distance) or moving targets usually relies on the detection of brightness contrast [fish (Schaerer and Neumeyer, 1996); insect (Giurfa et al., 1997); bird (Osorio et al., 1999)]. Chromatic contrast also plays a role in detection. The relative importance of chromatic and achromatic information can depend on background complexity (example of fruit detection in birds, Schaefer et al., 2006) and on the relative achromatic and chromatic contrasts offered by the prey against the background (example in blue tits, Stobbe et al., 2009) and on the colour content of the prey itself.

Visual cues indispensable for detection and recognition are processed while additional information is overlooked in some cases. For instance, the grasshopper mouse uses visual cues mostly for prey detection. Once the prey is detected, visual cues allowing a precise recognition of specific species seem to be overlooked in the decision to attack; this may be due to the generally limited vision of these nocturnal animals which forage in low light conditions (Langley, 1989). Another extensively documented example is that of jumping spiders which are fundamentally guided by vision. Jumping spiders feeding on both spiders and insects generally show a preference for spiders (Jackson and Li, 2004). They do not seem to analyze the entire prey shape or contour but more to concentrate on specific visual cues that rapidly inform them about the validity and profitability of the prey. Optical cues, like the location or shape of prey eyes, are sufficient for these predators to make the difference between spiders and insects or between conspecifics and prey (Harland and Jackson, 2000, 2002; Jackson, 2000; Nelson and Jackson, 2007).

Finally, different predators attend to different visual cues to detect and recognize their potential prey. Training pigeons to differentiate wasps from various species of mimetic hoverflies, Dittrich et al. (1993) showed that some species that appeared poor mimics to human eyes were judged to be good mimics by pigeons. While humans appreciate hoverflies’ mimicry on colour pattern mainly, pigeons use a more varied set of visual features to distinguish between different types of prey (Bain et al., 2007). The set of visual cues used by predators is flexible and depends on predator’s past experience (Mostler, 1935; Bain et al., 2007). Mostler (1935) gave the first clear evidence for that flexibility in his well-designed large-scale experimental approach to testing the theory of mimicry. He showed that inexperienced birds of several insectivorous
species attacked three noxious hymenoptera (wasps, bumblebees, honeybees) as well as their hoverfly mimics. Yet, they would rapidly learn to reject the noxious species and avoid attacking their mimics if offered after an encounter with a noxious model. Hoverflies gained their protection from their colour pattern, a visual feature to which naïve and experienced birds did not give the same importance. Similarly, in Bain et al.’s (2007) study, pigeons rewarded wasps used colour attributes (number of stripes, stripe colour) when asked to avoid flies while pigeons rewarded flies used mostly antennal length and also colouration to distinguish them from non-rewarding wasps.

In general, any enhancement of the differences in spectral content or intensity between the insect and the background facilitates detection (Troscianko et al., 2009). For example, Remmel and Tammaru (2009) have shown that bird preference for larger insect larvae is accentuated for conspicuous prey. Because this preference is independent of prey colouration, the authors suggest that detectability more than acceptability is important in determining size-dependent predation risk in this case. Similarly, a high brightness contrast elicits a higher attack probability in the praying mantis (Yamawaki, 2000). Conversely, any increase in similarity in intensity or spectral content between the insect and the background, the production of high-contrast internal detail (internal markings) more salient than the edge or false edges likely reduces detection probability. The enhancement may be more efficient for some prey–background combinations: prey configuration (shape, size and movement) being defined, toads respond more to a black prey against a white background than to the reverse (Ewert et al., 1982), probably because neurons display different responses to abrupt darkening and brightening of the visual field (Ewert, 2004).

Prey motion is also an important visual cue for detection and attack. Motion helps to segregate objects from similarly textured backgrounds (Srinivasan et al., 1999) and generally facilitates detectability. In toads, motion is crucial: an object must move to be categorized as prey (Ewert, 2004). More specifically, motion is analyzed in relation to prey size and shape. Elongated objects moving in the direction of their long axis are preferred while the same objects moving in the direction of their short axis are categorized as non-prey; this preference does not change with prey speed (Ewert, 2004). In the praying mantis, the probability of strike increases when prey motion increases (Iwasaki, 1990). Similarly, lizards prey more on moving prey than on other less active but equally palatable insects (Civantos et al., 2004). Grasshopper mice attack more moving than stationary prey (Langley, 1989). In chironomid larvae, immobility decreases predation risk by sticklebacks Gasterosteus aculeatus, but only in cryptic prey (Ioannou and Krause, 2009). Like edge detectors, motion detectors are neural structures that are sensitive to colour and brightness. Increased contrast between target and background facilitates detection of moving objects in the environment (Ewert et al., 1982; Livingstone and Hubel, 1988; Ewert, 2004). Conversely, motion camouflage (detailed in a subsequent section) can efficiently reduce detection probability.
2.2.2 Visual cues informing about prey profitability—predator preferences

Even if the prey is recognized as a valid prey type, it may not be attacked depending on the level of profitability expected from the attack. A prey item can be unprofitable if the attack is likely not successful, if the attack and the consumption requires more energy than the energetic content expected from the prey, or if the prey is unpalatable. Several visual features, like prey size, movement, colouration, are used by predators to determine if they should attack a potential target. This decision is subject to speed–accuracy tradeoffs (Chittka and Osorio, 2007) which are crucial in shaping the evolution of both prey appearance and predator behaviour.

First, insect size can inform on attack profitability. Although larger insects are readily more detectable, the increased detectability may not translate into an increased predation risk. If adult birds prefer large prey (Remmel and Tammaru, 2009), small or inexperienced birds prefer medium size prey over large prey because they require less handling (Moreby et al., 2006). Similarly, for predators of smaller size, there exists an optimal prey size above which predation becomes less profitable—higher chance of escape for the prey, longer time for prey handling or consumption. This of course depends on the type of prey and may not hold for slow-moving insects like caterpillars. For instance, grasshopper mice prefer to attack smaller prey (Langley, 1989). Optimal prey size increases with predator size in dragonflies (Olberg et al., 2005). The praying mantis pays special attention to prey volume and area but prey volume is the most important for attack decision; they attack in average smaller prey than those they pay attention to in the first place (Iwasaki, 1990) and from a large range of prey size, they prefer intermediate size (Iwasaki, 1990). Similarly, odonats presented with prey of various sizes prefer small prey (Shelly and Pearson, 1978; Rashed et al., 2005).

Second, prey movement can inform on prey profitability. Palatable and unpalatable prey exhibit different flight patterns, speed and movement predictability (review in Sherratt et al., 2004), all cues that can be used by predators to assess potential target profitability. These aspects will be studied in more detail in a subsequent section of this review.

Third, prey colouration can also inform the predator about the level of prey profitability. If some colours are associated with high levels of profitability while others are associated with low levels of profitability, relative preferences or avoidances for specific colours or colour patterns can evolve in the predators. At the same time, these preferences may shape the evolution of colours and patterns in insects. Attending to visual cues may be economical for predators and save them from un- or poorly rewarding attacks. Specific sections of this review will be dedicated to warning colours seen by predators or to specific cognitive processes of prey recognition (image search). Here, we want to put forward some interesting aspects of colour avoidance or preference, namely the
universality of the information content of prey colouration and the role of the background colouration in the construction and the expression of a preference or an avoidance for a specific colour.

Predators can prefer or avoid specific colours and patterns. This has been extensively studied, mostly in birds (references in Ruxton et al., 2004), but also in other insect predators such as insects or lizards. Most insectivorous species show unlearned avoidance for red relative to other colours such as brown, green or grey, which are preferred (Sillén-Tullberg, 1985b; Roper, 1990; Moreby et al., 2006; Gamberale-Stille et al., 2007). Not only colours but also patterns can elicit preferences or avoidances. Black and yellow patterns do not generate any avoidance in various insectivorous species, as shown by the high predation observed on striped hymenoptera and hoverflies (Mostler, 1935). Conversely, black and yellow patterns inhibit prey attacks in naïve domestic chicks, even for their first prey eaten (Schuler and Hesse, 1985). Aversion is not shown when black or yellow is presented separately or adjacent but not in stripes (Schuler and Hesse, 1985). A similar process can be seen in mantids (Tenodera aridifolia) for which black or orange solid colours are less aversive than black and orange striped patterns (Bowdish and Bultman, 1993).

The informative content associated to a given colour applies to different prey types. For instance, partridge chicks preying upon different insect species—heteroptera, coleoptera, orthoptera, hymenoptera—show a general preference for yellow-green colours over black and brown (Moreby et al., 2006). However, the informative content associated to a colour has by no means a universal value. First, it is prey-type dependent. For instance, birds’ avoidance of red is applicable only to insects or insect-like elongated objects while it does not exist for fruit or fruit-like round objects for which red is often preferred (Gamberale-Stille and Tullberg, 2001). Similarly, dragonflies show an aversion for yellow-black striped patterns for flies but not for wasps (Kauppinen and Mappes, 2003). Second, the informative content of a colour is also predator-type dependent. Avoidance of yellow-black striped patterns is present in a large range of insectivorous bird species but it is absent in non-insectivorous birds (Dittrich et al., 1993) and turns into a preference in bee-eaters (Koenig, 1950).

Aversion or preference for specific colours is maintained regardless of the colour of the background against which these colours are presented, as long as the background colour does not significantly interfere with prey detectability (Sillén-Tullberg, 1985b; Roper, 1990; Moreby et al., 2006). Associating a colour or a pattern per se and not a contrast between prey and background to the level of prey profitability is likely an efficient strategy since it can compensate for the spatio-temporal variations in contrast between the prey and the background. It may be particularly advantageous if prey frequent different environments, or if predators feed on a variable or large range of prey. Background colour has little effect at the time when aversion/preference is expressed, but it can have a significant effect on building, reinforcing or deactivating preferences. First, familiarity with a colour, presented in the background and
not in the food itself, increases the preference for this colour (Roper, 1990) or can convert a natural aversion into a preference, as shown for chicks reared in environments presenting black and yellow elements (Roper and Cook, 1989). Second, the visual environment affects the salience of colour for young birds, probably in relation to changes in relative attractiveness or memorability. For example, chicks are more easily trained to respond to orange than to blue, although they show no innate preference for either colour (Miklósi et al., 2002). Third, if background colour can increase familiarity, it has little power to convey information about prey palatability, as shown by experiments on unpalatability learning (Gamberale-Stille and Guilford, 2003). For domestic chicks, learning prey unpalatability is faster when prey colour and not background colour can be used as an indicator of this unprofitability. When both cues are available, prey colour is used as the only indicator of prey unprofitability. Moreover, learning is not possible when the only cue available is the level of contrast between the prey and the background and not colours per se (Gamberale-Stille and Guilford, 2003). Avoidance of unpalatable prey is learnt faster for more conspicuous prey (Harvey and Greenwood, 1978).

Predators do perform generalization based on object colouration. The experience of an association prey colour—prey profitability can be generalized to different prey types or to different colours. Such cognitive flexibility likely helps predators to adapt their foraging strategy to changing prey. First, all objects of a particular colour previously associated to a level of profitability can be assumed to bear the same profitability level. Although aversion to red is restricted to specific targets, preference for brown is generalized to all brown objects when birds are fed on brown food (Roper, 1990). Second, generalization can be applied to colours, especially in the case of novelty. For instance, birds conditioned to associate a colour to a reward can be exposed to a novel colour associated to unpalatable prey. They learn to avoid this prey based on its colour and avoid any further novel colour, showing that a generalization was made based on novelty (Schlenoff, 1984). In domestic chicks, exposure to novel food is sufficient to deactivate neophobia. Deactivation is similar regardless of the number of novel colours to which animals are exposed and is obtained even with a brief exposure (Marples et al., 2007). Yet, dietary conservatism (reluctance to incorporate novel food in a diet) is stronger than neophobia (reluctance to taste novel food) and reactivation is always much more easily achieved than deactivation (Marples et al., 2007). This limited flexibility in terms of reaction to colours, coupled to memorability, increase foraging efficiency by fostering safer and faster decision making.

Decision of attack can be shaped by visual information borne by insect size, colour and pattern. However, the decision can be made by integrating not only information coming from vision but also from other sensory channels as well. Communication—not only between conspecifics but also between prey and predator—is fundamentally multimodal, as shown by a growing body of evidence (Partan and Marler, 2005). For instance, lizards rely on visual cues to
decide which prey to pay attention to and approach; yet, unpalatable insects camouflaged into visually palatable insects are approached but not attacked, which suggests that information about palatability can be provided by visual cues but is also accessible through olfactory cues (Hasegawa and Taniguchi, 1994).

2.2.3 Role of visual input in capture mechanisms

2.2.3.1. Visual estimation of distance to prey  To successfully strike their prey, predators have to reliably estimate distance to them for stationary targets, and visual angle, angular velocity and distance for moving targets. For predatory insects, estimating distance is more difficult than for vertebrates. Insects have their eyes fixed relative to the head, and their compound eyes are not capable of focusing mechanisms, which could provide an indicator of distance. There are still three different mechanisms for distance estimation: image size, stereopsis and motion parallax. For an object of known size, image size measured by the number of photoreceptors excited on the retina can give a direct indication of the distance to the object. This mechanism may be used to estimate distance to conspecifics (Olberg et al., 2005) but is likely of restricted relevance in the case of prey of variable size. In the case of stereopsis, the distance to an object is encoded by the difference in retinal position between right and left eyes. For insects, the amount of visual information that can be extracted by binocular vision is limited by the small head and the close distance between the eyes which reduce the information provided by the angular disparity of view between the eyes. Extraction of visual information about distance is thus mainly restricted to short distances. For example, the dragonfly *Libellula* sp. is able to accurately discriminate distance up to 1 m but models have shown that stereopsis can only contribute to determinate distance up to half a meter (Olberg et al., 2005). The major mechanism used for distance estimation is motion parallax. In that case, distance is encoded by the movement velocity of its retinal image caused by the self-motion of the predator. The image of a close object is displaced faster than that of a distant one. This information does not require any binocular input. Experiments have shown that this mechanism is widely used in a large variety of insects, such as tiger beetles, mantids and mantispids or dragonflies (Poteser and Kral, 1995; Toh and Okamura, 2001 and references therein; Olberg et al., 2005). For instance, the praying mantis performs peering movements, that is lateral movements of the head along a line, to estimate its distance from stationary targets and the appropriate jump distance (Poteser and Kral, 1995). Peering characteristics depend on the visual environment from which to extract visual information. For instance, *M. religiosa* lives in grassland where background elements are uniform, aligned and closely spaced. The basic peering movements it performs (Kral and Devetak, 1999) have been experimentally shown to be most efficient against horizontally or vertically striped background (Poteser and Kral, 1995). In this species, peering velocity changes with background and peering amplitude increases with prey
distance. Conversely, *Empusa fasciata* which lives in habitats of shrub consisting of irregularly, variably aligned elements, translates its entire body sideways and performs back–forward movements resulting in peering of higher amplitude adapted to extract visual information from a visually more complex environment (Poteser and Kral, 1995).

### 2.2.3.2. Visual input during prey pursuit

Pursuing moving targets is also a complex visual challenge for predators. Target detection poses problems to moving predators; the image of the prey is degraded by the relative angular velocity of the moving predator and the prey (Gilbert, 1997). Different strategies have evolved to overcome this prey localization problem. After locating their prey, some vertebrates like toads close their eyes during their fast movement to approach their prey (Lock and Collett, 1979). Suppressing any visual input may be more advantageous than coping for distorted visual information.

In some cases, visual input of the position of the prey is not even needed. This is the case of the archer fish. These fish shoot water at insects flying above the water surface and they catch their dislodged prey exactly where it falls into the water. Distance to the prey is estimated from monocular cues with an extreme precision (error of 1 mm at 80 cm), with a correction for optical distortions due to air–water interface (Schuster *et al.*, 2004). Not only memory of past experience but more likely the extrapolation of laws (concerning the changes of apparent size with distance) seem to be at play for distance estimation (Schuster *et al.*, 2004). They only need information about direction speed and prey distance in order to ‘calculate’ the point of incidence of the target on the water. These cues can be extracted during the first 0.15 s following target strike; the animals do not perform any visual feedback afterwards. This absence of visual feedback can be easily deduced from the unchanged ballistic trajectory reaction of individual fish towards targets for which the post-strike trajectory has been experimentally changed (Rossel *et al.*, 2002).

Motion is a real challenge for prey detection and pursuit. Because photopigments have a finite integration time, the retinal image is subject to motion blur (just as in photography) when eye and surroundings move relative to each other (Land, 1997). This occurs more strongly at high angular velocities and insects chasing their prey have evolved mechanisms to compensate for image blurring. For instance, tiger beetles are tracking predators. They often track their prey by making regular stops and goes; stops help them to relocate the prey and minimize image blurring. Experiments have shown that for some visual combinations—high visual contrast between prey and background, large prey size—tiger beetles perform tracking without stops, suggesting that visual feedback and compensation for blurring may be costly and is avoided when not indispensable for successful capture (Gilbert, 1997).

Dragonflies have evolved capture tactics which are interesting to relate to the evolution of their visual performance. First, while most insects track their prey basing their own movement to the current position of their target, dragonflies...
intercept their prey. Be they sit-and-wait predators or hawks, they fly in a relatively straight line which intersects the projected flight path of their target. This strategy is likely economic in terms of visual feedback. These animals have evolved a highly developed visual system. They have evolved behaviours that make an optimal use of their visual equipment. They keep their target in their fovea—region of highest visual acuity—which is optimized to detect insect prey moving against the blue sky (Sauseng et al., 2003). Their highly performing retina is relayed by neurons specialized in the detection of small features in the environment such as moving prey. These neurons are primarily sensitive to brightness (luminance) contrast and they show a maximal response for a high brightness contrast between prey and background (O’Carroll, 1993), which is highly beneficial to backlight dark prey against the light sky. These neurons are built to respond to a moving prey showing no difference in velocity compared to the background (Nordström et al., 2006) which is advantageous for predators that are moving when chasing their prey.

2.2.4 Prey visual cues and predator versatility

Predators have evolved flexible capture tactics which are adapted to prey visual ability and behaviour. Jumping spiders stand probably as one of the best examples of this predator versatility (Curio, 1976; Harland and Jackson, 2004). Jumping spiders of the genus Portia, which feed on spiders and insects, adopt a cryptic stalking behaviour towards salticids: they freeze when faced by their prey and walk with their palps back. Conversely, they adopt a normal stalking behaviour towards prey other than salticids, not freezing when faced nor holding their palps back (Harland and Jackson, 2000). Visual cues that determine the type of stalking adopted is firstly the presence of eyes typical of spider principal eyes (Harland and Jackson, 2000). Normal stalking is chosen when eyes are absent, reduced or square-shaped; cryptic stalking is chosen for normal or enlarged eyes or when one eye only is visible (Harland and Jackson, 2002). Spiders adopt an ambivalent behaviour for spider-mimicking beetles or ants (Harland and Jackson, 2001, 2002), suggesting that the eyes may not be the only prey feature used by spiders to decide which capture tactic to adopt. Not only the type of stalking but also the decision to engage an attack depends on the prey and on the visual cues offered by the prey. Jumping spiders of the genus Phaeacius engage an attack towards salticids only if they are camouflaged from their prey by a cryptic background and if their prey is not facing them (Li et al., 2003). For the other types of prey, the probability of attack does not depend on background colouration or prey orientation, suggesting that prey visual performance is not sufficient to select for more complex predation behaviours.

Predators also adapt their behaviour according to prey escape ability. When they chase prey with a low escape potential like Thysanoptera or lepidopteran larvae, salticid spiders approach their prey frontally and release them after venom injection. Conversely, when they chase prey with a high escape potential
like homopteran or orthopteran species, they orientate sideways, make a rapid movement masking approach and do not release their prey after venom injection. Similarly, the praying mantis adapts its approach behaviour to the amount of prey motion (Yamawaki, 2003).

3 Methods to investigate insect colouration

3.1 MEASURING COLOURATION

Most studies of insect colouration, especially those conducted before the 1990s, involve a qualitative measurement of insect colouration, mainly through scores or human vision-based colour categorization, like ‘green’, ‘brown’ or ‘black’ (e.g., Kettlewell, 1955a; Sandoval, 1994; Harmon et al., 1998; Civantos et al., 2004; Hochkirch et al., 2008). This categorization did not only apply to insects, targets or fruit items in general but also to light and visual background. At first, such a categorization may seem convenient and fairly robust, especially for animal colouration. Indeed, natural pigments and structures show a limited variation around typical reflectance spectra (e.g. pigments colouring birds’ feathers; Burkhardt, 1989). For instance, ‘green’ colours typically have a main reflectance peak in the green range, with only secondary peaks in other regions like UV. Categorization and reflectance measurements are likely congruent in this case, making categorization a valid surrogate of reflectance spectrum, at least for species more sensitive to green than to UV wavelengths. Nevertheless, colour categorization presents numerous pitfalls (list in Endler, 1990). Scoring a colour patch is a subjective assessment; because perception is based on comparison, the scoring of a colour patch can be affected by adjacent colour patches. Similarly, it is subject to fluctuations due to lighting conditions in which scoring is performed. Finally, it is based on human vision. Colour categorization reduces variation to the human range of sensitivity, excluding regions like UV to which insects and most of their predators are sensitive (Table 1). Moreover, it ignores metamerism, that is, that several wavelength distributions can produce the same visual impression. Metamerism is common for human manufactured objects (backgrounds in experiments) and artificial lights. Yet, two colours seen as metameres by humans are likely not metameres for a different visual system. Finally, making categories implies gathering colours into groups: two colours of the same category—two greens for instance—are perceived as more similar in colouration than two colours of different categories—one green and one yellow—even if both pairs generate equal difference in photoreceptor responses. Location in wavelength of boundaries between groups, and the amount of distortion of photoreceptor responses depend on the visual system. Ideally, categorization should only come as a complement to help the researchers to interpret their results or to make their message more pedagogical to a general audience but not as a primary and unique colour measurement.
Given that insects and insectivorous predators (perhaps with the exception of some insectivorous primates) have visual systems that differ from ours in terms of range of sensitivity, photopigments and visual information processing, it is essential to objectively measure colouration (Endler, 1990; Bennett et al., 1994; Cuthill et al., 1999). This can be done by the means of spectrometry, a powerful method which can easily be adapted to the range of sensitivity of interest by using appropriate lamps, spectrometers and optic cables. Spectrometry provides spectral data which are objective and precise quantitative measurements. Reflectance spectra give the proportion of the incident light that is reflected by the colour patch (insect colour patch or background colour patch) while irradiance spectra give the light intensity available at each wavelength (see extensive and argumented practical help in Endler, 1990; Endler and Mielke, 2005). All spectral data are based on photon counts. This approach has been successfully applied to insect colouration (e.g. Stobbe and Schaefer, 2008; Théry et al., 2008; Stobbe et al., 2009).

Another way of measuring colouration is to use video or photography. Photography can be particularly useful to quantify the relative importance of colour patches within a pattern or to characterize the spatial relationships between different colour patches (shapes, transitions, patch homogeneity), even about temporal changes in colour aspects (Stevens et al., 2007b). Compared to spectrometry, photography is often viewed as a convenient and inexpensive means to rapidly collect large quantities of data. Nevertheless, different adjustments are needed if photography is used to investigate how insect colours are seen by potential predators.

Stevens et al. (2007b) provide a useful help guide to accompany potential users in all needed correction steps. They list the important technical characteristics to pay attention to when choosing a camera, they explain the calibration protocol and the process to linearize camera’s response to light intensity, how to correct the response of RGB channels to extract information about brightness. Finally, they detail how to transform data into camera-independent quantitative measures of colouration to compare measures from different cameras or to incorporate the data into models of animal vision. They draw attention to two main problems that are particularly relevant for studies of insect colouration. First, most cameras exclude the UV range to which humans are blind but to which most insect predators are sensitive. It is not difficult to do UV imaging (see application for the study of flower colouration, Kevan, 1972) and it may be a useful complement to classic photography (Stevens et al., 2007b). Second, information delivered by the camera’s sensors is biased towards specific wavebands which spacing is a closer approximation to visual systems (like that of birds) with regularly spaced sensitivity than to human’s vision. Working not on the RGB responses but on linear combinations of these responses may be useful to adapt to specific visual systems (example of mapping in Stevens and Cuthill, 2006).
3.2 BUILDING ARTIFICIALLY COLOURED STIMULI

Investigating how predators see insect colours and identifying the visual cues most relevant to predators requires an experimental approach. This imposes the manipulation of specific visual aspects of the prey (colour, shape, contrast, pattern, size) and/or the background to test their separate effect on predators’ reaction. This can be done by using dead versus live prey (e.g. Eklöf et al., 2002) artificially painted targets or manufactured objects (e.g. Bowdish and Bultman, 1993; Gilbert, 1997; Cuthill et al., 2005; Hyden and Kral, 2005; Marples et al., 2007; Wennersten and Forsman, 2009) and computer images or pictures (e.g. Dittrich et al., 1993; Bond and Kamil, 2002, 2006; Bain et al., 2007). Background is often ‘manipulated’ simply by performing laboratory experiments and choosing white, grey or black background (Harland and Jackson, 2000; Yamawaki, 2003) or by constructing computer images of visual structures (Bond and Kamil, 2002, 2006).

These manipulations—for example, painting targets, taking pictures, or setting ambient light and background—are often done without controlling visual conditions created for the experiments, which may compromise the validity of the results observed. As an example, Harmon et al. (1998) tested predators’ reaction to different combinations of natural red and green prey morphs against artificial green and red backgrounds. They assumed that a red target was cryptic on a red background, which is not a trivial assumption. Paints are based on colourants that highly differ in terms of reflectance from natural colourants. Since they largely call for metamerism in human vision, paints likely appear really different to a different visual system, especially under artificial illumination. A red target may show a visual contrast for the tested predator and not for humans. Ignoring the receivers’ view of the combinations target background may lead to an incorrect interpretation of the results. Measuring both object and background colouration as well as ambient light is indispensable to conduct thorough experimental tests of the role of insect colouration on predation.

Using videos or images present specific problems. As we saw above, computer screens and cameras are built to render objects as humans perceive them in nature. As a consequence, they likely fail to render insect colours as most predators perceive them in nature. Videos or image colours should be modified to match receivers’ vision if they are used for the purpose of testing vision (Fleishman et al., 1998). This manipulation consists in a change of the RGB combination for each colour patch independently and require the knowledge of receiver’s vision, object natural colouration and natural illuminants (Fleishman et al., 1998) as well as the response of display device to light intensity (Stevens et al., 2007b). Again, there are two limitations: since videos do not include UV, they should be used in conditions where UV is not relevant—receiver insensitive to UV, prey showing no reflectance in the UV, light conditions rendering inefficient the exploitation of
the UV range. In addition, videos create a gradient of light intensity and should be primarily dedicated to explore vision in diurnal predators.

3.3 ANALYZING COLOURATION DATA

Once colouration is measured, data have to be analyzed to extract biologically relevant visual information about achromatic and chromatic aspects of colouration. At this stage, two main options are available for quantitative data.

3.3.1 Characterization of spectral shape

Relevant characteristics of spectral shape can be extracted using different methods. They have in common to require information about the range of wavelengths to which the study animal is sensitive. In addition, all these methods assume that all wavelengths are treated equally by the visual system, an assumption convenient for computation but obviously violated by all biological systems. Such calculations can be performed directly on reflectance spectra but they can advantageously be performed on radiance spectra. Radiance is the fraction of the ambient light that is reflected by the object and that reaches the eye of the receiver, that is, the product of irradiance by reflectance. Such calculations are particularly interesting in the absence of knowledge of the visual system of the species of interest (or a closely related species with similar visual system).

A first possibility is to perform a principal components analysis (Cuthill et al., 1999). This kind of analysis presents severe limitations. It assumes independence of observations while reflectance at different wavelengths is correlated over large bands of wavelengths. In addition, outputs are highly sensitive to the set of colours analyzed, and decomposition between achromatic and chromatic components has to be forced to be biologically relevant (see Endler and Mielke, 2005 for discussion about the limitations).

A second possibility can be a direct computation of parameters that characterize achromatic (brightness) and chromatic (hue and chroma) components of colouration. Brightness can be computed as the average reflectance/radiance over the total range of sensitivity (Endler, 1990), hue (colour in its common sense) as the location in wavelength of the maximal reflectance/radiance or most important change in reflectance and chroma (colour purity or saturation for pigment-based colouration) as a ratio to estimate the prevalence of a certain range of wavelengths (examples in studies of bird colouration: Örnborg et al., 2002; Doutrelant et al., 2008). This approach has major limitations. First, the simple and ‘all-purpose’ formulas to obtain these parameters lead to the incorrect, although tempting, consideration that these parameters describe inherent properties of an object. Brightness, chroma and hue are perceptual terms and as so, they should be fed by a thorough understanding of perception to be relevant for a particular species. Conversely, the simplistic formulas ignore important perceptual mechanisms. For instance, computing hue as maximal reflectance or
as many chroma values as peaks in a spectrum ignores the fact that chromaticity comes from the comparison between different wavebands. Similarly, brightness perception is assumed to be uniform over the range of sensitivity while it is not. These limitations should invite researchers to make effort and feed more biology and physiology into colour data.

3.3.2 A more integrated approach: analysis using ‘physiological’ models

To date, different ‘physiological’ models are available in the literature, among which the most popular and conceptually interesting are Chittka’s colour hexagon (Chittka, 1992), Vorobyev and Osorio’s discriminability threshold model (Vorobyev and Osorio, 1998) and Endler and Mielke (2005) model for analyzing colour patterns. The aim here is neither to present the models in detail nor to compare them in terms of efficiency for studying particular signals. However, it is interesting to comment on several points.

All visual information comes ultimately from the capture of photons by photoreceptors in the eye. All models rely on photon capture as the first step (Eq. (1)). Applying such equations to data collected from digital photographic equipment and corrected to be camera independent can help to analyze insect colours using models of predator vision (Stevens et al., 2007b).

\[
q_{i}^{\text{object}} = \int_{0}^{700} L(\lambda)S_{i}(\lambda) \, d\lambda
\]

where \(L(\lambda)\) is the spectrum of the light entering the eye and \(S_{i}(\lambda)\) is the spectral sensitivity of the photoreceptor \(i\). The number of types of photoreceptors determines the number of quantum catches values obtained. The neural response of the photoreceptor \(i\) is not a passive electric transfer of the photon catch but it increases non-linearly with light intensity and reaches a maximum (eq. (2), also called Michaelis–Menton equation applied to photoreceptor response). The coefficient \(k\) (also called von Kries coefficient) is the reciprocal value of the photon flux evoking a response that is half the maximal response of the photoreceptor (Eq. (3)). This coefficient considers the fact that a photoreceptor gets adapted to its light environment.

\[
V_{i}^{\text{object}} = V_{i}^{\max} \left( \frac{kq_{i}^{\text{object}}}{(kq_{i}^{\text{object}})^{n}} \right)^{n} + 1
\]

where
\[ k = \frac{1}{q_c^o} \]  

\[ V \] as a function of \( \ln(q_c) \) is a sigmoid, where \( n \) represents the slope of the curve of response of the photoreceptor (\( n = 1 \) for many species). Photoreceptor’s adaptation to light is a dynamic and reflexive process so that it is possible to consider that the mean photon flux of the field of view becomes \( q_c^o \).

Taken alone, a photoreceptor only records information about light intensity level (brightness) but cannot perform any wavelength discrimination. For objects, the spectrum of the radiant light can be seen as the proportion of the ambient light that is reflected by the object, that is the product of \( R_{\text{object}}(\lambda) \) the reflectance spectrum of the object viewed by \( I(\lambda) \) the irradiance spectrum of the ambient light illuminating the object. A visual system with \( n \) types of different photoreceptors can exploit information coming from \( n \) different independent photoreceptors. It can thus be represented by a colour space with \( n \) dimensions (Wyszecki and Stiles, 1982; Kelber et al., 2003; Endler and Mielke, 2005). Being the principle of photon catch, information about brightness is accessible to all visual systems, even the simplest ones containing only one photoreceptor type. It can be seen as one dimension of the receptor space. The remaining \( n - 1 \) dimensions constitute the chromatic space. For two, three and four photoreceptors, the chromatic space can be represented by a line, a triangle and a tetrahedron, respectively.

Chittka (1992) proposed a model for trichromatic bee vision—the colour hexagon—which relies on simple assumptions. This model takes the photoreceptor responses to build a space that can be regarded as representing colour opponent relations. The model built as a stimulus space and not a perceptual space has been widely used to study how insects view flower (e.g. Chittka, 1996) or animal (e.g. Thiéry and Casas, 2002) colouration and can be used for exploring colour patterns. Nevertheless, distances are not meant to be perceptual distances. In addition, some options of calculation of receptor excitations make statistical tests of differences between sets of colours more complex than in a fully developed colour space (see Endler and Mielke, 2005 for discussion).

A perceptual perspective has been chosen by Vorobyev and Osorio (1998) in their discriminability threshold model. Considering that visual performance is primarily limited by errors in photoreceptor responses, they aimed to inform about whether a given difference in colouration between two objects translates into a perception that these objects are different in colouration. As in earlier perceptual models of animal vision (model for bee vision, Backhaus and Menzel, 1987), Vorobyev and Osorio considered that colour was coded by opponency mechanisms and that discrimination was limited by noise (but see differences in Vorobyev and Osorio, 1998). Their model has been validated as successfully predicting discrimination thresholds in di, tri and tetrachromatic...
species in bright illumination (Vorobyev and Osorio, 1998). Modifications of receptor noise computation allowed to extend its application to conditions of restricted photon captures (dim illumination or dark objects Osorio et al., 2004). In this model, the chromatic distance $\Delta S$ between two objects A and B can be expressed for a trichromatic visual system as:

$$
\Delta S^2 = (e_1^2(\Delta f_3 - \Delta f_2)^2 + e_2^2(\Delta f_3 - \Delta f_1)^2 + e_3^2(\Delta f_1 - \Delta f_2)^2)/((e_1e_2)^2 + (e_1e_3)^2 + (e_2e_3)^2)
$$

The terms $e_i$ refers to the error associated to the type of photoreceptors $i$ and $\Delta f_i$ the differences in responses of the photoreceptor $i$ for objects A and B.

$$
\Delta f_i = \ln\left(\frac{q_i^A}{q_i^B}\right) = \ln\left(\frac{{\int_{700}^{500} R_A(\lambda)I(\lambda)S_i(\lambda) d\lambda}}{{\int_{700}^{500} R_B(\lambda)I(\lambda)S_i(\lambda) d\lambda}}\right)
$$

(4)

Endler and Mielke (2005) made an interesting link between eqs. (3) and (5). In eq. (3), the fact that a photoreceptor adapts continuously to the average light in its field of view results in the fact that its response is always in the linear part of the sigmoid curve, near the half maximal response. As a consequence, a good approximation of eq. (2) can be $V_i^{\text{object}} \approx \text{constant} \cdot \ln(q_i^{\text{object}})$. It is then easy to see that the logarithm expression in eq. (5) reflects the assumptions that a photoreceptor shows a nonlinear response with light intensity, saturation and adaptation to light and that $\Delta f_i$ reflects a difference in photoreceptor response between two different stimuli.

In eq. (4), photoreceptors’ responses are weighed by the confidence (related to the error $e$) associated to each photoreceptor type and the colour space resumes to a scale of $\Delta S$ values. Equal values of $\Delta S$ correspond to equal confidence surfaces, thus becoming perceptual distances which are expressed in JNDs (just noticeable differences). Equation (4) is a signal-to-noise ratio which describes the confidence given to visual information in its totality. The value of 1 JND is often taken as the discrimination threshold: distances below 1 indicate objects similar in colouration while values above 1 indicate objects that are perceived as different in colouration. This model performs well at predicting what happens around discrimination thresholds and stands a useful tool to determine for instance which spectral tuning of photoreceptors would offer maximal discrimination of a group of natural objects (visual background features in Chiao et al., 2000) that could be insect prey.

Nevertheless, this model presents two major limitations. First, it assumes that the perceived magnitude of suprathreshold difference is proportional to the minimum number of JNDs separating two colours. In fact, the model extends the assumption made for threshold stimuli to suprathreshold stimuli, a hypothesis that cannot model cognitive processes such as colour categorization. Formulated
in terms of JNDs, colour categorization is the fact that two colours of the same category are perceived as more similar than two colours of different categories even if both pairs show equal dissimilarity in terms of JNDs. Colour categorization has been found in several species which belong to insectivorous groups such as birds, insects, primates or fish (references in Ham and Osorio, 2007) and is likely a general cognitive process. Second, this model is designed to compare only two colour patches at a time. Comparing sets of colours (like colour patterns) requires building multiple pairs of comparisons. Results are difficult to interpret perceptually given that chromatic distances tell nothing about the relationships between colour elements nor about how they differ and if they concern the same wavelength regions of not. Some attempts have been made to circumvent this problem (e.g. Hästad et al., 2005) but they are not satisfactory simply because the model is not meant to deal with that kind of question.

Recently, Endler and Mielke (2005) proposed a simple way of analyzing colour patterns based on unconstrained colour spaces (lines, triangles, tetrahedrons), which are parsimonious in assumptions about vision mechanisms and which provide a convenient geometrical system in which spatial statistics on differences between sets of colours are possible. Going back to colour spaces allows to study not only the distance separating the colour points in the space but also their relative location within the space. This new formulation incorporates receiver’s visual system as well as the visual environment in which visual signals are viewed. Even if the incorporation of receptor noise is not routinely taken into account as in Vorobyev and Osorio (1998), it can be easily calculated to give supplementary information. This representation can conveniently incorporate data on patch relative size by weighing colour points by their relative frequency in the analyzed pattern even if, as all existing models, it cannot represent the spatial organization between colour patches, an important asset for prey detection (e.g. Cuthill et al., 2005; Stevens et al., 2006b, 2008a, 2009c).

It is noteworthy to point two interesting conclusions. First, all the models discussed here have in common to discount achromatic mechanisms. This can be a major issue, especially when considering (see Section 1) that prey detection depends on the achromatic contrast between the prey and the background, particularly in the case of small and/or moving targets. In addition, most of the experimental investigations of predators’ reaction to insect colouration have consisted in manipulating brightness and not chromatic contrast. Second, although some adaptations have been made to deal with restricted light conditions (Osorio et al., 2004), these models are fundamentally adapted for vision in bright light. Dim light conditions exert specific constraints on visual systems. Photon capture by photoreceptors is complemented by neural mechanisms of temporal and/or spatial summation of photoreceptor outputs to compensate for low photon capture. Warrant (1999) proposed a model to incorporate such mechanisms and reconstruct animal sensitivity. Although this model has not been fully developed in a colour space model, it can be helpful to analyze visual signals seen by nocturnal insectivorous species. More generally, each model has its limitations (Kelber et al., 2003;
Endler and Mielke, 2005) but also its valid fields of applications. Further work on vision modelling should focus on interesting but hitherto overlooked aspects of visual systems such as integration of chromatic and achromatic information, eye regionalization, colour categorization, variable or dim light conditions. It could also be interesting to build synthetic models combining photoreceptors functioning at different levels of light intensity (typically rods and cones in vertebrates) to explain transitional perceptual processes, such as colour vision based on rods and cones at dusk (Reitner et al., 1991).

3.4 COLOUR INVESTIGATION: PRACTICAL RECOMMENDATIONS

To be implemented, physiological models have to be fed with data on object colouration, eventually background colouration, ambient light and receiver’s visual sensitivity. Object colouration is often the elements for which most information is provided (see Endler, 1990 for information on how to acquire these data). Spectral data can be measured. Information about the location and spatial organization of colour patches within an animal or background pattern has to be collected separately. Information about the relative contribution (patch size) of colours to a pattern can be gathered separately, for instance as in Gomez and Théry (2007) or can be acquired through the spectral measurements themselves, as recommended by Endler and Mielke (2005). For instance, one can apply a grid on the animal pattern and measure one spectrum for each cell; the number of spectra collected will be a rough indication of the area occupied by each colour type on the animal.

Theoretical work on background influence on the evolution of colour signals has underlined how important it is to consider the background in its complexity (Merilaita, 2003). However, its practical incorporation in studies of colouration in relation to vision is nearly absent (few exceptions in studies about bird colouration; Endler et al., 2005; Hästad et al., 2005). Measuring background variability deals with 3D complexity, a technically challenging task. A good estimate of background visual complexity can be given by hyperspectral imaging, a technique which consists in taking a picture of the environment that would collect for each pixel not a small (three for typical cameras) but a high number of values which can describe an entire radiance spectrum. Without calling for this expensive technique, incorporating at least a minimal amount of background spatial heterogeneity can reveal differences in visual performances between close visual systems (Hästad et al., 2005) that had apparently same performance in the case of an average background (Gomez and Théry, 2007). Models like that of Endler and Mielke (2005) offer the mathematical and statistical grounds needed for a synthetic comparison of more realistic viewing scenes. For instance, Merilaita’s (2003) finding that visually complex environments lead to the evolution of less cryptic prey can be easily spatially visualized. Visual similarity between two sets of colours is represented in a colour space by the overlap, or the inclusion of the clouds of points corresponding to these sets
of colours. Visually complex backgrounds are represented in colour spaces by more disperse clouds of points, in which a higher number of insect colour patterns (clouds of points) can fit in, resulting in similar levels of crypsis.

Information about ambient light should be collected in the same environmental conditions and at the time of day that the colour patches displayed by insects are normally seen by predators. If direct measurement is not possible, standard illuminants can to some extent be satisfying substitutes. Some standards exist for open areas from dusk to midday environments and are provided by the CIE (Commission Internationale de l’Eclairage).

Finally, the knowledge about visual sensitivity can be directly acquired on the species of interest through physiological and/or behavioural investigations. Although models of colour analysis vary in their requirements on this point, they have in common to need at least the spectral sensitivity curves of the different types of photoreceptors involved in vision. Curves only available from printed articles can be digitized using software like Winding (Lovy, 1996). If no curve is available, photoreceptor absorption functions can be mathematically computed based on few data (mainly peaks of absorbance of photoreceptors) and templates. Templates have been determined for insects (Stavenga et al., 1993) and for vertebrates (Govardovskii et al., 2000). For some groups such as birds, complementary templates for optical filters are also needed (Hart and Vorobyev, 2005). For vertebrates, it is also possible to model the visual effect induced by ocular media filters (Endler and Mielke, 2005). Even if templates may appear awkward in their mathematical formulation, they can be easily generated with a computer. One should prefer to use the information available for the species of interest whenever available.

As a conclusion, a thorough investigation of colours should be based on the method of measurement best adapted to the question asked. Although time-consuming and effort-demanding, objective and detailed measurements of the sets of visual elements important for prey detection should be performed. Special attention should be paid to signal perception if artificial prey targets are to be used. In all cases, spectrometry is a useful tool for measuring colour targets or controlling the biological validity of visual stimuli. A range of possible options is available to reconstruct insect colours as they are likely perceived by predators. Choosing a model should be guided by the type of question explored. Ideally, model choice should precede data collection in order to build a protocol best adapted to the question asked.

While models on animal colour vision are continuously attacked with the argument that they do not reflect exactly the visual system, it is important to notice that models are not meant to be perfect but to capture the essential elements. Vision models take into account the indispensable steps to explain the behavioural action spectra linked to visual detection (see assumptions in Vorobyev and Osorio, 1998). Nevertheless, they leave aside other aspects (shape and spatial organization of colour patches, behaviour) which may be important to consider for a skeptical and fruitful interpretation of the results, and even in the planification of the study.
4 Features of insect camouflage

One way to understand how insects are viewed by their predators is through the study of camouflage. Indeed, insect camouflage is often interpreted as the result of natural selection to avoid detection and recognition by predators, frequently involving body colouration. Therefore, identifying the features of camouflage could reveal how predator visual systems might be lured by insect prey. However, since the landmark books of Thayer (1909) and Cott (1940), research on natural camouflage has not progressed rapidly (Stevens and Merilaita, 2009a). This is notably due to the fact that camouflage has often been considered as obvious, not requiring formal testing. In addition, camouflage has mostly been viewed through human eyes, and not from the perspective of the appropriate receiver, the predator. It is only in the 1980s that the objective quantification of animal colouration and visual environments (Endler, 1978, 1984) promoted a more rigorous study of insect camouflage. More recently, the development of visual and computer sciences greatly facilitated the study of camouflage and induced an explosion in the number of scientists in this field, as evidenced by a recent compilation of works from biologists, visual psychologists, computer scientists and artists (Stevens and Merilaita, 2009a).

The term camouflage encompasses ‘all strategies involved in concealment, including prevention of detection and recognition’ (Stevens and Merilaita, 2009a). According to this recent review, there are four main tactics of camouflage: crypsis—which includes disruptive colouration, background matching, self-shadow concealment, obliteratorive shading, flicker-fusion camouflage, and distractive markings—masquerade, motion dazzle and motion camouflage. In this chapter, we will focus on the mostly studied form of camouflage in insects, crypsis, and review the relatively rare insect examples of masquerade and motion camouflage.

4.1 CRYPSIS

Most studies of insect camouflage have been conducted with birds as predators (Table 2) because birds are highly visually oriented predators and one of the main groups of insect predators. In addition, it is often possible to identify bird predation of insects in the wild, for example through damage on the wing of live or artificial insects.

4.1.1 Disruptive colouration and background matching

Among the different means of crypsis, disruptive colouration has been the most studied, and most often in insects (Table 2). Disruptive colouration ‘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
TABLE 2
Experimental tests of strategies used for visual camouflage by insects

<table>
<thead>
<tr>
<th>Strategy</th>
<th>Prey</th>
<th>Predator</th>
<th>Support</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Crypsis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Disruptive colouration</td>
<td>Peacock butterfly</td>
<td>Birds</td>
<td>No (?)</td>
<td>Silberglied <em>et al.</em> (1980)</td>
</tr>
<tr>
<td>Marginal pattern elements</td>
<td>Artificial moth</td>
<td>Birds</td>
<td>Yes</td>
<td>Cuthill <em>et al.</em> (2005); Schaefer and Stobbe (2006)</td>
</tr>
<tr>
<td></td>
<td>Artificial prey</td>
<td>Great tit</td>
<td>Yes</td>
<td>Merilaita and Lind (2005)</td>
</tr>
<tr>
<td></td>
<td>Artificial moth</td>
<td>Bird edge detection model</td>
<td>Yes</td>
<td>Stevens and Cuthill (2006)</td>
</tr>
<tr>
<td></td>
<td>Artificial moth</td>
<td>Humans</td>
<td>Yes</td>
<td>Fraser <em>et al.</em> (2007)</td>
</tr>
<tr>
<td>Maximal disruptive contrast</td>
<td>Artificial moth</td>
<td>Birds</td>
<td>Yes</td>
<td>Cuthill <em>et al.</em> (2005)</td>
</tr>
<tr>
<td></td>
<td>Artificial moth</td>
<td>Birds</td>
<td>No</td>
<td>Stevens <em>et al.</em> (2006b)</td>
</tr>
<tr>
<td></td>
<td>Artificial butterfly</td>
<td>Birds</td>
<td>No</td>
<td>Stobbe and Schaefer (2008)</td>
</tr>
<tr>
<td>Coincident disruptive colouration</td>
<td>Artificial moth</td>
<td>Birds</td>
<td>Yes</td>
<td>Cuthill and Székely (2009)</td>
</tr>
<tr>
<td>Disruption of surface</td>
<td>Artificial moth</td>
<td>Birds</td>
<td>Yes</td>
<td>Stevens <em>et al.</em> (2009c)</td>
</tr>
<tr>
<td>Asymmetrical patterns</td>
<td>Artificial moth</td>
<td>Birds</td>
<td>Yes</td>
<td>Cuthill <em>et al.</em> (2006a,b)</td>
</tr>
<tr>
<td>Background matching</td>
<td>Moth</td>
<td>Blue jay</td>
<td>Yes</td>
<td>Merilaita and Lind (2006)</td>
</tr>
<tr>
<td></td>
<td>Lepidoptera larvae</td>
<td>Bird with UV vision</td>
<td>Yes (five out of six spp.)</td>
<td>Pietrewicz and Kamil (1977)</td>
</tr>
<tr>
<td></td>
<td>Artificial prey</td>
<td>Great tit</td>
<td>Yes</td>
<td>Church <em>et al.</em> (1998)</td>
</tr>
<tr>
<td></td>
<td>Moth</td>
<td>Jumping spider</td>
<td>Yes</td>
<td>Merilaita <em>et al.</em> (2001), Merilaita and Lind (2005)</td>
</tr>
<tr>
<td></td>
<td>Artificial moth</td>
<td>Birds</td>
<td>Yes</td>
<td>Moss <em>et al.</em> (2006a)</td>
</tr>
<tr>
<td></td>
<td>Artificial moth</td>
<td>Humans</td>
<td>Yes</td>
<td>Fraser <em>et al.</em> (2007)</td>
</tr>
<tr>
<td></td>
<td>Artificial moth</td>
<td>Humans</td>
<td>Yes</td>
<td>Johnsson and Kjällman-Eriksson (2008)</td>
</tr>
</tbody>
</table>

(continues)
<table>
<thead>
<tr>
<th>Strategy</th>
<th>Prey</th>
<th>Predator</th>
<th>Support</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distractive markings</td>
<td>Artificial moth</td>
<td>Birds</td>
<td>No</td>
<td>Stevens et al. (2008a)</td>
</tr>
<tr>
<td></td>
<td>Artificial prey</td>
<td>Blue tit</td>
<td>Yes</td>
<td>Dimitrova et al. (2009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Birds</td>
<td>Species dependent</td>
<td>Speed et al. (2005)</td>
</tr>
<tr>
<td>Masquerade</td>
<td>Caterpillars</td>
<td>Birds</td>
<td>Yes</td>
<td>De Ruiter (1952)</td>
</tr>
<tr>
<td></td>
<td>Beetle larva</td>
<td>Ants</td>
<td>No (not visual)</td>
<td>Eisner et al. (1967)</td>
</tr>
<tr>
<td></td>
<td>Chrysoptera larva</td>
<td>Ants</td>
<td>No (not visual)</td>
<td>Eisner et al. (1978)</td>
</tr>
<tr>
<td></td>
<td>Assassin bugs</td>
<td>Spiders, gecko, centipede</td>
<td>Yes, from gecko</td>
<td>Brandt and Mahsberg (2002)</td>
</tr>
<tr>
<td></td>
<td>Assassin bugs</td>
<td>Jumping spider</td>
<td>Yes</td>
<td>Jackson and Pollard (2007)</td>
</tr>
<tr>
<td></td>
<td>Aphid</td>
<td>Jumping spider</td>
<td>Yes</td>
<td>Moss et al. (2006b)</td>
</tr>
<tr>
<td>Motion camouflage</td>
<td>Chironomid larva</td>
<td>Three-spined stickleback</td>
<td>Yes</td>
<td>Ioannou and Krause (2009)</td>
</tr>
<tr>
<td></td>
<td>Mantid</td>
<td>Mantid, lizard</td>
<td>Yes</td>
<td>Watanabe and Yano (2009)</td>
</tr>
</tbody>
</table>

? Denotes a study which conclusion has been severely criticized.
Four main principles of disruptive colouration have been investigated, three of which are largely supported (Table 2). First, ‘marginal pattern elements’ placed on the edge of the body, which are predicted to be more disruptive than patches placed inside (Cott, 1940). Second, highly contrasting patterns, which should be more effective than less contrasting patterns (‘maximum disruptive contrast’, Cott, 1940). Third, continuous patterns that range over different body parts and can be used to conceal revealing body parts, such as eyes (‘coincident disruptive colouration’, Cott, 1940). Fourth, false edges which can be used to create an appearance of different shape and hinder recognition of the body outline (‘disruption of surface’, Cott, 1940). It must be noted that these different hypotheses are not mutually exclusive and can be tested simultaneously: for example, Cuthill et al. (2005) have tested both the principles of marginal pattern elements and maximal disruptive contrast. Another well studied means of crypsis is background matching, ‘where the appearance generally matches the colour, lightness and pattern of one (specialist) or several (compromise) background types’ (Stevens and Merilaita, 2009a). Because the study of disruptive colouration has often been conducted together with the study of background matching (Merilaita and Lind, 2005; Schaefer and Stobbe, 2006; Fraser et al., 2007), and since animals may use both techniques simultaneously, we will review these mechanisms in the same section.

Surprisingly, until the last 5 years, only one experimental test of the effectiveness of insect disruptive colouration against non-human predators existed (Table 2; Silberglied et al., 1980). This study did not consider a specific mechanism of disruptive colouration, and to our knowledge stands as the only study of disruptive colouration conducted with living insects and predators in the wild. It was performed on a nymphalid butterfly highly palatable to birds, the banded peacock Anartia fatima, and apparently did not support the hypothesis of disruptive colouration. Since the butterfly frequented only one artificial clearing, the authors could capture and individually mark nearly the entire population, which allowed extremely high recapture rates and determining the minimum age of each butterfly at every capture and a minimum longevity for each individual in the population. The wing stripes of one part of the males was obliterated with black felt-tip marking pens, and equal numbers of individuals used as controls had the dye applied to the dark region basal to the wing stripe so that their appearance remained unchanged. Wing damages by birds were then monitored over 21 weeks. Unexpectedly, butterflies lacking disruptive colouration lived as long as those from the control group, a finding inconsistent with the theory of disruptive colouration. However, several objections were later made to this conclusion. First, the experimental modification might have made the butterflies look like an unpalatable species (Waldbauer and Sternburg, 1983) or directly modified their palatability (Cuthill et al., 2005). Second, obliterating the wing stripe may simply have converted the pattern from one background matching type to another background matching type of equal crypsis (Endler, 1984).
has not been demonstrated to be disruptive in function, so it may have another unrelated function (Stevens et al., 2006a). Clearly, more experimental support for the theory of disruptive colouration was needed, especially by taking into account the visual abilities of predators.

4.1.1.1. Marginal pattern elements  A clear improvement in the investigation of disruptive colouration was made with the study of Cuthill et al. (2005), who tested the prediction from Thayer (1909) and Cott (1940), that disruptive colouration occurs when patches on the body’s edge are more effective than patches placed randomly over the body (‘marginal pattern elements’). They offered predators artificial moth-like prey consisting of dead mealworms Tenebrio molitor on top of coloured paper triangles pinned onto oak trees. They carefully measured the colour contrast of artificial prey with the natural background by spectrometry coupled with the modelling of predicted photon catches of a typical passerine bird, the blue tit. ‘Prey’ survival was monitored over 24 h, and ‘predation’ by birds could be separated from predation by spiders and slugs because spiders suck fluids out, leaving a hollow exoskeleton, and slugs leave slime trails. The results were clear cut: artificial moths with markings overlapping the edge showed higher survival than the other patterns, whereas a ‘prey’ with randomly selected markings survived better than a model with the markings that were on the edge had been brought inward so that they do not overlap the edge. Black and brown uniform models survived worst of all. This clearly supports the hypothesis of disruptive colouration. Stevens and Cuthill (2006) analyzed digital images from the second experiment of Cuthill et al. (2005) with an edge detection algorithm combined with the photon catches of starlings Sturnus vulgaris. They showed that disruptive colouration is effective because ‘false’ edges are detected within the body of artificial moths rather than on the body outline, therefore hindering detection of the body outline of prey by its predator. These studies, together with others mainly studying background matching (Merilaita and Lind, 2005; Schaefer and Stobbe, 2006; Fraser et al., 2007), all supported the hypothesis of disruptive colouration through marginal pattern elements (Table 2).

4.1.1.2. Maximum disruptive contrast  As proposed by Poulton (1890), Thayer (1909) and Cott (1940), it could be important for concealment that some colour elements contrasting in tone and different from the background should be highly conspicuous (‘maximum disruptive contrast’). This question was investigated in the second experiment conducted by Cuthill et al. (2005), which showed that highly contrasting colours enhance the disruptive effect, again strongly supporting the theory of disruption in the field, independently of background matching (Sherratt et al., 2005; Stevens et al., 2006a). However, in Cuthill et al.’s (2005) study, all components of disruptive patterns presented colours in common to the natural background, which might not allow a proper test of the theory of maximum disruptive contrast. In order to avoid this
potential bias, Stevens et al. (2006b) used grey and black artificial moths (rather than brown and black in Cuthill et al., 2005) with the grey luminance matching, or mismatching, the background oak bark. Therefore, the targets did not match the colour of oak bark. The results confirmed the higher survival of edge disruptive patterns, and showed that disruptive patterns have a survival advantage compared to background-matching patterns which are not disruptive. As predicted by Thayer (1909) and Cott (1940), disruptive patterns still provide camouflage when the pattern elements are not matching the background, suggesting that an animal, presenting conspicuous patches involved in intraspecific communication, for example, can benefit from having them placed disruptively. However, heightened achromatic contrasts of marginal patterns did not increase the disruptive effect. Because moth models did not match bark colouration, the fact that two-tone background-matching patterns were more difficult to detect than monochrome targets supports the idea that pattern detection involves brightness contrast in birds (Osorio et al., 1999; Jones and Osorio, 2004). Stobbe and Schaefer (2008) also tackled the principle of maximum disruptive contrast by using artificial models of the diurnal white admiral butterfly Limenitis camilla differing in the chromatic but not the achromatic contrast of their wing stripes to the background as well as to the adjacent brown colouration of the wings. The visual contrasts on oak trees were modelled using the visual sensitivities of blue tits and the prevailing ambient light. The results showed that the strength of chromatic contrast was negatively correlated with survival probability. Therefore, as in Stevens et al. (2006b), these experiments do not support the predictions of maximal disruptive contrast.

4.1.1.3. Coincident disruptive colouration

Apart from disguising the body outline, disruption can also function to conceal other characteristic body parts, such as eyes, antennae and limbs (Cott, 1940). Concealment is obtained by using continuous patterns joining different body parts and the outline between them, and termed ‘coincident disruptive colouration’ (Cott, 1940). Patterns could be dark eye stripes that conceal the eyes, or two-tone body on wings with a two-tone central section, with dark and light sections of the wings and body coincident. The first and only experimental test of this form of disruption has been conducted by Cuthill and Székely (2009) by using artificial moths, preyed upon by wild birds, in which coincidence of colour patterns of wings and bodies was varied. They also conducted a visual search experiment on humans watching pictures of oak bark with or without artificial moths. Both experiments confirmed Cott’s (1940) principle of coincident disruptive colouration.

4.1.1.4. Disruption of surface

Another way of visual disruption than ‘marginal pattern elements’ breaking up the body outline is obtained by creating ‘false edges’ away from the body outline not corresponding to any animal feature (‘disruption of surface’, Stevens and Merilaita, 2009b). While most studies of disruption have focused on marginal pattern elements, only one recent
study experimentally tested the concealment effect of surface disruption (Stevens et al., 2009c). This study used artificial moths of different outline and surface patterns, and of different luminance contrasts, presented to wild avian predators. It also used the avian visual model and the algorithm of edge detection used by Stevens and Cuthill (2006). High luminance of markings increased the effectiveness of disruption, and markings with highest contrast placed away from the body outline were highly effective, supporting Cott’s (1940) idea of surface disruption. The avian edge model showed that surface disruption is not obtained by creating false edges away from the body outline, and that it may be related to a different visual mechanism.

4.1.1.5. Asymmetrical patterns Another challenge was to determine if symmetrical patterns, common in moths, are effective in disrupting body outlines to predators. It is indeed intuitive and demonstrated in humans that symmetry can facilitate visual search of cryptic prey, but this had not been tested in animals. All studies to date have confirmed the survival advantage of asymmetrical patterns. Again using spectrometry and artificial moths baited with mealworms, Cuthill et al. (2006a) tested the conspicuousness to bird predators of highly cryptic prey with or without bilateral symmetry in the matching of oak tree colouration. Following the ‘survival’ of targets over 5 days, they identified a small but significant fitness increase of asymmetry in insect models. The question of why asymmetry is not more common in cryptic colouration remains to be answered, and could be a challenge for developmental processes. Using the same techniques, Cuthill et al. (2006b) showed that symmetry of prey colouration has the same detrimental effects with regard to bird predation for both disruptive and non-disruptive background-matching patterns. Using captive great tits and artificial prey models, Merilaita and Lind (2006) confirmed the existence of a cost to cryptic prey for bilateral symmetry, even if not all bilaterally symmetric, cryptic patterns generate similar cost (one symmetric pattern in their experiment even generated no cost, but predators were very close to the prey substrate; see Cuthill et al., 2006b).

4.1.1.6. Background matching and its relation with disruptive colouration Most studies conducted on background matching have supported this principle (Table 2). An early experimental study in insects has been conducted by Pietrewicz and Kamil (1977) who trained blue jays Cyanocitta cristata to respond to the presence or absence of bark-like Catocala moths in slides. Moths were less likely to be detected by birds if they were presented on their naturally colour-matching substrate, and this concealment was increased when moths were in their natural resting orientation (head down or up depending on the species) compared to a horizontal position. Prey orientation has little effect for moths placed on a non-matching substrate, showing that background matching combined with orientation are important components of crypticity for these moths.
Endler (1978) proposed that ‘a color pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat where the prey is most vulnerable to visually hunting predators’. Despite numerous studies showing that prey are more difficult to detect when they have a high degree of resemblance with their visual background, Endler’s (1978) idea of camouflage through random sampling of the background had not been experimentally tested until Merilaita and Lind (2005). This study investigated the risk of detection of artificial prey by great tits Parus major in captivity. The ‘prey’ had two patterns randomly sampled from the background (difficult and! easy to detect) and a disruptive pattern. Two sets of prey were used: one with pattern elements broken on the outline, and one with full pattern elements touching the outline. The results showed that prey colouration matching a random sample of the visual background was not sufficient to maximize background matching, in contradiction with Endler’s (1978, 1984) suggestion. In addition, the disruptive prey and the best background-matching prey were equally cryptic. This was true for both prey sets, with whole pattern elements on the prey outline or with elements cut on the prey outline. This supports the principle of disruptive colouration, but also shows that random visual sampling of the background is neither sufficient nor necessary for efficient camouflage.

Another interesting study of background matching was conducted by Merilaita et al. (2001) who used great tits searching for artificial prey on two different visual backgrounds, either small or large patterned. Two prey types had the same patterns as the backgrounds, either small or large, whereas a third type had an intermediate pattern. Search time of prey was longer on the large-patterned than on the small-patterned background. Logically, the small-patterned prey was most cryptic on the small-patterned background, and the reverse was true for large-patterned prey on the large-patterned background. The compromised prey showed an intermediate crypticity on the small-patterned background, but was not significantly less cryptic than the large-patterned prey on the large-patterned background. Most interestingly, the compromised colouration had lower predation than the matching colourations, indicating that it might be the best strategy for a prey in heterogeneous habitats.

A first attempt to consider the full range of predators’ visual sensitivity in a study of background matching was made by Church et al. (1998), who examined whether crypsis of lepidopteran larvae found on oak trees extended in the UV. The reflectance of oak leaves and of six caterpillar species was measured by UV/visible spectrometry, in the full range of wavelengths to which insectivorous birds are sensitive. For five out of the six species, crypsis of these green caterpillars extended in the UV. However, one species which appeared moderately cryptic to the human eye was found to be very conspicuous to a UV-detecting avian predator. This showed how crucial it is to take into account the visual sensitivities of predators. Stobbe et al. (2009) examined the underlying visual mechanisms of background matching with two artificial prey types differing in their chromatic contrast in the UV/blue range, but achromatically identical as seen in the eyes of
blue tits. The backgrounds were either matching or mismatching the prey colouration. The results showed that chromaticity in the UV/blue range, as well as achromatic cues, are used by bird predators to search for prey. However, it remains to be studied if chromaticity in the medium and long wavelengths is as important as colour contrast in the short wavelengths for the visual search of avian predators.

In order to disentangle the camouflage functions of disruptive colouration and background matching, Schaefer and Stobbe (2006) designed five artificial models of the peach blossom moth, *Thyatira batis*, differing by their visual contrasts and disruptive patterns, as measured in the blue tit visual system, which were glued on differently coloured trunk backgrounds. A dead mealworm was glued underneath the wings so that less than half of the mealworm was visible to predators, and prey survival was monitored over 24 h. Interestingly, they found that chromatic contrast is more efficient than achromatic contrast to reduce predation: low chromatic contrast of cryptic moth reduced its predation risk to the level of disruptive prey. They confirmed the lower mortality of disruptively coloured forms compared to the cryptic form, and showed that disruptive forms on the body outline have higher survival in a wider range of habitats than the background matching form even though the disruptive patterns are symmetrical. Disruptive forms on the body interior provide, as background matching, efficient camouflage, but their protective value is specific to a particular background. Overall, their results confirmed the prediction of Cuthill et al. (2005), that disruptive colouration is more efficient on the body outline, independently of background matching.

Apart from the study of Fraser et al. (2007) with ‘human predators’, only three studies have considered other predators than birds. The first is the investigation of background matching of grass moths *Orocrambus flexuosellus* preyed upon by jumping spiders *Trite planiceps* and *Marpissa marina* (Moss et al., 2006a), who showed that spiders were less efficient to detect and capture moths on a matching than on a contrasting visual background. The second involves maggots preyed upon by wild brown trout parr *Salmo trutta* on a matching or contrasting background (Johnsson and Kjällman-Eriksson, 2008). This study also found that search time for prey was increased on the colour-matching background. The third study involved predatory beetles *Jauravia* sp. feeding on coccids *Saissetia filicum* found either on fern sori where they appear cryptic, or on vegetative leaves where they appear conspicuous (Patra et al., 2008). It showed that the degree of predation by beetles is higher on conspicuous than on cryptic coccids. However, it should be noted that these three studies inferred matching or contrasting backgrounds only by using human vision.

### 4.1.2 Distractive markings

In addition to disruption, prey can also avoid predation by using distractive markings (Thayer, 1909), which are highly visible patterns or patches that distract the predator attention toward them, and away from the body outline.
The first experimental test of that form of crypsis has been conducted by Stevens et al. (2008a) using artificial moths preyed upon by wild birds. The models used varied by the shape (irregular or circular) and the intensity of visual contrast of the markings with respect to the model (Fig. 1). A dead mealworm partially covered by the model provided an edible component to the predator. Contrary to Thayer’s predictions, potentially distractive markings decreased survival of artificial moths, and circular markings were as likely detected than irregular ones. In their recent experiment, Dimitrova et al. (2009) used blue tits searching in a cage for artificial prey with different levels of distractive markings on different types of visual backgrounds. The backgrounds also differed by their degree of distraction. Their results confirmed Thayer’s principle of distractive markings in prey improving camouflage. Interestingly, backgrounds with distractive features also increased search time of predators, independently of prey appearance. This suggests that camouflage may be favoured in highly visually contrasted habitats.

4.1.3 Countershading

Countershading is a means of crypsis in which animals have a darker pigmentation on the body surface mostly exposed to ambient light. It allows prey concealment through two strategies (Stevens and Merilaita, 2009a): self-shadow concealment, ‘where directional light, which would lead to the creation of shadows, is cancelled out by countershading’, and obliterator shading, ‘where countershading leads to the obliteration of three-dimensional form’ (see also Rowland, 2009). In insects, as in most animal groups, countershading has most often only been supported by indirect evidence, interpreting camouflage through human vision (for a recent review see Rowland, 2009). This was for example the case in the studies of Thayer (1909), de Ruiter (1956) and Tinbergen (1957). Few experimental tests of the adaptive value of
countershading have been conducted but, because of methodology or sample size, it could not be concluded that crypsis was improved (see Rowland, 2009). More rigorous experiments were conducted by Edmunds and Dewhirst (1994), who exposed artificial prey differing by their countershading patterns to predation by wild birds and found a higher survival value of countershaded prey. However, Speed et al. (2005) conducted a similar experiment and found no reduction in attack of countershaded prey. None of those studies took into account the visual sensitivities of avian predators. This led Rowland et al. (2007) to try solving this discrepancy using similar methods, but this time including spectrometric measurements and a model of avian colour vision. In both experiments, one in which artificial prey were presented on lawns to a range of bird species, the other in which prey were presented on green boards to individual blackbirds Turdus merula, countershaded prey had lower levels of predation than controls. Rowland et al. (2008) also conducted more realistic field experiments in which they used artificial prey resembling Lepidoptera larvae presented on the upper and lower surfaces of beech tree branches to wild bird predators. When prey items were presented on the upper surface of branches, the countershaded prey had higher survival than the uniformly coloured prey. When they were presented on the underside of branches, the prey with a reversal of the orientation of countershaded colouration had highest survival. This clearly provides evidence that an increase in pigmentation on the side of the prey closest to the light source offers camouflage in the eyes of the predator. In her recent review on the function of countershading, Rowland (2009) presented the first measurements of visual contrasts of countershaded lepidopteran larvae on their food-plant visual backgrounds, showing that countershading is stronger in the achromatic channel than in the chromatic one. However, it cannot support the principle of background matching since the illuminant spectra were the same for larvae presented on the upper or underside of branches, which is a crucial parameter to consider in countershading theory. Although much is left to be done in its study and that several objections to countershading as a mean of concealment have been raised (see Rowland, 2009), our understanding of countershading has progressed rapidly in recent years, partly due to the use of more rigorous consideration of the colour of prey and of the visual sensitivity of predators.

4.2 MASQUERADE AND DECORATION

Masquerade is used when prey ‘mimic inedible objects such as leaves, sticks and bird droppings, that is, objects of no inherent interest to the potential predator’ (Ruxton et al., 2004). Research on this camouflage tactic has been relatively limited, probably because adaptive advantages appear quite straightforward to understand (Fig. 2). Therefore, we mainly have descriptions of insects resembling inedible objects (e.g. references in Edmunds, 1990; Robinson, 1990; Canfield et al., 2009), but rare experimental demonstrations
of the survival value of this tactic. An early experiment was conducted by De Ruiter (1952) who offered caterpillars of canary-shouldered thorns *Ennomos alniaria*, oak beauty *Biston strataria* and *B. histaria* to Eurasian jays *Garrulus glandarius* and chaffinches *Fringilla coelebs*. Birds were first familiarized with sticks, of the same dimension as caterpillars, taken from the trees where caterpillars were collected. Dead caterpillars were then introduced in the experimental cage, mixed with sticks. Birds had great difficulties at finding caterpillars, obviously not discriminating prey from sticks. However, birds could discriminate caterpillars from twigs of other trees. In other experiments with living stick caterpillars, prey were found and eaten as soon as they moved. Avian predators obviously could not discriminate motionless caterpillars from sticks found of the trees on which they fed. However, in this experiment, it is difficult to conclude that predators detected and misidentified prey (masquerade) rather than simply failing to detect prey (crypsis). In an ingenious experiment, Skelhorn et al. (2010) showed that the cognitive strategies of predators, rather than their sensory abilities, drive the evolution of masquerade. They exposed three groups of naïve domestic chicks to a hawthorn branch (the host plant of twig-like caterpillars used as prey), three groups to a hawthorn branch bound in purple cotton thread to change its visual appearance, and three groups to an empty arena. The chicks with a prior experience of twigs were slower and more cautious to attack and handle twig-like caterpillars or twigs than chicks exposed to the purple twig. Chicks with no prior experience of twigs were even faster and less cautious to peck and handle twig-like prey or twigs. Because test items were strongly contrasting on the arena substrate, these results clearly show that masquerade functions in the absence of crypsis and can provide an entirely additional benefit to it.
Another form of masquerade has been described in species that cover their body with leaf, flower parts, lichen, faecal droplets, moulted skins and other organic or non-organic material. For example, the camouflage role of the trash packet held on the back of several insect larva species has been investigated by Eisner et al. (1967) who exposed larvae of the thistle tortoise beetle Cassida rubiginosa to Allegheny mound ants Formica exsectoides. It was found that ants easily detected prey, but that larva used their ‘faecal shield’ to avoid being bitten and killed by ants, therefore rejecting the visual camouflage function. Eisner et al. (1978) also studied larva of the green lacewing Chrysopa slossonae that feeds on wooly alder aphids Prociphilus tesselatus and copes with ants protecting the aphid colonies by masquerading as an aphid. To do so, larvae tears away waxy tufts from aphids and loads this material on its back, closely resembling its aphid prey. Both shielded and denuded larvae were presented to ants (black carpenter ants Camponotus pennsylvanicus, C. noveboracensis, Formica sp.). In all cases, ants rapidly detected the larvae, but only removed denuded ones from aphid colonies. Again, this form of masquerade appears to provide protection from predators, but not through visual perception. Other evidences suggest that this trash-carrying behaviour is used as defense, not visual camouflage, against insect predators (see Eisner et al., 1978).

However, in other cases, masquerading prey appears to avoid being visually identified by predators. For example, Brandt and Mahsberg (2002) studied the disguise of West African assassin bugs Pareodocla sp., Acanthaspis petax and Acanthaspis sulcipes with respect to their success in hunting ants (Dorylus nigricans, Crematogaster sp., Camponotus sp.) and to protection from predators (wall spiders, African house gecko Hemidactylus brooki, centipede Scolopendra morsitans). These bugs’ nymphs have the peculiarity to cover their whole bodies with dust, sand or soil (‘dust coat’), and to pile a ‘backpack’ of larger objects (prey corpses, other animal and vegetable matter) on their abdomens. Experiments with prey showed that better hunting success could be obtained with the dust coat impeding chemical and tactile recognition by ants. However, in experiments with predators, the main protective effect was attributed to the backpack which enhanced the concealing effect of the dust coat and confused the visually oriented predators (geckos). Jackson and Pollard (2007) also studied predation of masked or naked assassin bugs A. petax, but this time by three salticid spider species that also have acute vision. They confirmed results obtained by Brandt and Mahsberg (2002), showing that masquerade induced a failure of visual recognition of prey by predators. Moss et al. (2006b) conducted different experiments with the wooly apple aphid that covers itself with wax, Eriosoma lanigerum, attacked by the jumping spider M. marina. Their results suggest that wax is indeed hiding visual cues used for prey identification, notably the head which was sufficient for spiders to identify the aphid. Canfield et al. (2009) described larval decoration and morphological plasticity in larvae of Southern emerald moths Synchlora frondaria. They showed that larvae use anthers, pieces of petals and small leaves to cover their dorsal
surfaces. Interestingly, they also showed that larvae acquire the colour of their host plants by consuming flower parts. Although both mechanisms were interpreted as obviously providing crypsis on their visual background, no test of protection from predators was conducted in this study.

4.3 MOTION CAMOUFLAGE

To our knowledge, the only study of motion camouflage involving insects in the context of predation is that of mantids *Hierodula patellifera* avoiding detection by predators (conspecific mantids and Japanese five-lined skinks *Plestiodon japonicus*) when they are exposed on vegetation moving by the wind (Watanabe and Yano, 2009). Both in the field and in the laboratory, mantids walked and swayed their body more frequently when the wind blew harder, which is suggested as adaptive in reducing the risk of predation because predators were less likely to discover prey in the swaying leaf condition.

5 Warning colourations and patterns viewed by predators

The effectiveness of warning colouration has been largely supported in a wide range of wild and domestic insect predator species (Table 3). Colours avoided by predators are often red and black-and-yellow stripes. One caveat of studies of warning colouration is the frequent absence of appropriate colour measurement and consideration of predators’ visual sensitivities. To our knowledge, only Lyytinen *et al.* (2001), Schultz (2001), Gamberale-Stille (2001), Tullberg *et al.* (2005) and Prudic *et al.* (2007) used spectrometry to measure and study warning colouration. None of those has undertaken photon catch modelling.

5.1 WARNING COLOURS: LEARNT OR INNATE?

One important aspect of research on warning colouration is to determine if avoidance is learnt or innate. It has long been thought that predators learn to avoid warning colouration of prey, implying that the function of warning colouration is to facilitate avoidance learning and prey recognition (references in Schuler and Hesse, 1985). In his elegant work, Mostler (1935) underlined the importance of colour pattern in learning. Naïve insectivorous birds fed upon black and yellow hoverflies, showing no innate aversion towards striped patterns. Yet, they rapidly learnt to avoid noxious striped hymenopteran species (wasps, honeybees, bumblebees) and subsequently avoided hoverflies with striped patterns. Hoverflies gained their protection from their visual resemblance and colour patterns played an important role in avoidance learning. Since the 1950s, unlearned (in the sense of innate) avoidance of different coloured food has been demonstrated in a range of wild and poultry birds (references in Ruxton *et al*., 2004). Using hand-reared naïve birds captured in
<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Prey</th>
<th>Predator</th>
<th>Support</th>
<th>Avoidance</th>
<th>References</th>
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<td>Warning colour</td>
<td>Butterflies</td>
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<td>Yes</td>
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<td></td>
<td>Butterflies</td>
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<td>No</td>
<td>No avoidance of white</td>
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<td>Black/yellow stripes</td>
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<td>Black, black-yellow stripes, red</td>
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<td>Red</td>
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<td>Red</td>
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<td>Firebug</td>
<td>9 passerine spp.</td>
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<td>Red and orange</td>
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<td>Harlequin bug</td>
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<td>Milkweed bugs</td>
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<td>Brightness contrast helps detection</td>
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<td>Carabid beetle</td>
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<td>Black with yellow spots</td>
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<td>Artificial prey</td>
<td>Great tit</td>
<td>No</td>
<td>No aversion to UV</td>
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<td>Wasps, flies</td>
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<td>Black-yellow stripes in wasp only</td>
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<td>Natural, artificial</td>
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<td>Yellow-pink spot on jet black body</td>
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<td>Large, symmetric</td>
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<td>Symmetry in colour, shape and size</td>
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<td>Birds</td>
<td>No</td>
<td>No advantage of symmetry</td>
<td>Stevens et al. (2009b)</td>
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* Avoidance is observed in small insectivores but not in large insectivores or granivores.

The table is not exhaustive since we have not considered all studies on insect aposematism.
the USA (blue jays, red-winged blackbirds *Agelaius phoeniceus*, common grackles *Quiscalus quiscula*) fed with unfamiliar butterflies captured in Trinidad, Coppinger (1970) found a clear avoidance of novel foods and of red/black palatable butterflies (scarlet peacock *Anarthia amathea*) compared to brown and white butterflies similar in size (white peacock *Anarthia jatrophae*). Because birds were initially fed on brown food, Coppinger (1969) interpreted this result as the avoidance of novel colouration, neither learned nor innate, confirming earlier results with experienced blue jays. However, this was not a proof of the absence of unlearned avoidance of the black and red pattern. To investigate differences between the novelty and the innate avoidance, Schuler and Hesse (1985) offered naïve domestic chicks *Gallus gallus domesticus* mealworms painted either with black and yellow warningly coloured stripes or with a non-warningly coloured uniform olive green (a mix of the black and yellow paints). Chicks pecked at both prey types equally, but ate the warningly coloured ones at a much lower rate. The inhibition of attack after pecking was interpreted as resulting from the unlearned avoidance of the black and yellow colouration. To examine if the unlearned avoidance was related to particular colours and/or patterns of prey, Roper and Cook (1989) also used naïve chicks studied on their first feeding, which were offered green mealworms either painted with single colours (black, yellow or red), striped colouration (black/yellow, black/red, yellow/red) or half one colour half another (black/yellow, black/red, yellow/red). Chicks strongly avoided black prey, showed a mild aversion to black/yellow striped prey, and a mild aversion to red prey. Other colours and patterns were either neutral or preferred. It was concluded that stripes or bicolour prey were not more aversive than prey of a single colour, and that chick show specific aversions to particular colours and patterns, rather than to prey novelty or contrast. Interestingly, they showed that rearing chicks in black and yellow cages reduced or reversed their avoidance of black/yellow striped and black prey, and increased their preference for yellow and bicolour prey. Similarly, Roper (1990) showed that rearing chicks in red cages induced a preference for red prey over the usually preferred brown prey. This demonstrates that even if avoidance of particular colours and patterns are unlearned, they can be modified by experience (Mostler, 1935).

5.2 AVOIDED COLOURS

We have seen earlier that red and black-and-yellow stripes are most often colours avoided by predators (Table 3; Coppinger, 1970; Schuler and Hesse, 1985; Roper and Cook, 1989). Several other studies have confirmed these aversions, and extended our knowledge of chromatic and achromatic characteristics of warning colouration. Veselý et al. (2006) studied the aposematic colouration of red-black shieldbugs *Graphosoma lineatum* preyed upon by blue and great tits. They presented wild-coloured and non-aposematic brown-painted shieldbugs to birds, and found blue tits avoided both forms, whereas
great tits attacked both, but the brown ones more frequently. Schlee (1986) also confirmed the anti-predatory function of the red-black shieldbug colouration with European blackbirds *T. merula*. Exnerová *et al.* (2003, 2008) confirmed that different bird species react differently to aposematic and non-aposematic prey. Overall, small insectivorous birds avoid warningly coloured prey, whereas large insectivorous birds as well as granivorous birds often attack them. Exnerová *et al.* (2006) studied predation of the chromatically polymorphic firebug *Pyrrhocoris apterus* (red in its wild form, with white, yellow and orange mutants) by great tits, robins *Erithacus rubecula* and blackcaps *Sylvia atricapilla*. They found that red and orange colouration, and not the black melanin pattern, is essential to provide protection from avian predators. White mutants were not better protected than the non-aposematic brown-painted wild form, and the reaction of birds to the yellow form was species specific. This is consistent with the study of Lyytinen *et al.* (1999) who showed that the white colouration of pierid butterflies does not have a warning function. By manipulating the colouration of common glow-worm larvae *Lampyris noctiluca*, De Cock and Matthysen (2001) showed that the colour pattern consisting of yellow-pinkish lateral spots on the jet-black background was used to learn avoiding this distasteful prey by starlings. Kauppinen and Mappes (2003) have investigated the features that intimidate dragonflies *Aeshna grandis* to attack wasps *Vespula norwegica*. In a first experiment, they painted flies either black or with yellow and black stripes, and did the same for wasps. The dragonflies showed greater aversion to wasps than to flies. Yellow-and-black striped flies were more frequently avoided than black flies, revealing the selective advantage of yellow stripes. However, yellow-and-black wasps were not more avoided than black ones, showing that some other feature(s) should make wasps intimidating to predators. In further experiments, dragonflies were offered artificial prey that were painted with either yellow-and-black stripes, solid black or solid yellow. Again, dragonflies avoided more often striped prey. This study indicates that black-and-yellow stripes alone are effective in protecting prey, even palatable ones. Using a similar approach on the field, Rashed *et al.* (2005) extended the study of Kauppinen and Mappes (2003), notably by scoring responses of several species of dragonflies, and found that these predators were not avoiding the yellow-and-black patterns present in both aposematic and mimetic prey.

By manipulating the UV reflection of artificial prey offered to great tits, Lyytinen *et al.* (2001) examined whether UV cues might function as warning signals. They found no avoidance of UV-reflecting prey and no evidence that UV cues alone can work effectively as aposematic signals. However, it should be noted that most studies of warning colours do not take into account predator visual sensitivities or control for differences in brightness or colour contrast, as it has often been the case in the more recent studies of crypsis.

Few studies have also demonstrated that non-avian predators have the ability to learn the adaptive value of firefly larvae bioluminescence. De Cock and
Matthysen (1999) presented glowing and non-glowing prey dummies to toads *Bufo bufo* captured in areas where larvae of the common glow-worm were also observed. Toads showed lower frequency of attack and longer latency to attack glowing than non-glowing prey. Toads also found glow-worm larvae distasteful; after being exposed to these larvae, they increased their attack latency to luminescent prey, but not to non-glowing prey (De Cock and Matthysen, 2003). These studies confirm the aposematic function of glow-worm larva colouration, later used by adults as a sexual signal (Lewis and Cratsley, 2008).

5.3 THE IMPORTANCE OF CONTRAST WITH THE BACKGROUND

Contrast of warning colouration with the visual background has been studied in some detail. Results are ambiguous, a number of studies finding greater effectiveness of warning colouration on a contrasting background, others not. Sillén-Tullberg (1985b) investigated the survival of wild-type red aposematic individuals and grey mutant cryptic mutants of the harlequin seed bug *Lygaeus equestris* attacked by naïve zebra finches *Taeniopygia guttata*, and showed that although the survival of the aposematic larvae was higher than that of cryptic ones, the warning signal of the red form was not decreased on the matching background. Roper and Cook (1989) and Roper (1990) also found evidence that prey colours, rather than the degree of contrast against the visual background, defines unlearned feeding preferences in chicks. Similar results were found by Lindström et al. (1999) with hand-reared and wild-caught great tits predating mealworms.

In contrast with the study of Sillén-Tullberg (1985a), Veselý et al. (2006) showed that wild-coloured shieldbugs presented on matching backgrounds were attacked less frequently than those which were presented on a white background. Similarly, Gamberale-Stille (2001) demonstrated that aposematic milkweed bug *Tropidothorax leucopterus* larvae were attacked faster by domestic chicks on contrasting than on non-contrasting background, whereas there was no significant difference on attack latency on the palatable cotton stainer *Graptostethus servus* larvae. However, one may wonder if the domestic chick is really an ideal model predator.

To our knowledge, only one study considered the importance of brightness contrast on prey detection. It was conducted by Prudic et al. (2007) with milkweed bugs *Oncopeltus fasciatus* preyed upon by Chinese praying mantids *T. aridifolia sinensis*. Praying mantids were used because they are thought to have very limited or no colour vision. Therefore, it allowed investigating if brightness contrast (but not colour contrast) could function as a warning signal to a colour-blind predator. The palatability of milkweed bugs was manipulated by feeding them for two generations either on a diet of sunflower seeds (*Helianthus annuus*, palatable) or milkweed seeds (*Asclepias curassavica*, unpalatable). Prey were painted in either of two shades of grey and presented on a grey background. Increased brightness contrast facilitated detection of prey, predator aversion learning of unpalatable prey, and memory retention of the aversive response.
Tullberg et al. (2005) used human ‘predators’ searching on a touch screen for larva of the swallowtail *Papilio machaon* to investigate if colouration may constitute a combination between warning colouration at short distance and crypsis at longer range. Pictures of larvae were taken at different distances on shore and fen habitats, and images were manipulated to increase or reduce the warning colouration. Logically, detection times increased with distance for all colours and backgrounds. More interestingly, it was found that natural colouration is neither maximally cryptic at short range, nor maximally conspicuous at long range. Overall, the results constitute the first empirical support for the hypothesis that a colour pattern can combine warning colouration at short range with crypsis at long distance. However, human observers might not be considered as appropriate to assess camouflage or conspicuousness of prey when the natural receiver is likely different. In addition, necessary calibrations of the images or computer screens were not undertaken.

5.4 WING SPOTS AS ANTI-PREDATOR DEVICES

Wing spots, most often called eyespots, have been studied since the nineteenth century for their anti-predator function. Three principal hypotheses have been evoked to explain this function (Table 4). (1) The ‘intimidation hypothesis’ which considers that large circular spots located centrally on the wings mimic the eyes of the predators’ own enemies, intimidating predators and allowing the prey to escape. (2) An alternative version of the intimidation hypothesis is that wing spots intimidate predators because they are highly conspicuous and contrasting with the surrounding body region, and may be avoided as novel and rare features (the ‘conspicuous signal hypothesis’, Stevens, 2005). (3) The ‘deflection hypothesis’ which states that small spots at the periphery of the wings can deflect the attack of predators to non-vital regions of the body (review by Stevens, 2005). These hypotheses have been mostly tested with birds as predators, and received mixed support (Table 4).

5.4.1 Investigations of the intimidation hypothesis

Apart from highly qualitative experiments, this hypothesis had not been explicitly tested before Blest (1957). In this early study, European peacock butterflies *Inachis io* (Fig. 3) were presented to yellow buntings *Emberiza citrinella*. The butterfly has one pair of large spots on each wing; usually concealed, those are exposed when the butterfly is threatened and the movement is accompanied by a hissing noise. Living butterflies were used, either with wing spots or with eye spots removed by rubbing the forewings. It was found that butterflies with eyespots were given approximately four times as many overt escape responses from avian predators as those from which the eyespots had been removed. Blest (1957) also conducted eight other experiments presenting different spots of varied shapes and complexity to chaffinches, yellow buntings and great tits.
<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Prey</th>
<th>Predator</th>
<th>Support</th>
<th>References</th>
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<td></td>
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<td>Wiklund (2005)</td>
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<tr>
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<td>Yes</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>Birds</td>
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<td>Birds</td>
<td>Yes</td>
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? Denotes studies which conclusions have been severely criticized.
Overall, it was found that circular shapes were more effective in releasing escape response than bars or crosses, and that a model resembling an eye with a pupil was more effective than a single circle. Blest (1957) found similar effectiveness of circular eye-looking shapes by using an apparatus in which a dead mealworm placed in the middle of an image with symmetrical patterns was presented to avian predators. Despite their interest, Blest’s (1957) experiments raised a number of criticisms. First, as noted by Curio (1993, cited by Stevens, 2005) the own eyes of the human experimenter could have biased responses of birds to butterfly eyespots. Second, manipulation of the wings to remove eyespots could have altered the normal display behaviour of butterflies (Stevens, 2005). Third, Blest (1957) did not control for factors such as stimulus area, perimeter, width, the number of spot rings (Stevens et al., 2008b) or capture and handling processes (Ruxton et al., 2004). Finally, as pointed out by Coppinger (1969, 1970), birds may simply have avoided highly contrasting novel stimuli.

Although their sample was too small for statistical testing, further support of Blest’s conclusions was obtained by Cundy and Allen (1988), who used a mechanical butterfly often eliciting flight response of birds when displaying eyespots but rarely without eyespots. As Blest, Vallin et al. (2005) studied the anti-predation behaviour of peacock butterflies, painting over wing spots with a marker pen and/or removing the sound-producing parts of the forewings. Confirming the anti-predator function of wing spots, they found that only 1 out of 34 butterflies with eyespots was killed by blue tits, whereas 13 out of 20 butterflies without eyespots were attacked. The hissing sound did not provide increased protection from bird predation, although it clearly has a protective effect with respect to bat predation (Mohl and Miller, 1976, cited by Vallin et al., 2005).

FIG. 3 The European peacock butterfly Inachis io often used to study the hypothesis of intimidating eyespots. Joanne T. Kell ©.
In this study, the sound associated with the wing movement had no clear advantage for butterflies attacked by passerine birds. This was confirmed by Kodandaramaiah et al. (2009) who showed that motionless peacock pansy butterflies *Junonia almana* with intact wing spots have higher survival than motionless butterflies with paint-covered wing spots. Displaying the wing spots is known to be advantageous regarding bird predation, but is clearly detrimental regarding predation by European hornets *Vespa crabro* (Wiklund, 2005). By studying the differential survival of a cryptic butterfly (the comma *Polygonia c-album*), of the peacock butterfly, and of an intermediately cryptic species (the small tortoiseshell *Aglais urticae*), preyed upon by blue tits, Vallin et al. (2006) again confirmed the anti-predation function of wing spots. Experimenting butterflies and passerine birds of different body sizes, namely small peacocks and larger eyed hawkmoths *Smerinthus ocellatus* which have wing spots of similar sizes, preyed upon by both blue tits and great tits, Vallin et al. (2007) showed that wing spots of the same size do not provide the same protection from predators: the smaller peacock prey showed higher survival than the larger hawkmoth. Also, the larger bird species was less intimidated than the smallest one. Although Vallin et al. (2005, 2006, 2007) and Kodandaramaiah et al. (2009) clearly demonstrated the protective advantage of wing spots, they could not support the intimidation hypothesis through recognition of predators’ eyes per se. The conclusion of Stevens (2005), that ‘few, if any, studies have provided firm evidence that predators perceive eyespots as eyes, rather than just conspicuous or novel features’, is still valid.

### 5.4.2 Investigations of the conspicuous signal hypothesis

Stevens et al. (2007a) explicitly tested both the ‘intimidating’ and the ‘conspicuous signal’ hypotheses. As for the study of crypsis, artificial moth-like stimuli with a dead mealworm to attract bird predators were pinned to trees and their ‘survival’ was monitored in the field. This time, models differing by the shape and visual contrast of wing spots were used, and their design was calibrated using spectrometry and the vision model of an insectivorous passerine. The stimuli were printed on a grey scale because of the factorial increase in possible pattern complexity of coloured eyespots. A consistent result obtained across five experiments is that significantly higher survival was obtained for models displaying high internal contrast and high contrast with the target background, irrespective of the pattern arrangement. Interestingly, circular eyespots provided models with a higher survival than less eye-like shaped ones. However, this is interpreted more as a bias originating from the visual system of avian predators, which have circular receptive fields in their retina, than to the intimidating effect of predator eyes recognized by the butterfly predator. This contrasts with the results of Blest (1957) who showed that birds were more intimidated by circular models than by bars and crosses. However, Stevens et al. (2007a) used achromatic circles and diamonds, which would all appear circular from the initial viewing distance in
their field study, whereas bars and crosses viewed at short distance in the study of Blest (1957) and triangles used in the study of Stevens et al. (2007a) can clearly be separated from circles, even from a distance. This innovative study strongly supported the conspicuous signal hypothesis.

Stevens et al. (2008b) further tested the intimidating and conspicuous signal hypotheses by using achromatic artificial moth models with different numbers, sizes and shapes of the spots (Fig. 4A). The spots also varied by the displacement of their components toward or away from the target midline to investigate if it creates the appearance of a predator staring at its prey. Models were calibrated by spectrometry and through photon catches of the blue tit. Across three experiments, better survival was for models of large size and higher number of spots. Models with circular spots did not survive better than models with other conspicuous shapes such as bars. Models mimicking eyes staring at predators did not survive better. The same approach was used by Stevens et al. (2009a) who used different marking shapes (bar or circle), arrangements (eye-like and non-eye-like positions) or colours (red, yellow or blue ‘iris’, Fig. 4B). They found no effect of shape, arrangement, or colour on birds’ aversive responses. These results unambiguously support the conspicuous signal hypothesis and show that wing spots do not necessarily mimic eyes of other animals.

When testing the conspicuous signal hypothesis, it is important to determine if conspicuous wing spots are effective if they are present on prey which is either camouflaged or conspicuous against their visual background. This question has been investigated by Stevens et al. (2008c) with artificial moth-like prey calibrated using spectrometry and the blue tit vision model. As in the studies of Stevens et al. (2007a, 2008b), wing spots were effective in decreasing predation when they were placed on conspicuous prey. In contrast, results showed that spots increased predation risk of otherwise camouflaged targets.

Although rather simplified compared to natural wing spots, the models used in the ingenious experiments conducted by Stevens and colleagues clearly improved our knowledge on the features of insect warning signals. In the future,
experiments could be refined by using more complex models on different visual backgrounds, and include the use of different vivid colourations found in nature.

5.4.3 Investigations of the deflection hypothesis

In an early experiment, Swynnerton (1926) marked African butterflies of the genus Charaxes with artificial eyes, bars, etc., on the wing margins and released them on the field. When recapturing them at intervals, he found that marked butterflies survived longer and that those showing signs of having been attacked by birds bore beak marks and wing damage near the markings, confirming the deflection hypothesis. Blest (1957) tested this hypothesis by presenting yellow buntings with dead mealworms of three different kinds: either normal, painted with a white spot bearing a black pupil, or painted with a mealworm-coloured spot. Birds pecked more often prey that displayed an eyespot than control mealworms with a mealworm-coloured spot, therefore supporting the deflection hypothesis.

Lyytinen et al. (2003) used three forms of the squinting bush brown butterfly Bicyclus anynana (the spotless dry season form, the spotted wet season form and a double mutant line showing larger spots than the wet season form) which were presented to green anoles Anolis carolinensis and to pied flycatchers Ficedula hypoleuca (Fig. 5). The presence of marginal wing spots did not increase the survival probability, nor did it influence the location of strikes on the body or wings of butterflies. Results were similar for both birds and lizards, and do not support the deflection hypothesis. Lyytinen et al. (2004) found weak support for the deflection hypothesis, but only when spotted and spotless squinting bush brown butterflies were presented to naïve pied flycatchers. Again using squinting bush brown butterflies and Anolis lizards, but in a more standardized experimental design, Vlieger and Brakefield (2007) also found no support for the deflection hypothesis.

FIG. 5 The squinting bush brown butterfly Bicyclus anynana often used to test the hypothesis of wing spots deflection. William Piel and Antónia Monteiro ©.
hypothesis. As pointed out by Stevens (2005) differences in the support of this hypothesis obtained by Swynnerton and researchers using squinting bush brown butterflies is that prey had more opportunities to escape on the field than in laboratory experiments. In addition, squinting bush brown butterflies have several spots on the wings, which may direct predator attacks to different locations, reducing the opportunity to detect a positive effect. Furthermore, wing spots are small and not concealed in *B. anynana*, which may suggest that they are not used to deflect predator attacks, but may have another function. This latter explanation is supported by the fact that wing spots of *B. anynana* could be involved in female mate choice (Monteiro et al., 1997; Breuker and Brakefield, 2002; Robertson and Monteiro, 2005). Nevertheless, mate attraction and predator deception may not be totally conflicting. Using phylogenetic reconstructions of wing spot evolution and comparisons of evolutionary rates, Oliver et al. (2009) found that dorsal characters evolved at higher rates and more often displayed sex-based differences than ventral characters, supporting the prediction that dorsal characters may be used for mate signalling and ventral characters for predator avoidance.

One variation of the deflection hypothesis is related to the fact that some butterflies display wing spots and appendages resembling antennae or legs on the ventral part of their hindwings, which are interpreted as diverting the predator attack to the less vulnerable insect end (the ‘false head’ hypothesis, review by Stevens, 2005). Van Someren (1922) reported that lizards preferentially attack the ‘false head’ of lycaenid butterflies, allowing them to escape. Robbins (1981) tested this hypothesis on about 200 lycaenid butterflies. He measured their ‘predicted deceptiveness’ on the basis of the number of false-head wing patterns observed, and found that species with more false-head components had more frequent wing damage than other species. This was interpreted as reflecting the higher frequency of false-head patterns to deflect predators’ attacks. Wourms and Wasserman (1985) conducted two experiments in which they offered blue jays dead or live cabbage white butterflies *Pieris rapae* which were either normal or painted with six different patterns on the wings. In experiments with dead butterflies, only prey painted with wing spots showed a deflection of bird attacks towards the hind region. In experiments with live butterflies, birds redirected their handling on the head, fatal to prey, to the hind region in butterflies painted a ‘false head’. As a result, live butterfly with false-head markings had higher probability of survival, supporting the deflection hypothesis. These two experiments have been criticized because butterflies are very different from species naturally showing false heads (Cordero, 2001), because there is no control on the appearance of the paint with respect to natural colouration, and because experimental markings could have altered prey behaviour and palatability (Ruxton et al., 2004). By measuring the distribution of wing damage in the Burmese junglequeen butterfly *Stichophthalma louisa*, Tonner et al. (1993) found that symmetrical wing damages, presumably inflicted by birds when the butterfly is at rest and its underside markings visible, were obviously concentrated on the hindwing section displaying a dark spot on
the underside, resembling a false head. Asymmetric damage, inflicted in flight when the false head is not visible by the predator, occurred outside the false head region. In contrast to hypotheses stating that the colouration of the anal angle of hindwings is a primary visual attraction to predators, or that the false head attracts attacks toward the posterior end of prey, Cordero (2001) argued that the head is in fact the less vulnerable part of the butterfly because the eyes of the butterfly, which are their main predator detection devices, are on the head. In that case, the false head would repel predators’ attacks from the vulnerable end, and redirect them toward the true head, enhancing the opportunity of predator detection.

Evidence for the deflection hypothesis with small marginal wing spots are clearly contradictory and the use of wing damage patterns as evidence of deflected attacks has been criticized (review in Ruxton et al., 2004; Stevens, 2005). However, the false-head hypothesis is rather well supported by both field and laboratory experiments.

5.5 MOTION INFORMS ABOUT PALATABILITY

Motion is another visual feature used by predator to detect prey. Although it has long been recognized that conspicuous unpalatable species tend to have slower and more predictable movements than palatable species (references in Sherratt et al., 2004), different theories have been raised to explain this behaviour. Chai and Srygley (Chai and Srygley, 1990; Srygley and Chai, 1990a,b) considered that unprofitable prey should not evolve rapid movement since they have no need to escape from predators, and particularly if rapid movements are energetically costly. Slow movement may also be selected to reduce recognition errors in experienced predators (Guilford, 1986; Srygley and Chai, 1990b). Hatle and Faragher (1998) studied survivorship of the highly conspicuous chemically defended Eastern lubber grasshopper Romalea guttata preyed upon by northern leopard frog Rana pipiens. They found that lubbers moved much more slowly than undefended crickets both in the presence of a plastic or a living frog, and that slow-moving lubbers benefited of higher survivorship than fast-moving ones. Because movement triggers frog attacks, the slow movement of prey appears as an effective strategy to avoid attack by motion-oriented predators (see also Hatle et al., 2002). However, as pointed out by Sherratt et al. (2004), the motion orientation of predators could have evolved as a secondary consequence of the fact that unprofitable prey species tend to be slow. In addition, it is difficult to understand that if slow movements can deter an attack, why profitable prey would not use such behaviour? The above theories have been tested by Sherratt et al. (2004) using a computer program to simulate the evolution of locomotory traits seen by human ‘predators’. It was shown that unprofitable prey indeed evolve significantly slower movement than profitable prey, particularly when they are not more selected to avoid predation than profitable prey, or when it is advantageous for unprofitable prey to avoid being mistaken for
profitable prey. In that sense, they confirmed the hypotheses of Guilford (1986), Chai and Srygley (1990) and Srygley and Chai (1990a,b).

Another interesting set of studies concerns the relationships between motion cues and escape tactics in butterflies. Srygley (1994), studying morphological parameters related to flight in 18 butterfly species in the tribe Heliconiini and 10 of their non-heliconiine comimics, found that particular suites of the position of centre of body mass and of wing shape were associated with evasive flight, distastefulness and mimicry. The morphology of palatable species increases flight speed and maneuverability, whereas that of unpalatable species compromise flight performance. Although unpalatable species are less maneuverable, their more regular flight pattern allows considerable energy savings (see also Srygley, 2004). Most importantly, the morphology required for evasive flight in palatable species is different from the morphology of distasteful ones, making a ‘good’ Batesian mimic with the morphology and flight pattern of unpalatable butterflies unlikely to evolve. Therefore, by simply observing butterfly flight patterns (Srygley, 1994) and wing motion (Srygley, 2007), predators might guess if they target a palatable or an unpalatable prey. However, it remains to be determined if birds indeed react to tiny differences in butterfly wing motion and flight pattern. The fact that the butterfly flight pattern is the first stimulus seen by birds, not its colour pattern, has even led Kassarov (2003) to suggest that birds may not constitute the principal selective constraint leading to the evolution of mimicry and aposematism in butterflies.

5.6 WARNING-PATTERN SIZE AND SYMMETRY

The first experimental investigation of the effect of warning signal size and symmetry was conducted by Forsman and Merilaita (1999) who presented domestic chicks with artificial (black paper) butterflies either non-aposematic and palatable (associated with a chick-starter crumb) or aposematic and unpalatable (with a chick-starter crumb impregnated with quinine hydrochloride). Aposematic ‘prey’ had either symmetric small, symmetric large or asymmetric white circles on their wings. It was found that chicks avoid the larger warning signals, particularly if the aposematic pattern is symmetric. Although the level of asymmetry used is this study seems high (33% of the wing spot diameter) this result clearly shows the importance of size and symmetry in warning colouration patterns. Forsman and Herrström (2004) refined the study of Forsman and Merilaita (1999) by using different shapes, colours and levels of asymmetry in artificial butterflies presented to naïve chicks. They confirmed the detrimental effect of size asymmetry when asymmetry in size (spot diameter) was 7.5% or higher. They also showed that warning signals with symmetric colour pattern elements were better protected than asymmetric signals with pattern elements of different colour or shape. Therefore, there is strong evidence of the protective role of conspicuous colour patterns which are symmetric in colour, shape and size. Stevens et al. (2009b) conducted a field study of predation of artificial butterflies with two experiments: one testing the effect
of size asymmetry, between 5% and 50% (this time measured as spot area, not diameter), and the other the effect of shape asymmetry and asymmetry in position from the body midline. Results strongly differed from those obtained in laboratory experiments with chicks. Both experiments showed no survival advantage for symmetric size, position or shape. The discrepancy between these studies may be due to the fact that one study was conducted in the field, the others in captivity, to the use of wild or domestic species, or to the fact that asymmetry may be less important than other features of warning signals, like colour or size. In addition, in the field, prey items are usually encountered in a sequential manner, whereas in the lab experiments prey were presented in pairs, giving predators a choice between the symmetrical and the asymmetrical prey.

5.7 OTHER FEATURES OF APOSEMATIC COLOURATION AND MIMICRY

The question of learned, innate, or unlearned avoidance of warning colouration by predators is largely influenced by predator psychology and experience (e.g. Chittka and Osorio, 2007; Ihalainen et al., 2007, 2008), which goes far beyond our initial focus on predator vision of prey colouration. In addition, visual aspects of insect aposematism are generally combined with other signal modalities (olfactory, gustatory, auditory and/or behavioural) which often enhance unlearned biases and wariness (e.g. Skelhorn and Rowe, 2005; Hauglund et al., 2006; Lindström et al., 2006; Skelhorn and Rowe, 2006a,b; Lindstedt et al., 2008; Siddall and Marples, 2008; Skelhorn et al., 2008), but fall out of the scope of our review. Furthermore, the evolution of aposematic colouration has often been related to the degree of aggregation and to body size (e.g. Hatle and Salazar, 2001; Reader and Hochuli, 2003; Beatty et al., 2005; Despland and Simpson, 2005; Skelhorn and Ruxton, 2006). For a more general overview of processes involved in insect aposematism and mimicry, we also recommend the book of Ruxton et al. (2004).

6 Predator visual mimicry

In the preceding section, we have seen that butterfly eyespots have long been thought to mimic large predators’ eyes to deter predators from attacking prey. However, in that case, it was the predator’s predator that was supposed to be mimicked. Another rarely reported case is that of predator mimicry by insect prey. Both colouration and movement are important components to mimic a predator and effectively decrease predation risk. To our knowledge, the first experimental demonstration of predator mimicry is that of the snowberry fly Rhagoletis zephyria and the common zebra spider Salticus scenicus, its model and predator (Mather and Roitberg, 1987). The study compared responses of spiders to conspecifics, to house flies Musca domestica, to snowberry flies and to snowberry flies which wing stripes had been obliterated. The results showed that spiders treated snowberry flies as conspecifics, but that effect was not maintained in flies which had their wing stripes blackened. Most house flies were attacked, whereas few conspecifics
and intact snowberry flies were. It was not likely that the higher capture rate of flies with obliterated wing stripes was due to the obliteration process. Both the wings markings and the way they were displayed to predators seemed important components of the visual mimicry effect. A comparable case of predator mimicry was demonstrated by Greene et al. (1987) between the tephritid fly Zonosemata vittigera and the 11 species of jumping spiders. To investigate if the effect of the fly wing pattern and wing-waving display was involved in the mimicry of territorial displays of spiders, five prey types were presented: normal Zonosemata, Zonosemata with Zonosemata wings glued on (control), Zonosemata with house fly wings, house flies with Zonosemata wings and normal house flies. The wing pattern had a strong effect on predator retreat: normal Zonosemata and sham-operated control flies were attacked less frequently than the three other types. Indeed these flies vigorously waved their wings at the spider approach, and spiders reacted as when they observe the territorial display of a conspecific. Interestingly, Zonosemata with house fly wings displayed like normal Zonosemata, but were always attacked. House flies with Zonosemata wings never showed the wing-waving display and were always attacked and killed. Therefore, the wing stripes display of Zonosemata appeared to mimic territorial displays of salticid spiders and protect tephritid flies. Similar experiments were conducted with other predators: nonsalticid spiders Oxyopes salticus, mantids M. religiosa, assassin bugs Pselliopus zebra and whiptail lizards Cnemidophorus uniparens. The Zonosemata display was ineffective against these four types of predators, showing that Zonosemata is a specialized mimic of salticid spiders. Because many flies have leg-like wing patterns, jumping spider mimicry may be a widespread phenomenon. Very similar effects of wing flicking, combined with a jerky motion and sudden short flights, have been described in the fruit fly Z. vittigera and also provide protection from sympatric jumping spiders (Whitman et al., 1988). More recently, Rota and Wagner (2006) demonstrated that Brenthia moths mimic jumping spiders of similar size with wing markings, wing positioning, posture and movement. These moths elicit territorial display from spiders, which provides much higher rates of survival than other species which does not exhibit wing patterns and movements typical of Brenthia moths. A few other authors have suggested, but not demonstrated, that insects may mimic spiders (O’Brien, 1967; Santiago-Blay and Maldonado-Capriles, 1988; Zolnerowich, 1992; Floren and Otto, 2001). One case of visual mimicry has even been hypothesized between planthoppers and spiders from the early Jurassic (Shcherbakov, 2007).

7 Colour polymorphism

7.1 THE REPRESENTATIVE CASE OF THE PEPPERED MOTH

Colour polymorphism is commonly encountered in camouflaged insect species. Particularly, widespread in nocturnal moths (Kettlewell, 1973; Majerus, 1998), it is also common in other groups like grasshoppers (Dearn, 1990), walking
sticks (Sandoval, 1994), water boatmen (Popham, 1941), homoptera or mantids (Evans and Schmidt, 1990). How can polymorphism be maintained through evolutionary time despite the erosive actions of natural selection or genetic drift on genetic variation? Several different mechanisms have been identified to maintain high levels of polymorphism (references in Punzalan et al., 2005). What is the contribution of visual predation in this evolutionary process? Identifying the factors explaining the relative survival values of different colour morphs and assessing the exact influence of visual selective predation has been largely documented in insect species (e.g. Kettlewell, 1955b; Sandoval, 1994; Nosil, 2004). One of the most largely investigated issues is that of the melanic polymorphism, commonly found in Lepidoptera and Coleoptera (Kettlewell, 1973; Lees et al., 1973; Majerus, 1998). We will detail here the case of the peppered moth (B. betularia), one of the most widely quoted examples of evolution in action (Fig. 6).

The melanic polymorphism of this species, as in most other species (Lees et al., 1973; Brakefield, 1987), is controlled by a single gene locus with melanic allele dominant to the non-melanic ‘typica’ allele (Clarke and Sheppard, 1964; Lees, 1968). First recorded ca. 1848, the black form rapidly spread through industrialized northern England in half a century. It then remained for 70–80 years (or generations in this 1-year generation species) at high frequencies (above 90% and below 100%) in urban areas and low frequencies in rural areas. Coincident with the development of coal-based industrialization, similar rise of melanics was observed in several species (e.g. two spot ladybird Adalia punctata; Bishop et al., 1978) and synchronously in Britain, Europe and North

**FIG. 6** *Typica* and *carbonaria* morphs of the peppered moth *Biston betularia* on the same tree. This species has often been used to study colour polymorphism. Marteen Sanne ©.
Differential predation on different morphs appears the principal cause of the rapid evolution of colour polymorphism in the peppered moth. Active at night, moths rest on trees during the day, where they are preyed upon by birds. The ease at which the different morphs are found by the birds depends on how well they are camouflaged. Tutt (1896) was the first to propose that typical peppered moths were better camouflaged and hidden from avian predators on lichen-covered trees in unpolluted regions while melanics were better camouflaged than typical in areas where trees have been denuded of lichens and blackened by soot. This hypothesis of differential predation by birds was later tested experimentally by Kettlewell (1955b, 1956). Kettlewell’s experiments consisted in (1) quantitative rankings of camouflage effectiveness for human vision of pale and black moths placed on different backgrounds, (2) direct observations of predation by birds on moths placed on tree trunks, and (3) recapture rates of marked moths released onto trees in polluted and unpolluted woodlands. He convincingly demonstrated that the individuals most conspicuous for humans were the first to be eaten by birds and had lower recapture rates, providing strong qualitative support for the central action of differential visual predation. However, the estimates of morphs’ fitness values were less reliable and strongly criticized. Predation experiments involved the release of non-living prey items in abnormally high density, in non-natural over-exposed resting sites (Bishop, 1972) and a conspicuousness ranking not based on avian vision (Majerus, 1998). All these factors may have influenced birds’ hunting behaviour and relative predation rate on the different morphs. For instance, these predation experiments predated the demonstration that birds were sensitive to UV (Chen et al., 1984). Lichen species similar in appearance to human eye differ in their UV reflectance; non-melanic peppered moths at rest on lichens may be more cryptic to humans than to birds (Majerus et al., 2000). Again, this recent finding calls attention to the need to analyze insect colours from the predator’s point of view. Yet, Kettlewell noticed that the moths ranked as most conspicuous to humans were the moths first eaten by birds, confirming a roughly congruent ranking between humans and birds (Kettlewell, 1955b, 1956). At that level, the influence of lichens on moth crypsis had likely little importance. Despite methodological limitations (one can always find limitations or flaws in classic studies), the central role of differential visual predation in driving the evolution of polymorphism in the peppered moth remains undisputable (Brakefield, 1987; Majerus, 1998) and that is what should be retained from these studies.

Although heavily criticized, Kettlewell’s experiments were not renewed nor improved, underlining the difficulty for quantifying the selection exerted by visual predators on different morphs in realistic conditions. After Kettlewell’s qualitative evidence for visual predation, research effort orientated towards identifying the factors accounting for the dynamics and integrating them in different models (Mani, 1990). Conversely, little research effort aimed to acquire basic knowledge on prey and predator behaviour, on the mechanisms of prey
detection and on selection quantification, many issues that would bring valuable contributions to the understanding of the mechanisms of polymorphism evolution (Brakefield, 1987). Few studies have focused on morphs’ general behaviour and preferences in terms of resting sites, microhabitat or pairing. For instance, Kettlewell (1955a) showed that morphs of *B. betularia* settle on backgrounds they most resembled. A similar preference was later shown in the Scalloped Hazel moth *Gonodontis bidentata* (Kettlewell and Conn, 1977). Such morph-specific background preferences were also found by Grant and Howlett (1988). An active avoidance of non-matching backgrounds has been shown in several insect species (e.g. Edmunds, 1976; Owen, 1980; Sargent, 1981). The theory of multiple niche polymorphism posits that different genotypes should evolve preferences for the microenvironment in which they enjoy the highest fitness (Levene, 1953). Liebert and Brakefield (1987) studied the survival values of female peppered moths alone and in copula. They suggested that survival depended not only on the morph of the female alone but also on the morph of the male to which they were paired, since pairing implied in this species a relatively long physical association with potential vulnerability to predation.

### 7.2 Predator Perceptual Processes and Their Impact on Evolution Morph Frequency

If selective predation by visual predators were the only influence on colour morph frequency, it would lead to monomorphic populations (allele fixation) the appearance of which would depend upon which phenotype is most cryptic in the local population (Creed *et al.*, 1980). Several factors have been suggested to contribute to the generation and maintain of the geographical variation of melanics (review in Brakefield, 1987). Heterozygote advantage, migration or frequency-dependent selection is needed to maintain polymorphism (Creed *et al.*, 1980).

Negative frequency-dependent selection, where the relative fitness of a genotype decreases with its increasing frequency in a population, appears particularly interesting in the case of visual predation. In this context, visual predators consume different colour morphs not in direct proportion to their numbers but disproportionally more of the common ones and less of the rare ones. In other words, they switch away from once common prey when they become rare in a sigmoid functional response (Holling, 1965). With this behaviour, they can prevent rare prey types from being eliminated and constitute a powerful force able to maintain prey colour polymorphism (Punzalan *et al.*, 2005). Poulton (1884) was probably the first to recognize the importance of frequency-dependent predation and proposed it could actively maintain colour polymorphism in the geometrid moth larvae (*Cyclophora* spp.). The first experimental demonstration of this mechanism, also called apostatic selection (Clarke, 1962), was performed by Popham (1941) who found that the most abundant morphs of an aquatic insect, the water boatman (*Arctocorisa distincta*), were preyed upon faster than the others and not in direct proportion to their numbers.
Despite a high number of studies presenting evidence of frequency-dependent predation (review in Punzalan et al., 2005), evidence for the cognitive proximate mechanisms of such predation patterns remain scarce. Detecting camouflaged prey is a highly demanding visual task which mobilizes a large bandwidth in a visual system constrained by a limited visual information processing. Tinbergen (1960) proposed that predators selectively focus their attention on recently and commonly encountered prey types while ignoring the alternatives. Prior experience with a certain prey-type facilitates the detection of the same prey type in subsequent encounters. Guilford and Dawkins (1987) proposed the ‘search-rate’ hypothesis, whereby the detection of cryptic prey is not improved by the formation of search images, but only by a lower rate of visual search for more cryptic prey. By scanning a potential patch for a longer time, predators increase their probability of detecting cryptic prey.

These hypotheses are difficult to disentangle (Guilford and Dawkins, 1987) since they both posit that detection facilitation relates to immediate past experience with a short-time memory decay, and is more important for cryptic than conspicuous prey. These hypotheses differ on one important point: the search image hypothesis supposes that the construction of the search image provokes a reduced ability of detecting any other prey type, conspicuous or other equally cryptic prey types. Such an interference is not assumed by the search-rate hypothesis (Guilford and Dawkins, 1987; Punzalan et al., 2005). Only the search image process can produce frequency-dependent selection, which does not mean it actually does. The existence of colour polymorphism is by no means a proof that search image processes are operating. Other mechanisms such as migration can maintain colour polymorphism. Because the efficiency of the search image process directly depends on the level of prey crypticity and rate of prey encounter, this mechanism may be of restricted relevance in many situations, for instance, in the case of multiple backgrounds offering different crypticity levels.

However, exploring the relative importance of these perceptual processes is particularly interesting since it can provide information about the allocation of cognitive resources, how predators see their prey, what visual cues can be used for prey detection and the selective pressures driving the evolution of colour patterns. Bond and Kamil (1998, 2002, 2006) built a series of elegant experiments to assess the selective effects of visual predators on prey crypticity and phenotypic variance, in which individual blue jays searched for digital moths on computer monitors. Prey brightness (the only parameter determining colouration) evolved via a genetic algorithm by which morph frequencies in the virtual population were conditioned by moth detection probability by predators and by mutation events. Using a textured background, they showed that detection accuracy decreases with increasing dissimilarity between any two successive detected prey items, particularly not for moderately cryptic prey but for highly cryptic prey (Bond and Kamil, 2002). Results showed that birds failed to detect atypical prey among highly cryptic prey, suggesting the cognitive interference postulated by the search image hypothesis. Furthermore, this interference was higher for more cryptic
prey, confirming that search image was particularly relevant in the case of highly cryptic prey. They demonstrated that frequency-dependent visual predation promotes crypticity and phenotypic variance in the prey.

7.3 ROLE OF BACKGROUND IN MORPH DETECTION

Further experiments on virtual prey explored the role of background in the visual selection operated by predators on prey brightness patterns (Fig. 7; Bond and Kamil, 2006). Background structure has two types of effects on the evolution of colour pattern in prey. First, the scale of background heterogeneity directly determines the average level of crypticity found in prey (Merilaita, 2003). Visually complex backgrounds select for less cryptic prey than do ‘simple’ backgrounds. Background heterogeneity determines the type of brightness patterns found in the prey. Backgrounds with small-scale spatial variation (patches lower than moth size, Fig. 7) induce the evolution of generalists. Such backgrounds are relatively homogeneous but visually complex, with no large patch of distinctive substrate, but enough complexity to enable a range of diverse forms to be equally difficult to detect. Such fine-grained backgrounds can be for instance temperate grasslands, exposed rocks and soil, leaf litter or beach gravel. Because many different morphs can produce the same level of resemblance to the background, it is impossible to predict the number of expected different prey patterns from the background structure. Conversely, coarse-grained backgrounds with large-scale spatial variation (patches larger than moth size, Fig. 7) induce the evolution of specialists. In such heterogeneous environments divided into large, disparate substrate patches, individuals occupy only one substrate type at a time. As a consequence, there can be a strong selection for a close association between morphs and backgrounds. For instance, the walking stick Timema cristinae (Timemidae) shows a polymorphism on colour and pattern. Striped and unstriped green morphs are closely associated with different host plant species. Experiments using lizards and birds showed that morphs were associated to the plant on which they presented a higher survival (Sandoval, 1994). Further experiments show that morphs’ survival depended on the host plant species only in the presence of predators (Nosil, 2004), suggesting that the host preference is in fact a visual background preference. Predators operate a disruptive selection by reducing the survival of morphs on their non-preferred host plant. This reduced survival of ‘migrants’ can efficiently contribute to reproductive isolation and speciation, as shown in pea aphids, leaf beetles or butterflies (references in Nosil, 2004).

Second, background complexity also exerts additional selective effects mediated by differences in how predators search for and detect prey items. A background with high spatial variation induces slow, serial search processes where selective attention plays a central role (Bond and Kamil, 2006). When the background gets separated into larger coherent patches, it becomes beneficial for predators to focus on the currently most rewarding background.
patch type and search entire patches rapidly in parallel. Background complexity
determines predator searching behaviour and consequently the selective
pressure they exert on different colour morphs.

FIG. 7 Digital moths seen on disjunct (A), mottled (B) and speckled (C) backgrounds. The scale of background spatial heterogeneity is much higher than moth size (A), similar to moth size (B) or lower than moth size (C). Here, the same four moths are represented on the three backgrounds to compare their detectability. These moths evolved on the disjunct background and are the most cryptic of the individuals in their population. While on the disjunct background, moths are harder to detect on the patch they most closely resemble but can readily be located in a superficial scan, they are far more difficult to detect on backgrounds with high levels of noise at spatial frequencies comparable to moth size. After Bond and Kamil (2006). Alan Bond ©.
We have seen that prey detectability depends on the background against which it is seen. In some cases, there can be a strong selection for a close association between background and colouration. Some variations in colour are determined by the environment while others (and in fine all the limits to the variations in colour) are genetically determined. The dependence of colouration on environmental cues allows a more efficient and closer association between morph and background. The relative importance of these two levels of variation varies between species. For instance, two ground-hopper species of the genus *Tetrix* (Tettigidae, Orthoptera) show dimorphism on colour and pattern. Contrary to pattern, colour morph frequency in nymphs responds to background colouration perceived by larvae (Hochkirch *et al.*, 2008). Many grasshopper species exhibit homochromic response to background colouration; such a phenomenon is known from burnt sites where dark individuals predominate (Rowell, 1971). The colour morph of the peppered moth larva is influenced by the background colour to which it is exposed during the previous larval instars, with an induction mediated by visual input (Noor *et al.*, 2008). Similarly, the larvae of various hawkmoth species develop different colours if reared on different trees; for these folivorous insects, the leaf reflectance and not the food itself nor the leaf texture determine the coloured developed by the larva (Grayson and Edmunds, 1989). For other species like bush crickets, the environmental cue mediating colour determination is not visual. In this species, colouration varies with the season, with green individuals in spring and brown individuals in autumn; colouration is determined by water intake, which shows a seasonal variation (Lymbery, 1992).

Selection operates not only on colouration but more generally on behavioural components linked to background exploitation. Insects are ectothermic animals for which habitat use is constrained not only by predation avoidance but also by energetic requirements. Experiments conducted on the common ground-hopper *Tetrix undulata* (Tettigidae) showed that morphs select environments that are close to their optimal body temperature, actively avoiding high and low temperatures (Ahnesjo and Forsman, 2006). Dark individuals avoid high temperatures more actively. Besides this morph-dependent habitat preference, there is also a sex-dependent habitat preference originating from different temperature requirements in males and females. Consequently, different colour morphs (and sexes) select different habitat types due to their different thermal quality, even if at local points, the substrate seems to be chosen independently of morph type.

Colouration affects vulnerability to predation, directly through visual detectability and indirectly through thermoregulation ability and behaviour. For example, pale individuals warm up more slowly, bask more frequently for shorter periods compared to dark individuals. Because body temperature also influences escape behaviour, different morphs can show different escape potential and/or
strategies. Civantos et al. (2004) investigated the indirect effects of morph colouration on predation risk by performing experiments in the pigmy grasshopper (*Tetrix subulata*). They tested the escape potential of black and grey morphs to predation by a lizard (*Psammodromus algirus*). In the shade, both morphs show low activity and poor escape potential, and are equally vulnerable to predators. In the sun, black individuals are more active and show a higher escape potential than grey individuals. This increased activity translates into an increased attack probability but, because of enhanced escape potential, not into an increased predation rate. Counter to intuition, the existence of these indirect effects of colouration—here on thermoregulation and behaviour—makes it possible that the evolution of colouration in the prey could be selected by predators which not primarily rely on visual cues but on cues influenced by prey colouration. In other words, a close association between colour morph and background can lay the ground for a non-visual selection of morph colouration by predators.

7.5 VISUAL DETERMINANTS OF MORPH SELECTIVE VALUE

In conclusion, we can see that the survival value of a particular colour morph results from a combination of many factors, presented here in a non-exhaustive list. Vulnerability to predation primarily depends on the colour pattern of the individual itself as well as the background on which it stands since they determine the level of detectability of the prey. Prey colour and pattern, background spatial heterogeneity and complexity play an important role. Relative colour preferences shown by predators determine the relative value of the different colour morphs in a population. For instance, various coccinellid species differ by their preference for specific morphs of the pea aphid (*Acyrthosiphon pisum*). *C. septempunctata* prey on the morphs that most contrast on the background whatever their colouration while a closely related species, *Harmonia axyridis*, shows a significant preference for red over green morph (Harmon et al., 1998). The relative contribution of these predators to prey population dynamics determines which morphs are more advantaged in a population. Not only detectability but also prey motion and behaviour can also profoundly influence detectability. In insects for which mating implies a long association of partners, the phenotype of the partner also influences the survival value of a focal individual. This survival cost has been suggested for example in polymorphic moths (Liebert and Brakefield, 1987) or walking sticks (Nosil, 2004). More interestingly, predation risk also depends on the frequency of the colour morph in the population, rare morphs being relatively more protected than common ones (Popham, 1941; Bond and Kamil, 1998, 2002, 2006). Protection of rare colour morphs can be even more effective if predators are conservative in their search and choice of prey. A field test involving avian predators and prey consisting in pastry items of different colours assembled in monomorphic or polymorphic populations showed that red morphs perform worse in monomorphic than in polymorphic groups. This suggested that the
initial evolution and spread of specific signals may be promoted in polymorphic
groups (Wennersten and Forsman, 2009). Finally, predation risk of a given
colour morph depends on its spatial proximity to other phenotypes, particularly
to conspicuous ones. Kettlewell (1955b) first mentioned that some of the most
cryptic peppered moths were found and eaten by birds because of their proxim-
ity to conspicuous individuals. Such a facilitation found for a polymorphic
species has been recently tested in the case of different prey species showing
different conspicuousness levels. Zhang and Richardson (2007) showed that
trouts predating on active coloured stonefly larvae showed an enhanced preda-
tion on cryptic inactive mayfly larvae when prey individuals were in close
proximity. Finally, in aposematic species, the survival value of conspicuous
morphs is expected to decrease if the proportion of informed predators
decreases in the population, if the proportion of mimetic non-toxic morphs of
different species increases.

8 Discussion

This review has concentrated on decrypting how predators see insects’ coloura-
tion and more generally insects’ visual appearance and on detailing how pre-
dators use the visual information provided by insects to detect and capture them.
Through examples taken from various predator–prey systems, we have revealed
the evolutionary interplay between insect colouration and predator behaviour.
Visual predation generates an important evolutionary pressure that can
determine the evolution of specific colour patterns and behavioural strategies
in insects (countershading, disruptive colouration, masquerade, warning
colouration strategies). Insect colouration in its turn selects for the evolution
of flexible hunting tactics in predators (versatility of predator behaviour, selec-
tive attention to prey visual features).

Insect predators are highly diverse, not only in their taxonomic position but
also in the way they see insect colours and visual appearance more generally.
These multiple views of common targets arise from differences not only in
visual sensitivity but more widely in visual information processing—neural
mechanisms of visual perception, selective attention to specific cues borne by
insects, relative importance given to vision compared to other sensory channels.
Such diversity generates both methodological and conceptual challenges that
are progressively taken up. First, from a methodological point of view, the
diversity shown by predators in their visual performance imposes the necessity
to reconstruct colours as they are likely perceived by predators. Long submitted
to a convenient but misleading anthropocentrism, the measurement and analysis
of prey colours begin to incorporate predators’ visual systems and acknowledge
their importance in determining the evolution of insect colouration and colour
patterns. Although this approach often requires numerous and tedious measure-
ments of colours based on spectrometry (Endler, 1990) or digital image analysis
(Stevens et al., 2007b), the objective quantitative estimates permitted by powerful techniques convey a far greater potential to reveal biologically relevant perceptual mechanisms and evolutionary processes than traditional colour scoring or human-based categorization. Some new research questions have developed thanks to this change of point of view and important technical improvements. One of the best examples is probably the role of visual cues in nocturnal predation, an area where research is still in its infancy, calling for urgent experimental and modelling studies to get a better understanding of the evolutionary pressures exerted by visual predators on the evolution of nocturnal insects colouration. Second, discrepancies in predators’ view of their prey can be seen of course at high taxonomic levels but more interestingly at low taxonomic levels. Substantial differences have been observed between closely related species, for instance in visual performance, colour preferences or hunting strategies. As a consequence, investigators should acquire the knowledge about predators’ behaviour for their own predator–prey system, avoiding whenever possible to take close relatives as surrogate species and to make generalization about their validity of their results. Third, predators differ in the way they perceive insect colouration. This means that the information content of colour is not universal but depends on which prey displays it and which predator views this colour or pattern. This context dependence is even reinforced by the fact that insects move in an environment showing a high temporal and spatial visual variability which maintains variability in their visual appearance to potential receivers. The non-universality of the information transmitted also arises from predators’ cognitive processes, for instance unlearned preferences and avoidance for specific colours or patterns or recent experience of association between colour and profitability.

It is interesting to view the research conducted on insect colouration from a historical perspective. Most of the hypotheses about the adaptive functions of insect colours and patterns have been formulated long ago by Poulton (1890), Thayer (1909) or Cott (1940). These authors took advantage of their large naturalist culture and experience to propose conceptual advances that have proved highly relevant further on. After 1950, research on insect colouration entered an intense ‘hypothesis testing’ phase. Although they helped to decrypt important perceptual mechanisms (e.g. differential predation in polymorphic populations, image search hypothesis), these studies suffered from technological limitations in the measurement and analysis of insect colouration (e.g. investigations of the intimidation or deflection hypothesis for eyespots). The application of powerful techniques of colour investigation (spectrometry and digital photography) gives a new life to the study of the functional roles of insect colours and patterns at the end of the twentieth century. The impressive work of Stevens and colleagues (e.g., Cuthill et al., 2005; Stevens and Cuthill, 2006; Stevens et al., 2007a, 2008b, 2009b) is a good example of that ‘Renaissance’. Studies relying on a thorough colour measurement independent of human vision and the incorporation of predator vision in colour analysis helped not only to test existing hypotheses...
but also to formulate new ones. In addition, some ingenious experimental procedures allow to progressively incorporate more realistic viewing conditions or stimuli and to simulate long-term dynamics of colour evolution, an aspect that had been hitherto impossible to tackle (e.g. computer moths with complex patterns presented on increasingly complex backgrounds in the work of Bond and Kamil, 1998, 2002, 2006). At the same time, new models are available to interpret colours from a predators’ perspective (Vorobyev and Osorio, 1998; Endler and Mielke, 2005) that offer possibilities of getting closer to more realistic viewing conditions (incorporation of visual system limits, of background complexity). We should take advantage of the recent development of all these powerful tools and methods to fill some knowledge gaps that have developed all along the history of research on insect colouration and predators’ behaviour.

The knowledge acquired so far about insect colouration as viewed by predators suffers from several defaults. These defaults define where to focus future research effort. First, the traditional human-based assessment of colouration is now often replaced by more objective measures of colouration and the consideration of predators’ visual system, light and background spectral characteristics in colour analysis. This approach is far from being generalized (Civantos et al., 2004; Hyden and Kral, 2005; Hochkirch et al., 2008; Noor et al., 2008) and more effort should be put in reconstruct colours as they are likely perceived by predators in the specific viewing conditions of the study.

Second, research has concentrated on a restricted number of taxonomic groups, both on the prey and the predator sides. The large number of studies dealing with birds preying on butterflies for camouflage, warning colouration or polymorphism masks a striking lack of knowledge for what is going on in other predator–prey systems. Birds are interesting models from several aspects but they are largely inappropriate to explore questions like nocturnal vision. Similarly, Lepidoptera are not representative of insect behaviour in general. This questions the external validity of the hypotheses tested on these systems. For example, would eyespots bear the same function in insect groups other than Lepidoptera or for predator other than birds? Future research effort should try to explore a larger array of prey and predator groups to question the universality of predators’ perceptual mechanisms or the adaptive functions of insect colouration.

Third, research has completely left aside particular signals like iridescent signals. Yet, iridescence, that is the change of colouration with the viewing angle, is abundant in insects (reviews in Ingram and Parker, 2008; Doucet and Meadows, 2009; Seago et al., 2009). Investigation of iridescent signals requires measurement tools that have been traditionally used by physics (Vukusic and Stavenga, 2009) but are rarely used by biologists, probably because of their high level of technicity. As a consequence, it is still unknown (Doucet and Meadows, 2009) whether iridescence per se could provide decrease predation risk thanks to the flexibility it creates in the apparent colouration. It may increase camouflage in a visually complex environment, contribute to startle predators by creating sudden changes in brightness or colour or increase the efficacy of
warning colouration by providing highly detectable signals. These hypotheses have not hitherto been experimentally tested (Doucet and Meadows, 2009) but should open promising lines of research.

Fourth, experimental studies have often used simplistic artificial backgrounds and targets focusing on one predator species often placed in artificial viewing conditions (e.g. Iwasaki, 1990; Poteser and Kral, 1995; Kral and Poteser, 1997; Yamawaki, 2000; Gamberale-Stille and Tullberg, 2001; Miklósi et al., 2002). Future work should try to reproduce more realistic conditions by incorporating visually more complex backgrounds and more realistic stimuli not only incorporating achromatic components (Bond and Kamil, 2002, 2006; Stevens et al., 2007a, 2008b,c) but also chromatic components (Stobbe and Schaefer, 2008; Stobbe et al., 2009).

Fifth, studies tend to overlook the natural behaviours shown by both the insects and their predators; this is particularly striking in the investigation of colour polymorphism, for which the peppered moth is representative of the lack of interest for behavioural and naturalistic aspects. Yet, a better understanding of the biology and ecology of both prey and predators would help to design protocols, to interpret the results obtained in artificial conditions and to formulate new hypotheses.

Sixth, the vast majority of studies adopt an experimental approach using a system with a unique prey and/or a unique predator. Such an approach is indispensable to gain valuable information about the relative importance of different visual cues in predator’s hunting behaviour and to unravel the mechanisms at play in detection, recognition and capture. However, the monographic aspect of these studies restricts the potential generalization of the results obtained. It is time to go towards more integrative approaches at an interspecific level. Comparative approaches are powerful to gain understanding of the adaptive functions and the evolutionary pressures (natural or sexual selection) that determine the evolution of colouration and colour patterns. By making a priori hypotheses about the possible functional roles of colouration and by comparing the predictions to the realized patterns within a phylogenetic framework, it is possible to identify the communication strategies common to different species, their relationship to species’ visual environment and to test the validity of hypotheses at a large scale. Encompassing the diversity shown at species level, such approaches have shed new light on the evolution of bird (Gomez and Théry, 2007) or mammal (Ortolani and Caro, 1996) colouration. Comparative analyses on insect colouration are nearly absent. A valuable study at large interspecific level, but unfortunately without phylogenetic control or consideration of the UV, was conducted by Williams (2007) who compared colour patterns in all bumblebee species worldwide and related them to possible functions like thermoregulation or communication. A phylogenetic control could have allowed him to reconstruct the history of different colour pattern characters, to individualize colour characters according to their evolutionary trajectory and to reveal the evolutionary pressures operating specifically on
different components of insect colouration. More interesting is the comparative study conducted by Song and Wenzel (2008) on the evolution of colour plasticity in locusts. With a full phylogenetic control, this study established that locust basic colouration and black patterns are under different evolutionary pressures. It also showed the interest of applying the comparative method not only to fixed characters but also to plastic characters that change with environmental conditions. Although comparative methods require special effort to gather information about species biology and behaviour and phylogenetic relationships, they largely repay the effort granted. Now that a large number of hypotheses have been validated for a few species, it is time to give priority to large interspecific studies over monographic approaches in order to question the universality of predation mechanisms and insect colouration strategies.

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References


Poulton, E. B. (1884). Notes upon, or suggested by, the colours, markings, and protective attitudes of certain lepidopterous larvae and pupae, and of a hymenopterous larva. *Trans. R. Entomol. Soc. Lond.* **27**, 60.


