The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera

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ABSTRACT

Eyespots are found in a variety of animals, in particular lepidopterans. The role of eyespots as antipredator mechanisms has been discussed since the 19th Century, with two main hypotheses invoked to explain their occurrence. The first is that large, centrally located eyespots intimidate predators by resembling the eyes of the predators' own enemies; the second, though not necessarily conflicting, hypothesis is that small, peripherally located eyespots function as markers to deflect the attacks of predators to non-vital regions of the body. A third possibility is also proposed; that eyespots intimidate predators merely because they are novel or rarely encountered salient features. These hypotheses are reviewed, with special reference given to avian predators, since these are likely to be the principal visually hunting predators of the lepidopterans considered. Also highlighted is the necessity to consider the potential influence of sexual selection on lepidopteran wing patterns, and the genetics and development of eyespot formation.

Key words: eyespots, receiver psychology, antipredator signals, Lepidoptera, deflection, startle displays, false-head, visual signals, colour patterns.

CONTENTS

I. INTRODUCTION

The bodies of many insects and other animals bear a range of circular features, often complex in form and highly contrasting with the surrounding body patterning. These markings are generally poorly defined or not defined at all but are loosely termed 'eyespots'. In this article, eyespots are defined as an approximately circular marking on the body of an animal, composed of colours contrasting with the surrounding body area, often comprised of concentric rings, and occurring in bilaterally symmetrical pairs. Eyespots are most commonly found in the Lepidoptera, but also in the Coleoptera, Fulgoridae and Orthoptera. Additionally, other animal groups, specifically some tropical fishes, may possess eyespots.

The role and function of eyespot patterns has been considered for over a century, yet there are still many unresolved questions. Due to the widespread occurrence of eyespots, often with similar features and complex form, it is reasonable to suggest that they evolved in response to selective pressures, and are therefore adaptive (Tinbergen, 1974). It has long been assumed that eyespots function in interspecific encounters, conferring protection from predators.

The two foremost hypotheses for the antipredator utility of eyespots are: (1) that eyespots intimidate predators, by suggesting the appearance of the predator's own enemies, allowing the prey to flee (the 'intimidation hypothesis') (Fig. 1); and; (2) that eyespots draw the attacks of predators to non-vital regions of the body (the 'deflection hypothesis'; Poulton, 1890; Hingston, 1933; Cott, 1940; Blest, 1957; Tinbergen, 1974; Lyytinen, Brakefield & Mappes, 2003) (Fig. 2). In the case of the intimidation hypothesis, an alternative suggestion to eye mimicry is that eyespots intimidate predators since they are highly conspicuous and contrasting features, appealing to the predators' visual and psychological systems (the 'conspicuous signal hypothesis'). Larger, more-or-less centrally placed eyespots may function in intimidation, such as those of the eyed hawk moth *Smerinthus ocellatus*, whilst smaller, peripheral spots, such as in *Bicyclus anynana*, may be more effective in deflection (Blest, 1957; Coppinger, 1970; Edmunds, 1974*a*; Tinbergen, 1974; Brakefield & Larsen, 1984; Lyytinen *et al.*, 2003).

II. THE DEVELOPMENT AND GENETICS OF EYESPOTS

Each eyespot is essentially a set of rings of different colours, formed by wing scales containing different pigments, and with collections of scales reflecting and refracting light (Nijhout, 1990; Monteiro, Brakefield & French, 1994). Work throughout the last 25 years, largely on the butterfly *Bicyclus anynana*, indicates that a group of cells at the centre of a future eyespot (the focus) produces the eyespot in early pupal development (Nijhout, 1980). Early damage to this region prevents establishment of an eyespot or results in a reduced version, and grafting of the focus to a different location causes the formation of an ectopic eyespot (Nijhout, 1980; French & Brakefield, 1992; Monteiro *et al.*, 1994; Brakefield & French, 1995). Eyespot development may be explained by the production of an unstable 'morphogen' at the focus, that diffuses outwards forming a radial concentration gradient, with the epidermal cells producing specific pigments depending on morphogen concentration (Nijhout, 1980, 1990, 1991; French & Brakefield, 1992). A recent model proposed by Dilão & Sainhas (2004) explains eyespot development by a reaction-diffusion model, consisting of two diffusive morphogens and three non-diffusive pigment precursors. Threshold responses to morphogen concentration could determine the total size and proportions of the eyespot components (Monteiro, Brakefield & French, 1997*a*).

Advances in understanding the genetic control of eyespot development in *B. anynana* indicate that whilst the entire collection of an individual's eyespots may be regarded as a single 'character' (Brakefield, 2001), there is also the potential for independent change (Beldade, Koops & Brakefield, 2002). Carroll *et al.* (1994) showed that the gene *Distal-less* is expressed in the developing wing discs between the lacunae which form the wing veins, in between which *B. anynana* eyespots are located. Shortly before pupation, expression of the gene becomes enhanced in small circular groups of cells that correspond to the foci of future eyespots. Other genes have also been found, such as *Bigeye*, which increases eyespot size (Brakefield, 2001), and *Goldeneye*, which produces mutants with the outer gold ring expanded (Brunetti *et al.*, 2001).

Whilst selection on the size, location, and colour of eyespots has yielded rapid artificial selection results, selection for eyespot shape has been far more constrained (Monteiro, Brakefield & French, 1997*b*; Brakefield, 2001). Heritabilities for selecting 'fatter' or 'thinner' spots are low (approximately 15%), and limits to selection responses are quickly approached. Some changes to spot shape are also accounted for by changes in wing shape (Brakefield, 2001). Only two known mutations produce significant effects, both abrupt. The *Cyclops* mutant produces thinner elongated eyespots along the anterior-posterior axis, but produces its effect by altering the venation pattern, causing a fusion of adjacent eyespots, and is essentially lethal (Brakefield, 2001). The mutant *comet* is also an extreme pleiotropic mutant, with homozygotes having elongated eyespots along the L-R axis (Brakefield, 2001). The lack of less dramatic responses to selection for eyespot shape indicates that this feature is relatively limited in its plasticity. Indeed, a radial diffusion of morphogens may indicate why circular features are so common compared to other potential shapes.
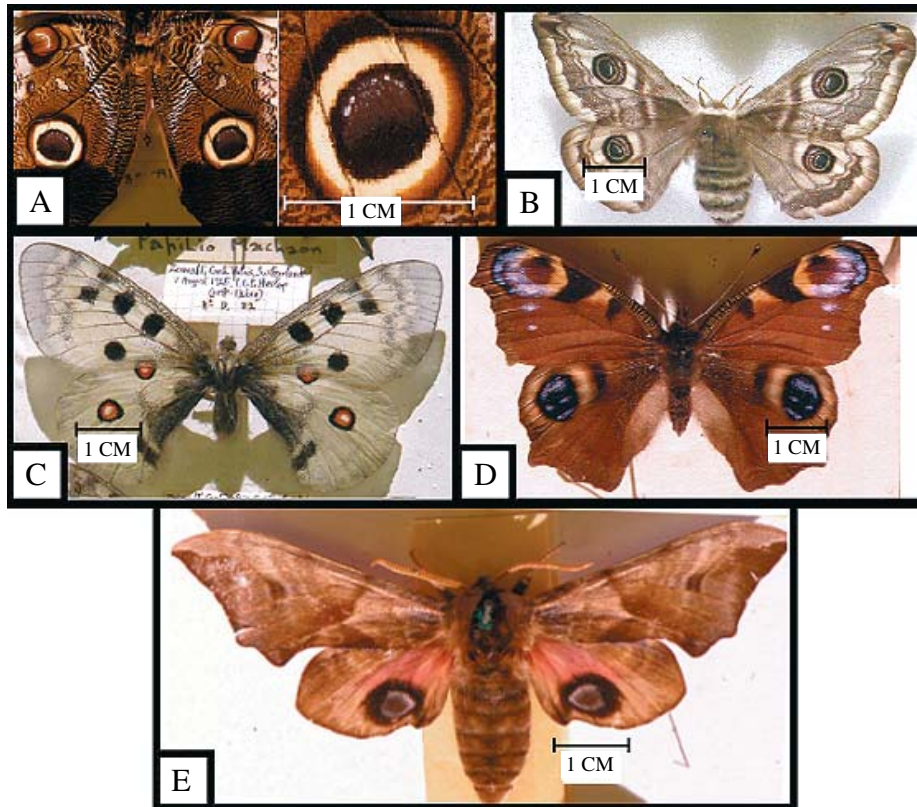
Fig. 1. Examples of potentially startling eyespots. (A) The main ventral eyespots of the owl butterfly *Caligo* sp., plus one of the spots enlarged, clearly showing several concentric circles. The pair of eyespots have often been quoted as resembling the eyes of an owl. (B) The four dorsal spots of the emperor moth *Saturnia pavonia*. Notice the high complexity of the spot and the asymmetry within each individual spot. (C) The red and black spots of the Apollo butterfly *Parnassius apollo*, which can vary substantially between individuals. (D) The complex eyespots of the peacock butterfly *Inachis io*, used in Blest's (1957) famous experiments. (E) The eyed hawkmoth *Smerinthus ocellatus* displaying its hindwing spots. The forewings are cryptic in appearance, and usually cover the hindwings, and therefore the eyespots. Bright saturated colours, appearing red, are found surrounding, and particularly above, the eyespots; a feature relatively common in many species of lepidopterans.

III. PERCEPTION OF EYESPOTS

(1) Receiver psychology and sensory systems

In considering the utility of any signal, it is unsatisfactory to inspect signals from a human perspective, unless the animal in question happens to have a visual system similar to ours. Rather, we must be aware of the visual and psychological systems of the predators involved (Guilford & Dawkins, 1991). Cott (1940) was aware of the interrelation linking visual perception and adaptive colouration, stating that 'characters serving as visual stimuli have evolved (in) parallel with the highly specialised sensory equipment of the animals towards which they are directed' (Cott, 1940, p. 191). Three aspects of signals are particularly important; (1) how easily a signal can be detected from the background, (2) how easily a signal is discriminated from other signals in the environment, and (3) how memorable a signal is (Guilford & Dawkins, 1991).

It is important not simply to examine specimens in artificial environments, a point long realised: 'We cannot appreciate the meaning of the colours of many animals apart from their surroundings, because we do not comprehend the artistic effect of the latter' (Poulton, 1890, p. 25). Apparently conspicuous markings may be superbly camouflaged in their natural habitats. Also, different environments vary significantly in their attributes, posing different selection pressures on signals (Endler, 1993).

(2) 'Colour' perception and avian colour vision

Colour perception depends upon assessments of the light reaching the receiver from an object, with comparisons of light from other objects around it, and with the ambient light (Brou *et al.*, 1986; Endler, 1990). So, whilst it is evidently convenient, it is inadequate to classify objects in relation to the colours they possess (Goldsmith, 1990). However, human perspectives have frequently been used to categorize or quantify colours and patterns, which could lead to spurious conclusions (Endler, 1990; Bennett, Cuthill & Norris, 1994; Cuthill *et al.*, 1999). Since birds pose significant selection pressures on insects, it is important to
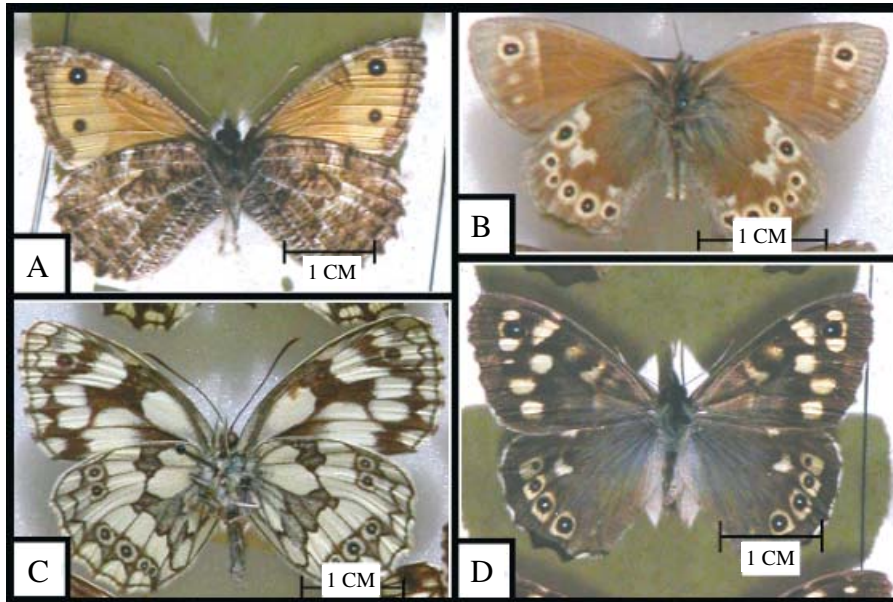
Fig. 2. Examples of potentially deflective eyespots. (A) The grayling butterfly *Hipparchia semele* ventral surface showing one larger and one smaller spot on each forewing. The eyespots may only be revealed if the butterfly perceives it may have been detected. (B) The ventral surface of the large heath butterfly *Coenonympha tullia* possessing a large number of small spots, particularly on the hindwings. (C) The marbled white butterfly *Melanargia galathea*, underside, showing a range of small spots, which do not stand out significantly from the other wing patterns. (D) The speckled wood butterfly *Pararge aegeria*, dorsal surface. This species has been the subject of several investigations into variations in spot number and behaviour among individuals and between the sexes.

consider avian visual systems, and how they differ from the human visual system.

Humans have three cone types, maximally sensitive to wavelengths of light of approximately 560, 530, and 420 nm (Dartnall, Bowmaker & Mollon, 1983; Yokoyama, 1999). Sensations of colour are produced by comparing the outputs of each cone type, and so relate to the spectral sensitivities of the different cones and differences in the photon catches received (Webster, 1996; Rodieck, 1998). Therefore, the same spectra produce different hues to animals with different absorption properties of their cone types. Additionally, Hering proposed in the late 19th Century that yellow and blue, plus red and green, represent opponent neural signals (Wandell, 1995; Webster, 1996; Chichilnisky & Wandell, 1999; Gordon, 2001). Opponent theory results from excitatory and inhibitory connections between the cone types. Excitation of a pathway causes us to perceive one colour, with inhibition causing a perception of the other member of the pair.

It has long been suspected that birds have colour vision involving four cone types, and that many species are sensitive into the ultraviolet spectrum (Huth & Burkhardt, 1972; Wright, 1972; Goldsmith, 1980; Chen, Collins & Goldsmith, 1984; Chen & Goldsmith, 1986). More recently, definite evidence has been found of four cone types (Maier & Bowmaker, 1993; reviewed by Cuthill *et al.*, 2000; Hart, 2001) and opponent processing (Osorio, Vorobyev & Jones, 1999*b*; Smith, Greenwood & Bennett, 2002). Hence birds will be able to perceive hues that trichromatic humans cannot. Ultraviolet vision appears to be a component of the vision of most, if not all, diurnal birds (reviewed by Cuthill *et al.*, 2000; Hart, 2001; recent data by Ödeen and Håstad, 2003), and is likely to function in various tasks such as mate choice, navigation, and foraging (reviewed by Cuthill *et al.*, 2000; Shi & Yokoyama, 2003; Church *et al.*, 2004).

These differences between human and avian vision are important since birds are thought to be the principal predators of lepidopterans, though other predators also pose significant visual selection pressures. Even bats may use vision in prey acquisition far more than previously realised; for example, brown long-eared bats *Plecotus auritus* have been found to prefer visual to sonar cues (Eklöf & Jones, 2003).

Most studies of eyespots were undertaken before the differences between human and avian sensory perception became apparent, and so consider patterns from a human perspective. Reconsidering previous studies in the light of modern evidence may yield differing conclusions. As such, a new hypothesis is presented below, the 'conspicuous signal hypothesis' (Section IV.2), arguing that some eyespots intimidate predators based on being highly conspicuous signals that appeal to the receivers' visual system.

IV. THE INTIMIDATION HYPOTHESIS

One of the main hypothesised functions of eyespots is that they deter predators by intimidation, preventing predators from initiating an attack. Most discussions of eyespots functioning as intimidation devices generally argue that eyespots

function by resembling the eyes of the predators' enemies. Startle displays may be associated with eye mimicry since eyespots may be revealed to give the impression of a suddenly apparent predator.

(1) Mimicry of eyes

It has long been known that some animals may use mimicry as a method of defence from predators: 'a considerable number of quite defenceless insects obtain protection from some of their enemies by having acquired a resemblance to dangerous animals,' (Wallace, 1889, p. 209). One method of mimicking potentially dangerous animals is to present features that mimic their eyes. Neudecker (1989) hypothesises that when eyespots are centrally located on the flank of fishes, and appear, or are accentuated at night, they may discourage potential predators by appearing to be an enemy. Similar theories have often been developed for lepidopterans.

Eyes are important visual signals in many animals, especially primates, and are the feature most capable of inducing fear in situations of social appraisal by others (Horley *et al.*, 2003). It is perhaps for this reason that eyespots are so easily associated with eyes by the human observer. Is this the case for other animals? Hingston (1933) states that 'the bird's eye, like that of the mammal, is the organ which most vividly reflects passion and sends threat most distinctly to the rival' (p. 143). However, this lacks experimental confirmation, especially in relation to insect eyespots. The eyes of predators have been thought to be a key feature for their recognition as enemies (Altbäcker & Csányi, 1990). For example, the short-eared owl *Asio flammeus* often attacks Darwin's finches *Geospiza* sp., and when the head of the owl is presented to the finches the eyes exert a high stimulus value in promoting mobbing, compared to a head with no eyes (Curio, 1993). However, the eyes have little effect as a stimulus when the whole body is visible (Curio, 1993), indicating that eyes may only be important features when other stimuli are unavailable.

Evidence that eyespots may be effective due to eye mimicry can be obtained from observations and experiments indicating that eyes represent salient features to many animals. Domestic fowl *Gallus gallus* chicks appear to avoid frontal views of each other, and even close their eyes when preening conspecifics (Jones, 1980). Visual avoidance has also been found in the lesser mouse lemur *Microcebus murinus*, (Coss, 1978) and could be widespread in animals. A range of experiments have investigated the effects of false eyes on *Gallus gallus* chicks. Jones (1980) presented chicks with circular pieces of black drawing board surrounded by a stylised 'head' and 'beak'. Importantly, Jones also tested the response of chicks to other shapes, such as diamonds, and to 'non-natural' configurations, such as two vertical eyes or three horizontal eyes. The results supported the intimidation hypothesis. With one or two eyes, chicks spent longer away from the stimuli than when there were no eyes, with the strongest effect induced by two eyes. Three horizontal eyes, two vertical eyes, or diamond-shaped eyes were not responded to in a manner that was different from controls. A problem with this and similar studies is that they fail to distinguish between circular stimuli and true mimicry of eyes. Also, a pair of eyes creates a bilaterally symmetrical signal, which may be important for image recognition (Kirkpatrick & Rosenthal, 1994; Forsman & Merilaita, 1999), and symmetrical patterns appear more effective as aposematic stimuli (Forsman & Merilaita, 1999, 2003; Forsman & Herrström, 2004). However, three eyes are equally symmetrical when the axis passes through the middle of the central eye, and in addition, the central eye provides a fixation point.

The physical surrounds of eyes are significant contributors to their stimulus value, and there may be considerable interaction between these features and eyes. This is supported by evidence from Inglis *et al.* (1983), who found that starlings avoided two eyes more than three, but only when surrounded by a simple head outline; otherwise, the result was reversed. To investigate these factors, Scaife (1976 *a*) exposed chickens to a stuffed hawk (the predator), and a stuffed kiwi (the 'strange' non-predatory bird). Chickens avoided the unaltered hawk more than they avoided an unaltered kiwi, and more than they avoided a hawk with no eyes. Perhaps most interestingly, the chickens avoided the kiwi with hawk's eyes more than the kiwi with its own eyes, indicating that some eyes are more aversive than others, though this could be due to differences in eye size.

In another experiment, Scaife (1976 *b*) looked at the effect of paired or singular eye-like stimuli on a hawk model or a 'strange' non-conspecific bird. As expected, two 'eyes' were more aversive than one, and circular markings had a larger effect than rectangular shapes. Avoidance of two eyes has also been found in lesser mouse lemurs (Coss, 1978), and paradise fish *Macropodus opercularis* larvae (Miklósi *et al.*, 1995; Miklósi & Csányi, 1999).

Blest (1957) also tested the effect of eyespot complexity on escape behaviour, using an apparatus with mealworms placed on a box in-between two shapes, which were illuminated from underneath when a bird approached. A circular model was more effective in causing escape responses than other shapes, and a single circle produced fewer escape responses than 'eyes' with 'pupils'. A reason to be sceptical of experiments involving false eyes was pointed out by Curio (1993): rarely in these studies have the experimenters considered the effect of their own eyes. Habituation to the two eyes contained in the human face could bias responses to other eye-like stimuli in otherwise naïve animals.

The experiments of Blest (1957), Jones (1980) and Scaife (1976 *a*, 1976 *b*) are intriguing as they indicate that the components of primary importance in the avoidance of potential threats are paired, bilaterally symmetrical circular features. However, it is unclear whether the chicks recognised the features as belonging to predators, reacted to novel features, or responded for other reasons.

(a) Evidence for the eye mimicry hypothesis

Perhaps the most convincing 'eye' spots are those found on the ventral surfaces of the wings of the neotropical butterflies of the genus *Caligo* (Fig. 1A), which can have eyespots up to 20 mm in diameter (Stradling, 1976). These crepuscular butterflies have eyespots bearing an uncanny resemblance to

the eye of some predators, such as an owl (Cott, 1940); the dark centre of the spot analogous to the pupil, and the golden ring around the centre of the spot mimicking the iris. The ventral wings, bearing brown and grey markings, are cryptic against tree bark (Stradling, 1976). Unlike many eyespots often associated with startle displays, the eyespots are continuously exposed when the individual is at rest, and are not surrounded by brightly coloured areas that would draw further attention to the area (Stradling, 1976). Stradling (1976) commented that when viewed from a distance, the eyespots on *Caligo* sp. do not interfere unduly with the crypsis of the ventral wing pattern and disputes that the eyespots resemble the eyes of an owl, arguing that the positions in which the butterflies are displayed when dead rarely match the poses adopted by living animals in the field. Furthermore, when the animal is active at dusk it flies erratically, so that the eyespots are not usually fully visible, and it is also unlikely that the butterflies would be taken by insectivorous birds at this time. Stradling (1976) instead argues that the eyespots protect against diurnally hunting predators: the eyespot and surrounding area mimic the head of predatory tree frogs of the genus *Hyla*. These frogs prey upon *Anolis* sp. lizards, which in turn serve as a threat to the butterflies. DeVries (1987) also argued that mimicry of owl eyes is not the selective force behind the eyespots, but disagreed that the eyespots mimic tree frogs. Thayer (1909) argued that the name 'owl butterfly' was a misnomer, due to the fortuitous resemblance between the owl butterflies' eyespots and owl eyes, instead suggesting that the eyespots function as distractive or 'dazzling' markings that draw the receivers gaze away from the outline of the body (also termed 'disruptive markings'; Cott, 1940).

In lepidopterans, false eyes are also found in larval stages. The larva of the large elephant hawk moth *Chaerocampa elpenor* bears two spots on either side of the body. When disturbed, the caterpillar draws its head and first three body-rings into the next two rings, mimicking the shape of a vertebrate head with two large eye-like spots; a display also found in other species (Wallace, 1889; Poulton, 1890; Hingston, 1933; Cott, 1940; Portman, 1959; Edmunds, 1974a). The front three pairs of legs are pressed close into the body (Portman, 1959), and when combined with elevating the front sections of the body, the appearance of a snake in a threatening posture, in form if not size, is created (Wallace, 1889). Anecdotal evidence indicates that this defence does startle birds, but does not determine whether the birds perceive the caterpillar as a snake, or are simply responding to a novel feature. In other situations, mimicry is less compelling. Behavioural experiments here would be of great interest: for example, to determine whether the likelihood of consumption of a snake-mimicking larva is affected by prior experience with the snake model. A positive result would provide evidence in favour of mimicry.

The classic experiments concerning the use of eyespots in intimidating predators were performed by Blest (1957), who presented yellow buntings *Emberiza* sp. with peacock butterflies *Inachis io*, which have two pairs of eyespots, thought to resemble vertebrate eyes (Fig. 1D). The eyespots are normally concealed, but when threatened, the butterfly wings are depressed, exposing the forewing eyespots, and the forewings are protracted, revealing the hindwing spots. A pause or aborted attack by the avian predator was counted as avoidance behaviour. Blest (1957) found that 'unaltered' butterflies caused about four times as many escape responses in birds compared to butterflies with the eyespots removed by gentle rubbing of the forewings. However, the mechanical rubbing of the wings to remove the eyespots could have affected the motivation of the butterflies to display. Habituation to the eyespots was usually rapid, indicating that eyespot displays may only be of survival value if they are uncommon, and are not exposed to predators too frequently (Edmunds, 1974a). Butterflies with dorsal eyespots often rest with their wings closed, and moths often have hindwing spots concealed beneath the forewings. This reduces the overall exposure of the eyespots to potential predators, and guards against rapid habituation, ensuring a startling effect when the eyespots are exposed.

Young (1997) argues that two eyes on the hindwings of moths imply that the mimicked face is large, causing small predators to flee; this would have the greatest effect for moths with well-separated large spots. Eyespots may therefore allow the true size of the insect to be easily recognised, discouraging smaller predators from attempting to consume them. There has been no systematic investigation of whether eyespots are generally found on relatively large lepidopterans. A selective force would also arise on small butterflies to have large eyespots to falsely convey the appearance of large size. If eyespots are used to advertise the large size of the prey animal, then perhaps eyespots should only be displayed to small predators. However, the response of a lepidopteran to a potential predator is likely to be instinctive, and it would be difficult for a lepidopteran prey to judge the size of a predator in the brief interval during which an attack is initiated. Startle responses to eye-spotted insect displays have been recorded in larger bird species, such as jays, that would be able to consume large insects (see Tinbergen, 1974), indicating a role for factors other than prey size.

Experiments have also tested the use of eyespots as scaring devices towards pest species. Belant *et al.* (1998) found that eyespots are ineffective as deterrents to starlings *Sturnus vulgaris* nesting in artificial cavities. They placed pairs of 22 cm diameter taxidermy eyes with black pupils 6 cm apart above the entrances to nest boxes. Compared to the controls, and to the other treatments, the eyespots had no effect in preventing nesting and reproduction. This result could be due to habituation to the stimuli, which would be less likely to occur with prey eyespots. Other studies have found that commercially available deterrent 'eye-spot balls' are more effective than regular 'beach balls' in deterring house sparrows *Passer domesticus* from visiting a bird table (McLennan, Langham & Porter, 1995).

(b) Criticisms of the eye mimicry hypothesis

Blest (1957) concluded that eyespots incorporate properties that make them maximally effective, including circularity, and suggested that eyespots may parasitize an inborn antipredator device in animals. Birds, for example, may have an innate avoidance of eye-like features (Edmunds, 1974a). Blest (1957) also argued that some eyespots generate a

three-dimensional effect by displacement of the concentric elements to one side of the pattern, imitating the pupil, with highlights giving the appearance of light reflecting from a spherical object. However, other spots are two-dimensional in appearance, and bear little resemblance to real eyes. Therefore, not all eyespots may mimic eyes. Tinbergen (1974) points out that it is obviously disadvantageous for the bird to react to eyespots, so why have they not been able to 'override' their harmful response? Firstly, the organisation of a bird's vision is so formed that a circular pattern, such as an eyespot, is more conspicuous than other markings, and birds may be cautious of any conspicuous pattern (see the conspicuous signal hypothesis below). An alternative view, favoured by Tinbergen (1974), is that escape responses are initiated by features that resemble enemies, such as eyes.

Blest's (1957) conclusions are criticised by Coppinger (1969, 1970), on the basis that birds may simply be avoiding highly contrasting novel stimuli. In experiments with blue jays, Coppinger (1969) found that inhibition of attacking novel insects was not related to a specific pattern, but rather was due to an interaction between the patterns of the prey and the jays' previous experience. There may be an innate tendency to reject novelty (neophobia) or novel features may promote dietary conservatism. This reaction may not be overridden if the rate of encountering eyespots is low enough to avoid habituation. Coppinger (1970) reports that half the birds in an experiment initially avoided even mealworms, and in Blest's (1957) experiments, insects without eyespots still caused startle responses; half (six) of the birds were removed from the study as they were so startled by the spotless butterflies that they no longer responded to any butterflies at all. The situation may be complex, as is frequently demonstrated in studies of aposematism. For instance, it is often assumed that naïve predators must learn to avoid unpalatable prey (Cott, 1940; Endler, 1988), although Alatalo & Mappes (1996) point out that the predators are not naïve in an evolutionary sense. Chicks at least may have inbuilt aversions for some colours (e.g. black) more than for other colours (Roper & Cook, 1989). Aversions may not simply be based on novelty alone, though Roper (1993) found that chicks learned to avoid distasteful solutions faster when the solution's appearance was novel. Furthermore, in direct contention with Blest's (1957) experiments with peacock butterflies, Hingston (1933) reports anecdotal evidence of birds actually attracted to peck at the front spots of peacock butterflies.

If we accept that eyespots mimic vertebrate eyes, do they resemble the eyes of a specific predator, or are they mimicking some general features of eyes? A common problem in the mimicry literature is that of 'imperfect mimics', such as the numerous hoverfly mimics of hymenopterans, where a species appears not to have maximised its mimicry with respect to a given model species, potentially because it is mimicking a range of species, occurring at different frequencies (Howse & Allen, 1994; Joron & Mallet, 1998; Edmunds, 2000; Sherratt, 2002). Also, some predators present a greater threat and the patterns of the mimic may be biased towards those models which represent a greater selection pressure (Edmunds, 2000).

Langerholc (1991) argues that mimicry of faces does not receive the treatment it deserves, and that 'it has been the brunt of ridicule by avowed evolutionists and shunned by mimicry researchers … Logic and reason have been marshalled on an unbelievable scale to discredit what anyone can now see for himself in the photographs'. Whilst sometimes we may trust our instincts, Langerholc (1991) has fallen into the unfortunate trap of failing to realise that our instincts, and indeed 'what anyone can now see', are not the same as the experiences of other animals, including the principal predators of the prey species.

(2) The conspicuous signal hypothesis

It has long been assumed that eyespots resemble vertebrate eyes, without considering the alternative, that the features may intimidate predators by simply being highly conspicuous and contrasting, and startle naïve predators based on the concept of neophobia (Marples & Kelly, 2001), or may promote dietary conservatism. Dziuraweic & Deręgowski (2002) argue that the term 'eyespot' is unjustified, as there is 'no evidence that the animals in question respond to the paired spots in such a way because they *see* them as eyes'.

One similarity between eyes and eyespots is circularity, but the fact that most eyespots are circular may have little to do with eye mimicry. Evidence from the development and genetics of eyespot formation in *Bicyclus anynana* (see Section II) indicates that circular features are developmentally easier to produce than other patterns, due to the radial diffusion of morphogens from the centre of a spot (there are cases of lepidopterans showing non-circular features, such as triangular markings in the Atlas moth *Attacus atlas*, so it would appear that some flexibility is possible).

Tinbergen (1974) raises the possibility that birds should be especially cautious of any conspicuous feature, and that eyespots could be one of the most conspicuous of all markings. Circular shapes may be more detectable than other shapes. For instance, Lythgoe (1979) points out that the spatial organisation of many vertebrate retinae is similar, and that ganglion cells forming part of the visual image pathway often have approximately circular receptive fields, divided into a central and surrounding region, though this is an idealisation (Wandell, 1995; Rodieck, 1998). A common feature is lateral inhibition, where the signals from a group of cells are inhibited when cells surrounding the receptive field receive stimulation (Lythgoe, 1979). In many fields, central excitatory areas are surrounded by concentric inhibitory regions ('on-centre, off-surround'); the opposite pattern can also be found ('off-centre, on-surround') (Wandell, 1995; Gordon, 2001). A stimulus on the central region increases the number of impulses from the ganglion cells, but the same stimulus falling on the surrounding region causes a decreased number of impulses; thus the optimum stimulus size is approximately proportional to the receptive field size (Lythgoe, 1979). Of course, approaching a spot, and changing the angle of viewing, would reduce the effect on this kind of receptive field since it will extend more into the inhibitory surround. However, it is possible that a range of ganglion arrangements exist that are maximally stimulated at different distances and orientations. Also, the

point at which an eyespot is revealed is probably quite stereotyped. This distance could also be where stimulation of the predator's receptive field is maximal, causing a strong startle response. Some ganglion cells fire when the illumination on the central field becomes dimmer, and are most sensitive to the presence of a circular dark marking exactly covering the central field, especially if surrounded by a lighter ring, which elicits no inhibition (Lythgoe, 1979). This is a common eyespot pattern and links to the concept of 'feature detectors', where animals respond selectively to certain aspects of stimuli, including simple features such as lines in particular orientations (Gordon, 2001). These detectors may be used in edge detection, and an eyespot is essentially a shape with highly contrasting edges against the wing background. Eyespots may be influenced directly by the spatial characteristics of the receivers' vision, and be highly effective in stimulating a predator's visual system to produce a behavioural response. Tinbergen (1974) also points out that any mutation causing a conspicuous wing pattern may have a selective advantage, with selection resulting in its further development into a circular shape. Whilst the above arguments are speculative in terms of the mechanisms involved, it seems credible that circular features are highly conspicuous.

The apparently universal pairedness of eyespots seemingly enhances their resemblance to real eyes. However, there is an alternative explanation. Symmetrical signals can enhance the ability of animals to perceive objects correctly, from different positions and orientations (Enquist & Arak, 1994), and may evolve as a by-product of how image recognition functions (Kirkpatrick & Rosenthal, 1994; Forsman & Merilaita, 1999). Also, most patterns appearing on bilaterally symmetrical animals are bilaterally symmetrical. Therefore, it is no surprise that eyespots are usually paired; this does not mean that they are mimicking a pair of eyes. Cott (1940) postulates that eyespots may actually, in some instances, be interpreted as highly concentrated warning signals, where bilateral symmetry enhances the signal (Forsman & Merilaita, 1999).

Another issue concerns how we explain non-eye-like features found in and around many eyespots, such as highly saturated areas of colour (Blest, 1957). These may highlight and draw the attention of the predator towards the eyespots, increasing the chance that the predator will detect and react to them (Guilford & Dawkins, 1991). Endler (1992) points out that patterns are most conspicuous when they contain adjacent 'light' patches (highly reflective unsaturated colours), and dark patches (low reflectance and chroma). Also, the colour of adjacent patches can affect the perceived colour of another patch (Brown & MacLeod, 1997). For example, changing the variance (contrast and saturation), but not the mean colour, surrounding another patch can induce a shift in the perception of contrast and saturation of the unaltered colour patch to humans (Brown & MacLeod, 1997). Hence, some patterns may stand out more if they are bordered by vivid colours, or especially if they are bordered by colours that differ significantly in brightness and chroma (Wyszecki & Stiles, 1982; Endler, 1990, 1992). Often, objects appear much more vivid and richly coloured against low-contrast, grey surrounds than they do against highly

contrasting, multicoloured surrounds (Brown & MacLeod, 1997). It would be revealing to determine if this method of patterning is common in and around eyespot features. Displays may attract attention without providing specific information, perhaps by exploiting innate preferences for bright colours or symmetrical patterns (Forsman & Merilaita, 1999; Osorio, Jones & Vorobyev, 1999a), and may be explained by the 'receiver bias hypothesis', where a bias inherent in the animals' recognition system can explain the evolution of exaggerated signals (Enquist & Arak, 1994; Jansson & Enquist, 2003).

(a) Neophobia

Many results attributed to an innate avoidance of eyes can be explained as a simple avoidance of novel features (neophobia; Marples & Kelly, 2001) (Coppinger, 1969, 1970). Blest (1957) attributed the escape behaviour of birds when presented with *Aglais urticae* butterflies to the bright and conspicuous colour patterns on the dorsal wing surfaces. Habituation to the displays was rapid, and the displays had little effect on experienced predators. Sargent (1978) also reports that blue jays *Cyanocitta cristata* rapidly habituated to and learned to catch *Catocala* sp. moths, generally within 12–15 experiences. If the stimulus does not pose a threat habituation can occur, whereas if there was a real danger, avoidance learning would take place. Lyytinen *et al.* (2003, 2004) found that inexperienced pied flycatchers *Ficedula hypoleuca* were less likely to attack butterflies with eyespots than experienced birds. This indicates that provided predators do not encounter eyespots at a rate that would allow rapid habituation, eyespots provide protection by causing neophobic responses in predators.

(b) Startle displays

Often, insect eyespots are concealed beneath camouflaged body parts, only being revealed when the insect is disturbed (Tinbergen, 1974). These 'startle displays' (also called protean displays) often function when usually cryptic prey have developed secondary defence mechanisms that operate after a predator has initiated an attack (Humphries & Driver, 1970; Tinbergen, 1974; Sargent, 1976, 1978; Vaughan, 1983; Schlenoff, 1985). Startle responses involve sudden, conspicuous changes in the appearance or behaviour of prey, including revealing eyespots, and are thought to confuse or alarm predators, providing a chance to escape (Humphries & Driver, 1970; Sargent, 1976, 1978; Vaughan, 1983; Schlenoff, 1985), and allowing reconcealment (Young, 1997).

The eyed hawk moth (Fig. 1E) employs a startle display exposing two large eyespots, described as grey in the centre, surrounded first with blue, then by a black ring (Newman, 1890). The moth moves rhythmically up and down, giving the impression of movement associated with the eyespots (Edmunds, 1974a). Motion may be incorporated to increase the detectability of the signal by the receiver (Fleishman, 1988; Guilford & Dawkins, 1991).

In the field, evidence of startle displays is often taken from the presence of V-shaped beak marks on the wings of the

insects, demonstrating release from an avian predator. However, as Edmunds (1974 b) pointed out, it is difficult to determine whether a high frequency of marks indicates a high rate of escape or a high incidence of predation.

Startle displays appear maximally effective when they incorporate visual signals that are highly salient, such as circular features, which are quickly detected by a potential predator. Whilst startle displays may provide protection by promoting a neophobic response, the displaying animal also gains protection by another mechanism; a sudden and conspicuous change in appearance and behaviour, rather than simply by looking odd. A pause in the attack will allow the prey time to escape and re-conceal itself. This point is often neglected in laboratory studies, since prey items may be unable to flee to relative safety (due to constraints on distance or cover).

The increased duration before a predator attacks, after an insect has performed a startle display, may also be explained by a delay in processing the signal due to the sudden presentation of a large amount of visual information. In studies with humans, Corbetta *et al.* (1990) found that subjects were less effective in discriminating changes between stimuli presented for 400 ms, separated by 200 ms, when dividing their attention between shape, colour and velocity cues, compared to when they focussed attention on a single attribute. Other animals must have similar limitations in their ability to process large quantities of information, and since eyespot patterns (shapes) are accompanied by a sudden expression of movement and colour cues, predators may simply hesitate as a result of the time required to process this information (cf. 'satyric mimicry'; Howse & Allen, 1994).

The conspicuous signal hypothesis is presented here as an alternative to that of eye mimicry in promoting an intimidation effect in predators. A variety of evidence indicates that eyespots, and their associated characteristics (startle responses, bright surrounding colours, etc.), could promote a response simply by appealing to the predators' visual and psychological systems. Further investigations of the effect of presenting circular features and bright colours on the visual systems of specific receivers are needed to obtain more conclusive evidence.

V. THE DEFLECTION HYPOTHESIS

The deflection hypothesis argues that eyespots function in drawing predatory attacks to less vital regions of an animal's body (Cott, 1940; Edmunds, 1974a). Poulton (1890) suggested that small spots on the wings of various butterflies may deflect the attacks of predators, allowing the prey to escape (Fig. 2). This has also been proposed in fish (Neudecker, 1989), tiger beetles (Kamoun, 1991), and tadpoles (Van Buskirk *et al.*, 2004). Eyespots located at the rear margin of the hind wing, and at the conspicuous apex of the forewing, both far from the body, are usually classed as deflection marks in lepidopterans. V-shaped beak marks on or around eyespots on the wings are often taken as evidence of a deflection marker function, with the beak marks regarded

as unsuccessful bird attacks (Edmunds, 1974b; Robbins, 1980).

(1) Evidence for the deflection hypothesis

In a simple experiment aimed at testing the deflection hypothesis, Blest (1957) painted spots on mealworms, and scored the number of pecks at the marked and unmarked ends. Significantly more pecks were directed to eyespot markings (white spot with black pupil), than to control markings (mealworm-coloured spots), indicating some evidence for a deflective role of spots.

Swynnerton (1926; cited in Tinbergen, 1974) marked butterflies of the genus *Charaxes* with artificial eyespots, and tested their survival against unaltered individuals in the field. Marked butterflies tended to survive longer, and they bore signs of failed bird attacks near the wing spots.

Lyytinen *et al.* (2003) tested the deflection hypothesis in *Bicyclus anynana* by comparing the survival of the spotless dry season and the spotted wet season morphs, plus a mutant with enlarged spots, when presented to *Anolis* sp. lizards and pied flycatchers. There was no evidence that the eyespots were advantageous. Eyespots did not increase the chance of escape, and there was no difference between the proportion of initial strikes aimed at the wings of spotted and non-spotted individuals. A later experiment also found little evidence that birds made misdirected attacks towards butterflies with eyespots (Lyytinen *et al.*, 2004). These results may have differed from those obtained by Swynnerton since the field situation offered butterflies a greater opportunity to escape than in the laboratory. Furthermore, *B. anynana* individuals have several spots on their wing margins, potentially causing the predators to attack a variety of regions on the wings, and reducing the likelihood of detecting a positive effect. The eyespots of *B. anynana* are relatively small, and not concealed, so are unlikely to have a role in intimidation.

Recently, a novel approach to investigating the deflection hypothesis was applied by Hill & Vaca (2004), who tested if conspicuous white marginal wing patches on the butterfly *Pierella astyoche* were relatively weak compared to homologous regions of the wing in closely related species without the patch. As predicted, the hindwing tear weight of the patch in *P. astyoche* was significantly lower than in *P. lamina* and *P. lena*. A lower tear weight means that an avian attack to this region more easily breaks off a section of the wing, potentially allowing the butterfly to escape with only wing damage.

Ecological variation in eyespot patterns on the ventral hindwings of the meadow brown butterfly *Maniola jurtina* has been well studied (Bengtson, 1981; Brakefield, 1982, 1984; Brooke, Lees & Lawman, 1985; Owen & Smith, 1990, 1993; Van Dyck, Matthysen & Dhondt, 1997; Merckx & Van Dyck, 2002), and provides a useful system for investigating the role of small peripheral eyespots, thought to function in deflection (Merckx & Van Dyck, 2002). Individual butterflies possess between zero and six spots on each hindwing (Brooke *et al.*, 1985). Brakefield (1984) designed a model for *M. jurtina*, predicting higher numbers of eyespots, and a more symmetrical eyespot pattern, in individuals that require greater deflective protection due to

high activity levels. Merckx & Van Dyck (2002) tested Brakefield's (1984) model by comparing *M. jurtina* with the hedge brown butterfly *Pyronia tithonus*, and found that the more active, but less mobile, *P. tithonus* had a higher number of more symmetrical eyespots. Due to a higher proportion of time spent in flight *P. tithonus* is likely to be more susceptible to predation, and so selection may favour greater deflective protection. Merckx & Van Dyck (2002) also found that within both species, the sex with the highest number and most symmetrical eyespots was also the most damaged. A study of *M. jurtina* in Sweden by Bengtson (1981) found that the frequency of beak marks was significantly lower in females than males (8 % of females, compared to 13 % of males), and related this to greater activity levels in males. Greater wing damage was found in individuals with more eyespots, presumably reflecting a higher incidence of escape from predators. An alternative interpretation is that eyespots may increase conspicuousness, resulting in heightened predation rates and greater wing damage in more highly spotted forms. Alternatively, Bengtson (1981) notes that these results could be due to earlier hatching and a longer lifespan in males, though it is unclear what differences exist in the rate of injury in the short-term (e.g. per day) between the sexes. Owen & Smith (1990) found similar results, and that damage in males was generally more asymmetrical possibly because males are more active, and suffer more damage during flight, with females damaged generally when at rest with folded wings.

Spot number has also been found to correlate with levels of activity and behavioural patterns in the speckled wood butterfly *Pararge aegeria* (Fig. 2D) (Shreeve, 1987; Van Dyck *et al.*, 1997). In *P. aegeria*, males competing for females either 'perch' in sunlit patches, or they may 'patrol' in search of females (Shreeve, 1984, 1987; Van Dyck *et al.*, 1997). Shreeve (1987) found that in an English population of *P. aegeria*, the majority of seasonal and habitat-related variation in male behaviour was related to hindwing spot number. Males of the three-spot morph were most abundant in open areas and engaged more in patrolling behaviour. In comparison, four-spotted males were most abundant in coniferous woodland and engaged more in territorial behaviour. Van Dyck *et al.* (1997) argue that Shreeve's (1987) study analysed interactions between males only in early August. They found little effect of spot type on interactions between males from April to September. Where they did find significant effects they were in opposition to Shreeve's (1987) results. Three-spotted males engaged less in patrolling flights, and tended to initiate more intraspecific conflicts than four-spotted males (Van Dyck *et al.*, 1997). Thus the situation in *P. aegeria* is unclear. The observation that four-spotted males engaged more in long flights supports the model that more active individuals require greater protection from predators such as by deflective markings, since the fourth spot is clearly visible only in flight (Van Dyck *et al.*, 1997).

(2) The 'false head' hypothesis

A variation in the theme of deflective markings is the hypothesis that some butterflies, notably from the
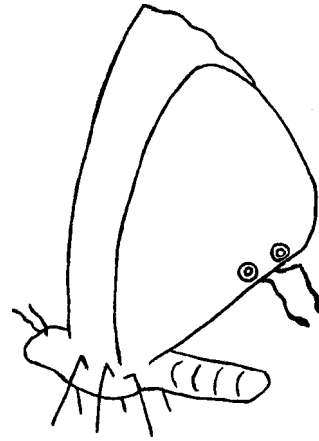

Fig. 3. A simplified illustration of the false head markings and structures seen in some butterfly species, particularly lycaenids. False head markings often include eyespots on the ventral surface of the hindwings, close to the posterior of the body. These eyespots are often accompanied by appendages that appear to mimic antennae or legs.

Lycaenidae, but also the Riodinidae and Nymphalidae, exhibit 'posture reversal,' by creating the impression of a false head at the posterior end of the butterfly (Kirby & Spence, 1818; Poulton, 1890; Edmunds, 1974a; Tinbergen, 1974; Robbins, 1980, 1981; Tonner *et al.*, 1993; Cordero, 2001). These frequently include eyespots on the ventral surface of the hindwings (Fig. 3). Van Someren (1922, cited in Robbins, 1981) demonstrated that lizards preferentially attack the false head of lycaenid butterflies, which often combine eyespots with false antennae and legs, and even walk in the direction of the false head, adding behavioural support to the morphological traits (Curio, 1976). The real antennae are held motionless so the true head is inconspicuous, whilst the false antennae are moved to enhance the probability they will be detected (Fleishman, 1988; Guilford & Dawkins, 1991). Additionally, many lycaenids rest on vertical surfaces with their heads pointing down, contrary to most other species, in which the head orientates upwards (Edmunds, 1974a). Poulton (1890) indicated that the true body of the insect is short, and does not extend as far as the false head, which may mean the insect avoids serious injury if captured. False head markings may also cause predators to misjudge attacks by anticipating that the prey will flee in the 'wrong' direction (Curio, 1976).

Robbins (1981) tested the deflection hypothesis by collecting specimens of 125 species of lycaenid butterflies and scoring the level of 'deceptiveness,' based on the number of false head components present. Species with more false head components had a higher frequency of wing damage than did species with less deceptive false heads. Tonner *et al.* (1993) counted the frequency of beak marks on different regions of the wings of wild Burmese junglequeen butterflies *Stichophthalma louisa*, which have a range of eyespots on the underside of the wings. They divided the wings into 13 sections and measured the distribution of symmetrical and asymmetrical wing damage caused by

birds. Symmetrical damage occurred primarily in the false head region, whereas asymmetric damage occurred in other areas. Tonner *et al.* (1993) argue that symmetrical damage is inflicted when the animal is at rest, with its wings held together, and asymmetrical damage is inflicted during flight. Robbins (1980) found a different probability of wing breakage occurs in different wing regions: the majority of beak mark damage was in regions where all four wings overlap and thus are more resistant to breakage. This casts further doubt on the use of wing damage to test rate of deflection (Edmunds, 1974*b*; Robbins, 1980).

Wourms & Wasserman (1985) determined the distribution of initial strikes and handling responses of blue jays *Cyanocitta cristata* on cabbage white butterflies *Pieris rapae*, painted with wing patterns similar to those found in lycaenids. They presented birds with dead unaltered butterflies as controls, and dead butterflies painted with one of six wing patterns, including several forms of lines converging on the anal angle of the hindwing, and a treatment with an eyespot near the posterior end of the hindwing. The only marking found to alter the initial attack strike distribution significantly was the eyespot, which directed attacks towards the hind regions. In experiments with live painted butterflies, jays switched from handling the butterflies in the true head region of controls, to the hind region in butterflies that had been experimentally marked. Hence, live butterflies showed an enhanced chance of being released by mishandling if they had painted markings. This is good evidence for the false head hypothesis, though critics could argue that the lack of a control for painting may have influenced the results.

In contrast to the hypothesis that false head markings deflect predatory attacks away from the vulnerable head region, Cordero (2001) argues that the head is actually *less* vulnerable to attack, since an attack to the head allows the butterfly to detect an oncoming predator earlier than would an attack aimed at the posterior end. The false head repels the attack of the predator away from the vulnerable posterior end, to the less vulnerable anterior region of the butterfly, enhancing the chance of detecting an attack earlier. This is a theory which is yet to be tested.

A useful avenue for future research would be to analyse the distribution of eyespots on butterfly wings. We should expect spots to draw the attacks of predators to non-vital body regions. Since the wing veins carry haemolymph to the wings and provide structural support, deflective spots may be less likely to cross over veins. The leading forewing edge is important to flight performance, and so deflective spots are unlikely to be located in this region (A. Thomas, personal communication; Wootton, 1992, 1993; Combes & Daniel, 2003). The effect of wing damage to these regions on the aerial performance of the butterflies has not been systematically studied.

Deflective spots and their components may have an optimal size: too small and they would not be detected, too large and they may not draw the attacks of predators or may reduce overall crypsis. By measuring the allometry of eyespot size against wing area, species with deflective spots would be expected to show an upper limit on eyespot size. This prediction would not hold for eyespots that function in intimidation which should occupy the maximum area possible, and show positive allometry.

VI. EYESPOTS AND SEXUAL SELECTION IN LEPIDOPTERANS

It has long been suggested that lepidopteran wing patterns function in sexual selection (Darwin, 1874), supported by recent studies (Silberglied, 1984). Surprisingly, few studies have investigated the role of eyespots in mate choice or intrasexual competition. Hingston (1933) argued that eyespots are divisible into two groups: those functioning in intraspecific encounters, and those functioning as anti-predator devices. Hingston (1933) suggested that eyespots were important in intrasexual competition as threat patches, and that many eyespots are located on the outer wing section, where they are most visible to competitors (an opposing theory to the deflection hypothesis). Eyespots represent very prominent visual signals, and so may make ideal stimuli to function as indicators of mate quality.

Eyespots may have multiple roles with conflicting functions, such as sexual selection and predatory avoidance. One of the classic studies of this trade-off in visual signals is on the guppy *Poecilia reticulata* (Endler, 1978, 1980, 1987, 1991), in which conspicuous male colouration, favoured by females in most populations, is counterbalanced in rivers with high numbers of predators.

Possibly the only investigations of the use of eyespots in sexual selection in lepidopterans have been undertaken with the butterfly *Bicyclus anynana*. Eyespots on the dorsal surface of *B. anynana* are generally not exposed to predators, and may function in female mate choice, with females preferring males with darker spots (Monteiro *et al.*, 1997*a*). Breuker & Brakefield (2002) found in *Bicyclus anynana* that females select males with larger dorsal wing eyespots, illustrating a role of eyespots in sexual selection.

Detailed analyses are needed to ascertain whether differences exist between males and females in the presence or absence of spots, and also for eyespot characteristics, such as colour and size. When present, eyespots are generally found in both sexes of lepidopterans, although exceptions exist. For example, female large white butterflies *Pieris brassicae* tend to have more visible black forewing spots than males, if the male has spots at all. The observation that eyespots are generally found in both sexes could indicate that they are primarily involved in a function other than sexual selection, but could also mean that eyespots are used by both sexes in mate choice. Differences between the eyespots of the sexes could arise due to differences in life-history strategies. For example, if one sex is more active, or more exposed to certain predators, it could be under greater selection pressure to develop defensive markings (see Section V). Before it is possible to conclude that eyespots function as antipredator devices, we should first investigate the possible role of eyespots in sexual selection.

Fig. 4. Examples of spot patterns that do not fit the definition of an eyespot. (A) The dorsal surface of the oak eggar moth *Lasiocampa quercus*, which has a small white spot on each forewing. A deflective role is unlikely given the location of the spot on the wing. (B) The brimstone butterfly *Gonepteryx rhamni* showing four small spots, one in the centre of each wing (the spots on the hindwings are larger). The wings appear either white or yellow to the human eye, and the spots appear orange. The spots are visible on both the ventral and dorsal surfaces. (C) Garden tiger moth *Arctia caja* with hindwings bearing multiple dark spots against a reddish-orange background. This pattern may be a characteristic feature of aposematic moths, in particular, the use of bright colours and numerous highly contrasting, though simple, spots.

VII. THE POTENTIAL COST OF EYESPOTS

Many animal signals may be the result of a trade-off between two opposing selection pressures. A trade-off between crypsis and the presence of conspicuous eyespots may exist, with eyespots potentially increasing the detectability of the prey animal (Edmunds, 1974*a*). This may be offset by behavioural adaptations, such as in the grayling butterfly *Hipparchia semele* (Fig. 2A), which only exposes its eyespots when disturbed (Edmunds, 1974*a*; Tinbergen, 1974). In fact, many satyrines, which often have one or two eyespots on the under-surface of the front wing, when at rest pull their forewings down between the closed hindwings thus concealing the eyespots (Hingston, 1933). In fish, some species of Trachinadae and Uranoscopidae conceal themselves in sand. However, if they are discovered before they have buried themselves, or perceive a potential source of danger once buried, they expose a black spot on their dorsal fin, signalling their toxic poison apparatus (Bedini, Canali & Bedini, 2003). Revealing a warning signal only once other lines of defence have failed, indicates that such signals can bear a cost.

An alternative method of avoiding the cost of bearing conspicuous spots involves the occurrence of 'seasonal polyphenism' (or 'seasonal dimorphism; Cott, 1940), where there is an annually repeating pattern of changing phenotypic ratios in successive generations under environmental control (Shapiro, 1976, cited in Brakefield & Larsen, 1984; Brakefield, 1996). Brakefield & Larsen (1984) discuss this phenomenon in butterflies such as *Bicyclus anynana*, where the spot pattern reflects a balance between conspicuousness to predators and the pattern's effectiveness in enabling the butterfly to escape an attack. Dry-season forms of *Bicyclus anynana* appear to be more camouflaged, with a reduction or elimination of eyespots compared to wet-season forms (Brakefield & Larsen, 1984). Individual forms develop into their respective phenotypes depending on body temperature in the larval stages (Zijlstra *et al.*, 2003; Lyytinen *et al.*, 2004). The wet-season form has ventral eyespots positioned close to the wing edges. When at rest, the wings are kept closed and the forewings fully exposed above the hindwings, exposing the marginal eyespots on both fore- and hindwings. In the dry-season forms eyespots are very small or completely absent, and are hidden at rest (Lyytinen *et al.*, 2004). Reflectance spectra measurements indicate that the wings of both phenotypes are well camouflaged against dead brown leaves, but both forms are highly visible against the green wet-season leaves (Lyytinen *et al.*, 2004). Lyytinen *et al.* (2004) propose that eyespots may serve a deflective function in the wet season, when crypsis of the brown butterflies against the green foliage is ineffective, but are absent in the dry-season forms since they may prevent successful camouflage. This theory is supported in aviary trials with great tits *Parus major*, where butterflies with eyespots were detected more quickly against a 'dry-season' background.

If brightly coloured markings make prey individuals easier to detect, how can they evolve? This problem was addressed by Cooper and Vitt (1991) with a simple mathematical model for an animal possessing a conspicuously coloured tail as a deflective target. The model showed that having a conspicuous marking can be favoured under some conditions, specifically when there is a high chance of an inconspicuous individual being detected, and when the increased probability of detection due to the deflective mark is small compared to the benefits gained from an increased escape probability.

This argument applies to *Bicyclus anynana*, where the background brown wing pattern confers little advantage against the green wet-season foliage, allowing for the evolution of conspicuous deflective eyespots. Importantly, the model shows that even if deflective markings cause an increase in attack rate on the bearer, they can still be favoured provided they increase the chance of escaping from an attack.

VIII. OTHER FUNCTIONS OF WING SPOTS

Lepidopterans, in common with many animals, often possess a range of circular markings that do not fit the definition of an eyespot as presented here, and which may have other functions (Fig. 4). For instance, the dark spots found on the otherwise 'reddish' hindwings of the garden tiger moth *Arctia caja* (Fig. 4C) probably function as an aposematic

signal, since the tiger moth contains toxins including choline esters (Kettlewell, 1965). If the term 'eyespot' is restricted to spots consisting of concentric circles, what function then do other 'types' of spot have, such as the monochromatic spots of the brimstone butterfly *Gonepteryx rhamni* (Fig. 4B)? Owen & Smith (1990) report that it is possible to pick out tiny spots on the wings of the meadow brown butterfly *Maniola jurtina*, and Thayer (1909) argued that small eyespots ('minor ocelli') are likely to involve background matching. Some moth species, such as many noctuids, have circular features that resemble small patches of lichen. There may be a succession of intermediate forms for background-matching spots, from small and inconspicuous to larger conspicuous spots, and it may be difficult to determine where one function ceases, and the other begins (Thayer, 1909). It is clear that there is a diverse range of spot types, with functions ranging from anti-predation to sexual selection, aposematism, or camouflage. To elucidate their possible roles further behavioural experiments are needed.

IX. CONCLUSIONS

(1) Eyespot patterns are widespread features in animals, especially lepidopterans, yet rigorous experimental tests investigating their functions are often lacking.

(2) The intimidation hypothesis argues that eyespots startle predators, allowing the prey to escape. This occurs because eyespots mimic the eyes of predators, or simply because they are highly conspicuous features. Few, if any, studies have provided firm evidence that predators perceive eyespots as eyes, rather than just conspicuous or novel features.

(3) The deflection hypothesis argues that small peripherally located eyespots deflect the attacks of predators to regions of the body that are non-vital. Evidence for this function of eyespots is contradictory, with some studies using wing damage patterns as evidence. Some butterflies possess eyespots and other features that give the appearance of a false head to deflect attacks from vital areas. This hypothesis is relatively well supported.

(4) There is likely to be a cost to bearing eyespots in the loss of camouflage that they may induce. However, this cost can be offset by life-history strategies, such as temporal polyphenism, or simply if the cost of the increased risk of predation is less than the benefit gained from an increased chance of escaping an attack.

(5) There are a range of spot patterns that do not fit the definition of an eyespot as given here. Some of these may function in sexual selection, camouflage or aposematism, but the role of many spots remains unknown.

X. ACKNOWLEDGEMENTS

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