

Do animal eyespots really mimic eyes?

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Abstract The diversity of anti-predator adaptations in the natural world has long been an active area of research in evolutionary and behavioural biology. A common visually-obvious feature found on prey are ‘eyespots’, being approximately circular markings often with concentric rings and conspicuous colours. These are found on a range of animals, especially adult and larval Lepidoptera and fish. One of the most widespread functions of eyespots seems to be to intimidate or startle predators: delaying, preventing or halting an attack. However, while the fact that they can influence predators in this way is uncontroversial, the mechanism(s) behind why they are effective is debated. Traditionally, they have been assumed to work by mimicking the eyes of the predator’s own enemies, and much research in this field is conducted under the implicit or explicit assumption that this theory is correct. However, eyespots might work simply by being highly salient stimuli that promote sensory overload, biases, or neophobic reactions in predators. A range of recent studies has aimed to test these alternatives. Here, we critically evaluate this work and what it tells us about the mechanisms underlying eyespot function. We conclude that although eye mimicry is plausible, there remains a lack of evidence to support it and most observations are at least equally consistent with alternative mechanisms. Finally, we also discuss how the debate can be resolved [*Current Zoology* 60 (1): 26–36, 2014].

Keywords Eyespots, Predation, Animal coloration, Mimicry, Warning signals

Predation is a major evolutionary influence on most animals (Ruxton et al., 2004, Stevens, 2013), and correspondingly many species have evolved a wide range of defensive adaptations, including protective coloration. Anti-predator defences can be defined as either primary, when a predator attack is prevented from occurring in the first place; or secondary, operating after the predator has begun an attack by reducing the likelihood that the attack will be successful (Edmunds 1974). A widespread visual feature of various arthropods, fish, and some other vertebrates are conspicuous circular features commonly called ‘eyespots’. These are thought to have a range of anti-predator functions, including startling or intimidating predators to delay, halt or prevent an attack, and deflecting the attacks of predators to non-vital regions of the body (Ruxton et al., 2004; Stevens 2005; Kodandaramaiah 2011). Eyespots involved with startling or intimidating predators are often thought to be relatively large and centrally placed on the body to stop attacks, whereas deflective spots are thought to be small and peripherally placed in order to attract or draw predator attacks to them (Stevens, 2005). The term ‘eyespot’ is often used to describe any marking on the body of an animal with features that to a human ob-

server can be reminiscent of the appearance of a vertebrate eye. Specifically, they are often paired (with similar marks appearing symmetrically on either side of the animal’s centreline), they are often round or oval, and they often comprise highly contrasting concentric rings. Widespread adoption of the name ‘eyespots’ is understandable, because some of these features can look strikingly like an eye to a human observer. As we discuss in this article, eyespots are often thought to work as a type of deception by tricking an observer into misclassifying them as real eyes belonging to a potential predator.

A range of experiments in the last decade has indicated that eyespots can be effective in delaying, halting or preventing predator attacks (see below). However, the reason *why* this is the case remains controversial. The most widespread and popular theory is that the predator misidentifies the eyespots on its prey as the eyes of a potential predatory threat to it (reviewed by Stevens 2005). This could involve either eyespots that are continuously visible or on display (such as on the owl butterflies of the Genus *Caligo* or emperor moths of the genus *Saturnia*), or eyespots that are suddenly revealed in a startle display (such as on the eyed hawk

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moth *Smerinthus ocellatus* or peacock butterfly *Inachis io*). This hypothesis can be traced back to some of the earliest experimental work exploring the function of such markings (Kirby and Spence, 1818; Blest, 1957). However, the theory's longevity, and its appeal to human observers, has perhaps contributed to its sometimes unquestioned acceptance in both the popular and scientific literature despite lacking a strong empirical foundation. In this paper we focus on work involving startling or intimidating spots because these have been most frequently used to test the eye-mimicry and opposing theories. In contrast, most work on deflection has focussed on whether deflective spots actually work as hypothesised, and not on the mechanisms underlying why they might work.

Many publications are based on the assumption that the theory that eyespots mimic eyes is an established fact. This phenomenon is so widespread that we confine ourselves to only a number of recent examples here. In a list of examples of purposed predator-mimicry, Rota and Wagner (2006) state that "eyesspots on the wings of giant silk moths and other Lepidoptera undoubtedly mimic eyes of mammalian predators." They offer no support for this assertion. Williams (2010) presented a feature article on a recent book by Howse (2010) dedicated to suggested examples of vertebrate mimicry by invertebrates. Williams presents predator mimicry as established fact, suggesting that Howse highlights "the extent to which lepidopterans have evolved mimicry of many vertebrate features to deter predators". The strength of evidence for this interpretation is not discussed, although the implication is that it derived solely from appearance to the human observer. Indeed, one of the photographic illustrations supporting the article (of the eyed-hawk moth, whose name derives from its prominent eyespot markings) is captioned "An eyed hawk moth presents remarkable similarity to the fox."

In a recent review, Howse (2013) states that the lepidopteran wing patterns "often closely resemble the heads and bodies of vertebrates (including birds and reptiles) and of various invertebrates." He further discusses a number of supposed cases of eyespots combined with other markings mimicking the whole form of an animal head. For example, the peacock butterfly and the peacock pansy *Junonia almana* apparently "show a strong resemblance in life to a bird's head when they are viewed head down. The thorax then comes to represent the beak." According to Howse (2013) resemblance to a

whole plethora of objects and animals can be seen in insect wings: including beaks, teeth, feathers, salamanders, frogs, snakes, alligators, bats, rodents, dogs, primates, millipedes, hornets, lepidopteran larvae, scorpions, and even tapirs. However, when reviewing photographs of these insects we often struggled to find these purported resemblances convincing. In any case, it is not how these animals look to humans that matters evolutionarily, but rather to their real predators, which often have very different visual and cognitive systems. It is common for humans to see illusions of objects that are not there because they have a significance or association to us. This is a manifestation of the well-studied psychological phenomenon of apophenia, where people perceive meaningful patterns or connections in random or meaningless data. This tendency in humans does not mean that other species see the same illusions of other animals in the markings of their prey that some humans perceive.

Janzen et al. (2010) claim to have discovered (in the title of their article) "a tropical horde of counterfeit predator eyes" in the markings of caterpillars and lepidopteran pupae. As this title suggests, the article is based on the assumption that these markings function as an anti-predatory defence through mimicry of predatory eyes. Again, the perception of human observers is the only evidence given for eye mimicry: "It is hard not to be convinced that the false eyes in Fig. 1 are not real, and we suspect even harder for a small bird when foraging." In fact, no clear definition of such eyespots are provided except that the 36 species showcased gave the illusion of false eyes to the authors. As their figure 2 makes clear, their definition of eyespots is broad enough to include a row of oval mono-coloured spots, one to each segment, running down the flank of a caterpillar. No evidence is presented that predators of caterpillars are responsive to such markings, never mind that such a response is driven by eye-mimicry. In the last three paragraphs, we have presented a selection of some the more extreme instances of assuming eye mimicry is true, but this assumption is found to a lesser extent in many other papers.

The above issues are not just a question of a lack of rigour and objectivity when investigating eye mimicry. As we will discuss below, we do not doubt the logical validity of eye-mimicry or that it remains a plausible theory. However, there are other competing ideas that could explain the presence of many eyespots without invoking mimicry and in many instances these are more

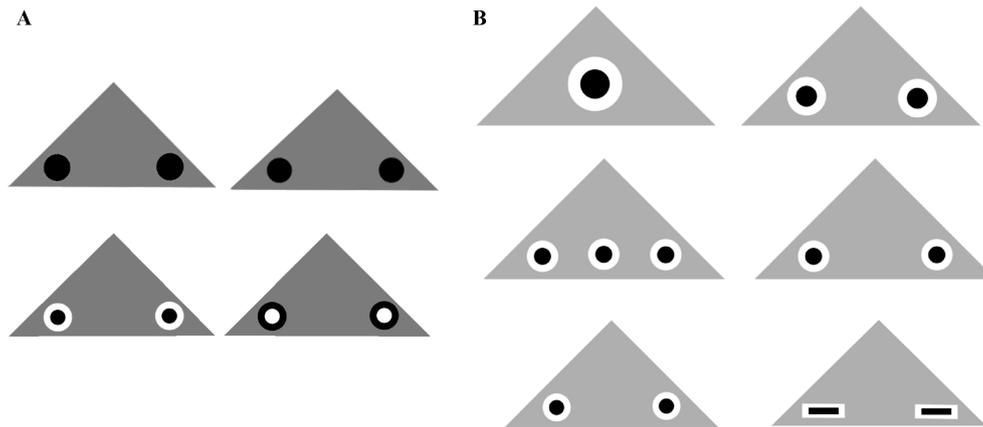


Fig. 1 A) Stimuli used in Stevens et al. (2007) that were presented to wild birds with different spot shapes and contrasts. Targets with high contrast spots had higher survival than those with low contrast. There was no difference between the survival of targets with spots with a black centre and white surround and the opposite arrangement of equal contrast. B) Stimuli from Stevens et al. (2008). Targets survived better with more spots and larger spots, but there was no advantage to prey with a pair of spots. There was also no difference between targets with different shaped markings.

parsimonious explanations because they do not need to invoke sophisticated cognitive misclassifications that must occur for an animal to mistake eyespots for a predator. Stevens (2005, 2007) suggested that eyespots could instead work based on an avoidance of highly contrasting or colourful stimuli that are especially effective at stimulating the predator's visual system and promoting neophobic reactions (Marples and Kelly, 1999; Marples et al., 2005) or dietary wariness (the 'conspicuous signal theory'). Similar suggestions were also made by Coppinger (1969, 1970). In addition, avoidance behaviour could stem from learnt or inherited biases in predators against conspicuous colours and patterns, akin to avoidance behaviours associated with warning signals found on toxic prey. With regards to startle displays, we would here suggest another, not-mutually exclusive theory; that eyespots work by inducing sensory or information overload. For example, humans can be less effective at processing information when having to divide attention between several different cue types (e.g. shape, colour and velocity) than one only (Corbetta et al., 1990). Similar constraints have also been demonstrated in auditory processing of different streams of information in bats (Barber et al., 2003), and could be a common limitation in processing information about stimuli (Stevens, 2013). Suddenly being presented with lots of different colours, patterns and movement, as occurs in a startle display, might cause predators to pause an attack simply due to having to take additional time to process all the new stimulation (Stevens, 2005). In fact, a sudden change in behav-

iour of a prey item by itself could be sufficient to trigger a pause simply because there is a change in circumstance/information that needs evaluation. Logically, this is likely to be a component of any startle display because many such displays do not contain eyespots but rather different colours and patterns (such as on underwing moths). Finally, many of the features of eyespots that are assumed to equate to eye mimicry can be explained by developmental and genetic factors. For example, spot circularity could arise for developmental reasons if these shapes are easier to produce than other non-eyelike shapes (e.g. Nijhout, 1980, 1990; French and Brakefield, 1992; Monteiro et al., 1997; Dilão and Sainhas, 2004). Likewise, many eyespots occur in pairs and this is assumed by many to relate to eye mimicry, but could purely stem from the fact that most animals are bilaterally symmetrical.

Therefore, we have several hypotheses that could explain the mechanisms underlying eyespot function: eye mimicry, sensory or information overload, and conspicuousness promoting neophobia and learnt or innate biases. In order to distinguish between these, experiments would need to demonstrate benefits of increased eye mimicry or conspicuousness independent of the other. We note, however, that these are not mutually exclusive and may differ in relative importance between species (see Discussion). In this review, we ask what objective experimental evidence there is in support of (or against) favouring the eye-mimicry theory over the alternatives, and conclude that at present, there is very little in favour of eye mimicry.

1 Aviary Experiments

Until recently, the only experimental evidence that eyespots were effective in startle displays to deter predators came from work by Blest (1957). He showed that birds were less likely to attack peacock butterflies with their eyespots rubbed off than those that were unaltered. However, one can criticise Blest's experiments on a number of grounds (see Stevens, 2005; Théry and Gomez, 2010) and clear evidence for eyespot function remained limited. Recently, however, a series of clever experiments by Vallin and colleagues has shown convincingly just how powerful eyespots can be in deterring predators (Vallin et al., 2005, 2006, 2007). They presented live peacock butterflies and eyed hawk moths to captive birds in aviaries. They painted over the spots on the wings, or control regions, and showed that birds were reluctant to attack butterflies or moths (especially the peacock butterflies) with their eyespots intact.

However, although these experiments clearly show that eyespots work in influencing potential predators, they are incapable of testing the reasons why they do so because they did not undertake any manipulation of how much the eyespots mimic eyes. The butterflies or moths without eyespots may have been attacked more simply because their wing patterns were made less conspicuous. Indeed, Coppinger (1969, 1970) criticised Blest's conclusions in this manner, by stating that the birds could just be avoiding highly contrasting novel stimuli (see also Théry and Gomez, 2010).

Recently, Merilaita et al. (2011) conducted an aviary experiment using prey made from the wings of dead peacock butterflies and a mealworm larva. They presented birds with butterflies with the eyespots removed, or with either all four or just two eyespots intact. They predicted that if eye mimicry is key then the strongest response (longest attack delay) should occur towards two spots, whereas if conspicuousness is important then four spots should elicit the strongest response. The authors found no statistical difference between two and four spots (with both being avoided more than no spots), and concluded that the evidence favoured eye mimicry more. We feel, however, that alternative interpretations are at least equally supported by the data. It is clear from their Fig. 2 that prey with four eyespots were actually attacked qualitatively more slowly than those with two, and the difference in attacks between spotted and unspotted prey was greater for the prey with four spots than two spots. Therefore, if anything, to us the results are actually in greater accordance with the con-

spicuousness theory. They certainly do not provide a strong case for preferring the *eye-mimicry* mechanism over the *conspicuousness* alternative.

In a recent study, similar to those of Vallin et al., Olofsson et al. (2013) presented live peacock butterflies to domestic fowl *Gallus gallus domesticus* with and without eyespots. They found that the chickens fled the startle display of the peacock butterflies in both treatments. However, chickens were less likely and slower to return to butterflies with eyespots, and produced more alarm calls towards these butterflies. The authors concluded that they had found evidence in support of with eye mimicry, because the birds produced more



Fig. 2 Stimuli used by Hossie and Sherratt (2012, 2013)

Top image shows an artificial caterpillar with an eyespot. Middle and lower images show artificial caterpillars with eyespots on prey that were either cylindrical or shaped more like a snake. Images courtesy of Thomas Hossie.

alarm calls consistent with the detection of ground-based predators when confronted with eyespot rather than eyespot-less prey. However, as with the work of Vallin et al. (2005, 2007), although valuable to show that eyespots work in influencing predators, Olofsson et al.'s experiment is not set up to distinguish between the conspicuous-signal and eye-mimicry theories. The results are equally consistent with conspicuousness effects because the eyespot stimuli were likely to be more conspicuous than the non-eyespot prey. Chickens make alarm and distress calls to a wide variety of stimuli, and it is expected that this should be elevated towards a more salient stimulus type. To strengthen the evidence for eyespots functioning through triggering misidentification as a terrestrial predator, it needs to be demonstrated that the specific type of calls given in response to butterflies are indistinguishable from those given in response to predators but identifiably different from those given in response to other equally-salient stimuli.

A different study (Brilot et al., 2009) also investigated an anxiety response of birds (starlings, *Sturnus vulgaris*) towards stimuli with eyespots or not, presented alongside different types of sounds, including control or non-threatening sounds (white noise or starling alarm calls) and predator (sparrowhawk) calls. Eyespots caused birds to spend less time near food and to be slower in approaching food, and the sounds caused anxiety responses. However, unexpectedly, there was no interaction between anxiety state towards the sound types and response to eyespots. The authors suggest that this lack of interaction could indicate evidence against eye mimicry because if eyespots do mimic eyes then they should lead to an increased anxiety/fear response and an interaction with the auditory stimuli. Furthermore, they found that the birds did not show differences in the amount of time they spent facing the eyespots, which can be a coarse measure of the perception of a threat, and as such did not seem to consider them an active threat. Finally, the eyespots had no effect on the initial latency of the birds to move, a measure sensitive to the alarm call treatment. These considerations led the authors to tentatively suggest that the results went against the eye mimicry theory.

2 Field Studies

The first experiments to directly aim to distinguish between the mimicry and conspicuousness theories were undertaken by Stevens and colleagues. In their experiments, they created artificial 'moth-like' triangular targets with a range of markings on them (Fig. 1).

These were attached to trees in mixed deciduous woodland in the UK, with a dead mealworm larva as an edible component for bird predators. Predation rates on different stimulus types were monitored over time. In the first series of experiments (Stevens et al., 2007), spots of greater visual contrast (black or white) against the target background (intermediate grey) survived longer than spots of lower contrast (dark or light grey). However, there was no difference between black or white spots. In two of three experiments there was also no difference in survival between targets with spots with a black centre and white surround (dark 'pupil' and light 'iris') and those with the inverse arrangement of equal visual contrast. Contrast perception between sensory stimuli is often encoded on a log scale by sensory systems, including for vision, and so in those two experiments visual contrast between black, white, and grey was calculated in this manner. In a further experiment in the same study, contrast was calculated on an absolute (linear scale), and there was a survival advantage of spots with back centres. However, in this instance, owing to the way the contrast of the stimuli was calculated, black colours would likely have been perceived as having greater visual contrast than white, which likely explains this different result.

Next, Stevens et al. (2008) tested the survival effect of different numbers of spots and different shapes. Circular shapes were no more effective than bars or squares, and displacing the central spot inwards (more eyelike) or outwards (less eyelike) had no effect. Furthermore, there was no advantage to having a pair of spots (pair of eyes) above other spot numbers (one or three), yet higher numbers of spots or spots of greater size (greater conspicuousness) increased survival. Finally, Stevens et al. (2009) tested the role of different orientations of spots, being horizontal (eyelike) or vertical (non-eyelike), and different spot colours including red and blue (warning and novel colours respectively, but rarely found in eyes) and yellow (often found in raptor eyes). They found no difference between any of these treatments. Overall, these experiments showed that continuously displayed spots can be highly effective in preventing predation (compared to unmarked controls). However, the results offered no support for the eye mimicry theory and were instead consistent with effects of visual salience or conspicuousness. Other experiments have shown that continuously displayed spots found on real butterflies are also effective in preventing bird attacks (Kodandaramaiah et al., 2009). However, as with the experiments of Vallin et al. (2005, 2007) above, Kodandara-

maiah et al. did not manipulate the form of the eyespots and so could not test for eye mimicry.

Many butterfly and moth eyespots have light patches somewhere near the centre of the feature. These highlights or 'sparkles' are often asymmetrical and have been suggested to mimic the patches of bright light reflecting back of the surface of eyes and to create a three-dimensional appearance of the eyespots. Recently, Blut et al. (2012) showed that such markings are common in lepidopteran eyespots and in most cases are found towards the top (towards the anterior) part of the eyespot. They also conducted predation experiments with artificial prey, similar to those of Stevens et al., and found that eyespots were more effective at deterring predators when they were larger, and when they had a conspicuous white 'sparkle' added. Blut et al. also found that the survival of the prey was higher when the sparkle component was on the top part of the eyespot, as opposed to other positions. They argue that light reflecting from the surface of eyes would normally occur on the top part of the eye, and so the eyespots are more effective when mimicking this. Therefore, if their argument about reflectance usually being on the top part of the eye is correct, then their experiments are consistent with the eye mimicry hypothesis. One thing to note is that white patches like this often reflect ultraviolet light very strongly, and have been shown to be important in mate choice in some butterflies (Robertson and Monteiro, 2005). Therefore, although not mutually exclusive with an anti-predator function, they may also be used in mate choice.

3 Eyespots on Insect Larvae

Compared to adult Lepidoptera, work on larval stages has so far been limited. Recent work by Hossie and Sherratt (2012), presenting artificial caterpillars made from dyed pastry to wild birds (Fig. 2), showed only a limited benefit of eyespots in preventing attack and that this advantage interacted with prey camouflage (countershading). Hossie and Sherratt (2012) suggested that eyespots improved survival on countershaded but not homogeneously pigmented models because the former could have been a more convincing snake mimic to birds. This idea was followed up subsequently by the same authors, who presented similar prey to birds, with or without eyespots, but this time with body shapes that were either cylindrical or widened at the posterior end in a manner akin to the defensive posture of caterpillars with eyespots and broadly resembling a snake's head (Hossie and Sherratt 2013). They found that both the

presence of eyespots and the widened head shape reduced avian attacks. However, there was no synergistic effect of these two modifications, which would be expected had the presence of eyespots contributed to enhancing any mimicry of snakes. The authors did not modify the characteristics of the eyespots (e.g. shape, contrast, number, and so on) and so it is hard to draw conclusions about whether such spots work due to mimicry or conspicuousness. These experiments could, nonetheless, afford a promising route to testing eye- and snake-mimicry in future, and one useful extension of the work would be to add in an element of behaviour to the models because many putative snake mimics also have behavioural traits that may enhance resemblance to snakes.

Finally, Hossie et al. (2013) describe two species of tropical caterpillar that can palpitate eyespots when approached or threatened. They suggest that this is a more advanced form of eye mimicry, resembling a blinking eye opening and closing. This is an interesting idea, and certainly warrants further investigation. However, one could also argue that the movement enhances the conspicuousness of the display.

4 Fear and Avoidance Responses of Animals to Eye-Like Stimuli

A range of studies, particularly in the 1970s and 80s tested how animals, especially birds, responded to cues that could convey the presence of a potential predator or threat. Such work presented subjects with stimuli that might indicate a predator and involved changing various features of these, such as the presence and type of eye-like objects. They found mixed evidence that animals respond to more eye-like features with enhanced avoidance behaviour or fear responses. Features used to identify the eyes of animals have generally thought to include circularity, pairedness, and horizontal orientation. However, as Scaife (1976a) points out, while these may be important in recognition they cannot be sufficient alone to recognise predators because this would not facilitate distinctions between predators and conspecifics.

Scaife (1976a) tested how domestic chicks responded to the presence of a threatening animal (a stuffed hawk) or a non-predatory species (a kiwi), with or without different looking eyes. Chicks avoided the predatory species more than the kiwi, and especially when the eyes were uncovered. In addition, putting hawk eyes (which Scaife 1976a suggests were more conspicuous than the other eyes) on the kiwi increased avoidance,

indicating that chicks were sensitive to both the presence and the specific appearance of the eyes. However, there was no difference in avoidance behaviour towards isolated pairs of circles or rectangles (both with a black 'pupil' and yellow surround), suggesting that when not paired with other predator features eye shape was not important. In a second study, Scaife (1976b) presented chicks with a range of three-dimensional stimuli in isolation (i.e. no model head), either singularly or in pairs, as circles or rectangles, and with gaze directions that either followed or looked away from the chicks. Here, all three stimuli types produced avoidance, but this was especially strong with a pair of circular tracking eyes. This suggests that chicks have heightened responses to more eye-like stimuli, even in isolation from other cues. However, why the results for shape here differed from Scaife (1976a) is unclear, and some aspects of the results are hard to disentangle from conspicuousness; for example, a pair of eyes presents a greater stimulus size than a single eye.

Jones (1980) presented chicks with a range of stimuli of varying similarity to eyes. In all experiments the stimuli were surrounded by a mask, superficially resembling part of a face and beak. First, he found that chicks showed greater avoidance behaviour and fear responses when presented with two circular eyes (with central dark 'pupils' and light surrounds) than one. As above, this could be due to increased stimulus area. However, Jones also found a lack of difference in response between a no-eye control and diamond shaped eyes, two vertical eyes, or three horizontal eyes; indicating that these stimuli were not responded to as eyes. The low response to three eyes suggests that stimulus number or conspicuousness alone was not important. Finally, Jones presented chicks with stimuli comprising circles either without a central pupil or as just the central pupil alone and no surround, or rectangular shapes with or without pupils. Again, it is difficult to draw clear conclusions about these findings because of the large differences in conspicuousness and contrast of the stimuli used. However, the results showed a general lack of effect of having stimuli without pupils, and, in particular, that rectangular stimuli were more effective than the other stimuli in eliciting avoidance (and akin to a pair of circular eyes in their effect). Therefore, the results of Jones (1980) study provide some results consistent with response enhancement towards more eye-like stimuli (two eyes avoided more than three) and some findings that are more consistent with conspicuousness (rectangular eyes avoided strongly).

Other studies have tested responses of birds to eye-like stimuli in different contexts. For example, Inglis et al. (1983) presented starlings with different eye-like stimuli in a foraging context that appeared when the birds landed on a feeding trough. As above, the results provided a mixture of support for both eye-mimicry and conspicuousness effects. On the one hand, starlings showed greater avoidance to stimuli with pupils and surrounds than towards simple circles alone. Pupil shape was not important but a circular outline was. Eyes with coloured irises were more aversive than black and white ones, but there was little effect of contrast. Conversely, increasing the number of eyes from one to three resulted in an increase in aversion, but this trend was not apparent when the eyes were surrounded by a head outline, in which case two eyes were avoided more. Furthermore, changing the orientation of the stimuli from horizontal to vertical had little effect.

In other taxa, Coss (1978) presented lesser mouse lemurs *Microcebus murinus* with stimuli comprising different numbers of circles (0–4) with a centre and surround, and measured gaze direction and time spent looking at the stimulus. Coss found that lemurs spent less time looking at stimuli with two spots than other numbers. In addition, lemurs spent less time looking at a horizontal pair of spots than spots arranged vertically or at a 45 degree angle. However, although these results are interesting, gaze aversion and avoidance is well known in primates and can be very important in social and dominance interactions (including in mouse lemurs; Coss 1978). Therefore, interpreting such results and applying them to the question of mimicry of the eyes of predatory threats is troublesome.

Overall, therefore, these studies can be taken to provide mixed support for both eye mimicry and conspicuousness. More specifically, they indicate that two aspects of context can be important in the way that animals respond to such stimuli.

First, the colours, patterns, and other features surrounding any eye-like stimuli may be key in driving a response (Scaife, 1976a). Similar findings regarding context and surrounding features have been found in tests investigating how fish identify and discriminate between cues that could indicate predatory and non-threatening species (Karplus et al., 1982). In the context of animal eyespots, this suggests that the presence of other features that mimic predators, in addition to eyes, may be important in causing prey animals to misclassify eyespots on Lepidoptera, fish, and other animals as eyes. Although such mimetic features on prey have been

suggested (such as avian beaks; e.g. Howse, 2013), there is no evidence as yet for such similarities (see above).

Second, the above studies imply that the behavioural context in which the eye-like features are seen is also important. When animals are already under heightened sensitivity to look out for predators, and are presented with other aspects of the predator, then they may respond to eyes. In other contexts then they may not actually respond to eye-like stimuli as if there is a predator.

Finally, it is important to remember that most of the above experiments were designed specifically to test how animals respond to the potential presence of a predator, and the cues that increase avoidance or fear responses. They were not set up to test whether other types of natural stimuli are effective by mimicking eyes. Therefore, the conclusions we can make from such work about eye mimicry are necessarily limited. All these factors mean that while eyes do seem to be an important feature that some animals are sensitive to, it is hard to draw clear conclusions about the implications of this for eye mimicry. In addition, the contextual responses of animals to eyes suggests that simply bearing circular eyelike markings may sometimes not be very effective in stimulating animals to classify them as eyes belonging to a predator. Given the apparent lack of any mimicry of other predator features in most animals with eyespots this could even be taken as evidence against eye mimicry. Nonetheless, the type of experiments described above, and akin to Olofsson et al. (2013) with chickens, may offer a useful avenue to test whether animals to respond to eyespots as eyes.

5 Conclusions and Future Work

In recent years there has been a wide range of studies aiming to test the eye mimicry theory, and hence whether eyespots really do work as a form of deception by providing misleading information about the identity of the animal that possesses them. However, although the study of Blut et al. (2012) provides some support for the theory, the majority of work is inconsistent with predictions of eye mimicry or not appropriately designed to discriminate between competing hypotheses. In contrast, several experiments have found consistently that conspicuousness is an important feature of eyespot effectiveness (for continuously displayed spots at least; see below). The key to providing strong support for eye-mimicry is to be able to show that more eye-like stimuli are better at promoting avoidance behaviour even when the level of visual conspicuousness is the

same or lower. At present, only perhaps the work of Blut et al. (2009) has done this, whereas the work of Stevens et al. (2007, 2008, 2009) has gone against the eye mimicry theory. Although work investigating fear and avoidance responses of animals to eyes is informative, so far it is hard to evaluate how relevant such work is to determining the mechanisms underlying eyespot function.

Regardless of this lack of evidence for eye mimicry, many authors implicitly adopt an approach that this theory is the null hypothesis that can be adopted in the absence of sufficient evidence to the contrary. However, we feel that a logical case for this privileged status has not been made. One might argue that parsimony suggests that in the absence of conclusive data the simplest explanation is to be preferred. In terms of the assumptions that must be made about the cognitive processes experienced by a predator in response to eyespots, it is not obvious that the eye-mimicry hypothesis is more parsimonious than alternatives (indeed it appears quite the opposite). However, given the challenges of studying the cognitive processes of non-humans we do not feel that arguments based on parsimony can provide a universally-accepted “default” explanation for predator responses to eyespots. Rather we would prefer to see researchers accept eye mimicry and other possibilities as currently equally valid alternative or complementary hypotheses. Further, as with any scientific theory, we should start from the basis that evidence needs to be found in favour of eye mimicry before this idea becomes accepted. However, even when a lack of evidence is found in favour of eye mimicry in experiments, many authors do not always take this conservative approach. An example of this was discussed earlier in the difference between the original authors’ interpretation of the experiments presented in Merilaita et al. (2012) and our own interpretation. A lack of objective and balanced treatment of the eye mimicry and alternative theories given current evidence (or lack of in the case of eye mimicry) by authors risks damaging scientific progress in this subject.

It is important to be clear that we do not dispute that some of the lepidopteran markings called eyespots have repeatedly been demonstrated to have a strong effect in delaying or aborting predatory attacks, and that mimicry of the eyes of predatory species is a plausible underlying mechanism for such an effect that should not be discounted. Our concern is that this mechanism has been prematurely adopted by many as the dominant or sole function of these markings. This leap of faith is

dangerous if it stifles research into this function and leads research on predatory-prey interactions down false trails. There has been a tendency for people to want to believe that the theory is true because it is a compelling and attractive idea. In order to discourage the perpetuation of this problem, it is important that scientists studying visual phenomenon in animal communication and camouflage are not overly swayed by the appearance of animals to them. The point has repeatedly been made that the receivers that have fitness consequences for animals, and that can select for visual traits, generally have very different visual and cognitive systems from humans; and it is essential that we make judgments based on our understanding of those non-human systems rather than our own. We do not take the view that the study of eyespots should entirely ignore the subjective perception of humans. Humans are primarily visual animals, and it would be a mistake not to use human perception as a way to stimulate ideas and identify potentially interesting case studies in the study of adaptive coloration generally. Further, there can be striking concordance between human and non-human observers, as in a study that demonstrated that humans and pigeons ranked different hoverfly species very similarly in terms of the fidelity of their mimicry of social wasps (Dittrich et al., 1993). However, while human perception can be a fruitful source of hypotheses on the evolution of anti-predator appearance traits, evaluation of those hypotheses must be based on the visual and cognitive systems of observers that better approximate those that would have imposed fitness pressures on the focal species concerned.

Clearly, more work is needed to resolve this controversy, and there is a range of further studies that could help. First, although the experiments of Stevens et al. (2007, 2008, 2009) are the only studies to date to systematically distinguish between the conspicuousness and eye-mimicry theories by using a wide range of stimuli types, their key limitation is that the spots were continuously visible. With a few notable exceptions, in most butterflies and moths, however, eyespots are often linked to a startle display (i.e. being triggered by close approach of a potential predator). Therefore, a logical extension is to repeat the general type of experiments and stimuli used in those studies, but present them in the form of a startle display (only being revealed in response to the close approach of a potential predator). Note, however, that many fish eyespots are continuously visible. In addition, work on the deflective function of eyespots has sought to test whether they work at

all, and has not so far considered the mechanisms as to why they might work. Whether eye mimicry is a valid mechanism for this (perhaps attracting predators to peck at the eyes of their prey) is at the moment unknown.

Further field experiments such as those undertaken by Hossie and Sherratt (2012, 2013) would be valuable given that little work has tested eyespot function in insect larvae. Here, two main approaches would be useful. First, it would be important to manipulate the form of the eyespots to alter their level of eye mimicry and conspicuousness and measure how this affects survival. Second, although challenging, it would be valuable to incorporate behaviour into the prey to test if they really do mimic snakes (see above). Likewise, almost all experiments investigating eyespots and intimidation have been done in terrestrial systems. Yet, eyespots are also common in fish too. One recent study by Kjærnsmo and Merilaita (2013) investigated whether stickleback fish *Gasterosteus aculeatus* would attack broadly camouflaged rectangular artificial prey when marked with a large eyespot. However, they found no difference in attack latency for prey with and without the spot. Therefore, whether intimidation works in aquatic systems, and why, awaits further work. The kind of 'sparkle' or reflectance patches that occur on eyes of terrestrial species should not occur in aquatic systems, and as such we would not expect eyespots in fish to have highlights. However, to our knowledge this has not yet been tested.

As we have discussed above, there have been a wide range of aviary studies testing the function of real eyespots on prey. These either present birds with live prey (able to produce startle responses) or dead prey or prey parts. However, although these experiments demonstrate that eyespots work, they do not test how. To distinguish between eye mimicry and conspicuousness effects, it is essential that future work investigating responses of birds, including latency to attack and putative alarm calls, is undertaken with prey with eyespots that have been carefully modified to change their resemblance to eyes and/or their conspicuousness. We admit that design of stimuli that vary in their resemblance to eyes to an ecologically-relevant non-human observer is a non-trivial challenge, but the study mentioned previously where pigeons could consistently rank hoverfly on the fidelity of their mimicry of social wasps suggests that such an undertaking should not be impossible.

The work of Stevens et al. (2007, 2008, 2009) and Hossie and Sherratt (2012, 2013) used artificial stimuli

that did not directly or closely mimic any real species. This has the advantage that any effects can be broadly generalised and used to understand general principles of eyespot function, whereas with real species is harder to apply principles beyond that animal. Conversely, the stimuli are relatively artificial and lack many of the other features and body coloration that real species have, and so the effects of this cannot easily be explored. As Hossie and Sherratt (2012) point out, many eyespots in the natural world only vaguely resemble real eyes to human observers. Close resemblance to eyes may not be needed if a predator has to make a rapid decision or has to evaluate a large amount information or complex stimulus, such as in a startle display (Janzen et al., 2010; Howse, 2013). However, it is nonetheless somewhat ironic that many of the experiments testing eye mimicry have been undertaken on peacock butterflies, a species with eyespots that (subjectively to humans) deviate considerably in shape, colour, and symmetry from real animal eyes. Therefore, experiments might also usefully be done manipulating the eyespot form of species that (to ecologically-relevant non-human observers) more closely resemble vertebrate eyes.

It seems likely that in species like the peacock butterfly (or, for example, the eyed hawk moth, which has red and blue colours in its spots), where aspects of the mimicry appear to our eyes poor, conspicuousness must be a valuable feature of markings even if eye mimicry is also important. Otherwise, why would species use such bright and elaborate colours that are rarely present in predatory eyes? As discussed above, the eye mimicry and conspicuousness theories are not mutually exclusive, and it is possible that a broad resemblance to eyes is important, but that the predator response is enhanced by greater conspicuousness beyond the mimicked stimulus; a supernormal stimulus stemming from sensory exploitation (Stevens, 2013).

Following the above, little work has as yet directly quantified the appearance of eyespots and compared them to real eyes. One study on fish has used multidimensional morphometric analysis of facial features of fish to investigate which cues could facilitate predator recognition, and found some evidence that eyespots on some fish species resemble the eyes of predatory fish (Karplus and Algom, 1981). Further studies along these lines would be valuable and could usefully be done with image analysis techniques, or even perhaps using artificial neural networks. However, there would be two particular challenges here requiring careful thought. First, a suitable null comparison would be needed to test mimi-

cry against. This would need to be carefully chosen so not to bias the result. Second, the actual species' model whose eyes the eyespots mimic needed to be identified. This could be challenging, especially in tropical systems. Furthermore, it is possible that eyespots may be imperfect mimics, or resemble the eyes of multiple species and be a compromise in form between the appearance of all of those (Stevens, 2005).

Eyespots remain one of the most widely studied features of animal coloration, having been frequently used to test not just anti-predator defences, but also genetics and developmental biology, developmental plasticity, and sexual signalling. Despite much work on them, we are still some way off truly understanding why they work and why they are so diverse.

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