# Eyespots

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Synonyms: Ocellus, Ocelli

Definition: Animal color patterns consisting of roughly concentric rings of contrasting colors.

## Introduction

Eyespots are animal color patterns consisting of (roughly) circular, often concentric rings of contrasting colors. Eyespots have received their name because (at least to humans) they often resemble the vertebrate eye. Eyespots are common in many terrestrial (land-living) animals such as insects (particularly in larval and adult moths and butterflies), birds and reptiles, but they are also widespread in many aquatic animals such as mollusks, flatworms and fishes (Poulton 1890). Eyespots are highly variable in appearance and occurs in a variety of sizes, number and color combinations. Laboratory studies on butterflies has shown that the processes that explains development of eyespot patterns are relatively simple, and that it requires only one, or at least very few changes in the regulatory genes to change the position, color and number of eyespots (Brakefield et al. 1996). This suggests in turn that the evolution of eyespots can occur relatively fast.

Because of their appearance and widespread occurrence in the animal kingdom, the function of eyespots have intrigued naturalists and biologists for more than a century (e.g. Poulton 1890). In some animals, eyespots may play a role in intraspecific (within species)

communication or reproductive signaling (Robertson & Monteiro 2005). For example, eyespots of the butterfly *Bicyclus anynana* has proven to be an important signal in mate selection, as females of this species prefer males with larger UV-reflective spots (the center of their eyespots) (Robertson & Monteiro 2005). Another, classic example is the Indian peafowl (*Pavo cristatus*), where the females are attracted to males with more eye spots on the tail. Although these examples show that the eyespots in some species are important in mate choice, eyespots are most well-known for their protective function against predators. There are two hypotheses that have been put forward to explain how eyespots in prey protect against predators: 1) *the diversion hypothesis* (also called the *deflection* hypothesis) and 2) *the intimidation hypothesis*.

*The divertive (deflective) effect of eyespots*

The common occurrence of (generally small) eyespots found on the wing margins of many moths and butterflies, as well as eyespots located on the caudal area in some species of fishes has been explained by the divertive function of such eyespots (Poulton 1890; Blest 1957). According to the diversion hypothesis, eyespots serve to direct the strikes of attacking predators towards less vital or defended parts of the prey body, or towards a direction that would facilitate prey escape (Blest 1957; Kjernsmo & Merilaita 2013). For example, in a study using yellow buntings (*Emberiza citrinella*) as predators, and mealworms (*Tenebrio molitor*) with a simple spot painted onto them as prey, Blest (1957) argued that the birds directed their attacks towards the eyespots, although firm conclusions could not be drawn as his study was not scientifically sound. However, some empirical evidence for the divertive effect of eyespots has been revealed recently in study systems using passerine birds as predators, and butterflies that have marginal eyespots as prey (Olofsson et al. 2010). Olofsson and others showed that the marginal eyespots of the woodland brown butterfly (*Lopinga*

*achine*) drew the attacks of blue tits (*Cyanistes caeruleus*) towards the eyespots, but only under specific light conditions where the UV-intensity of the light was high, and the intensity of longer light wavelengths were low (Olofsson et al. 2010). Many species of fish have eyespots located near of in the area of their caudal fins, and these spots have been shown to misdirect attacks from predatory fish (Kjernsmo & Merilaita 2013; Kjernsmo et al. 2016). The mechanisms behind the divertive effect, at least in the case of fish, may be because the specific shape of eyespots resemble the real eye (eye-mimicry), and confuses the predator (Kjernsmo et al. 2016).

*The intimidating effect of eyespots*

Another possible anti-predator function of eyespots that has been invoked to explain their existence in some prey is predator intimidation (Poulton 1890, Blest 1957). According to the intimidation hypothesis, generally large eyespots (for example those found in many species of butterflies and moths) could serve to intimidate potential predators, subsequently thwart, delay or otherwise prevent an attack from being successful. Recent studies have provided support for the intimidating effect of eyespots against passerine birds (Vallin *et al.* 2005; 2007; Stevens *et al.* 2007; Olofsson *et al.* 2012; De Bona et al. 2015). However, the question why some eyespots intimidate predators has so far been unresolved and debated. Two main hypotheses for the intimidating nature of eyespots have been proposed. The first is that eyespots resemble the eyes of the predator's own enemy (Poulton 1890; Blest 1957) and hence suggest the presence of a potential threat. The other is that the high conspicuousness of eyespots is a property that intimidates (Blest 1957; Stevens *et al.* 2007). Some studies has provided indirect evidence for the idea that predators might associate eyespots with the threat posed by their own enemies. For example, in a study using the domestic fowl as predator and the peacock butterfly (*Aglais io*) as prey showed that when the birds were exposed to

butterflies with intact eyespots, they were more vigilant and elicited more alarm calls than those that were exposed to butterflies that had their eyespots painted over (Olofsson et al. 2012).

## Conclusions

Even though eyespots in some species are involved in mate choice signaling and intraspecific communication, the existence of eyespots in many prey species can be explained though their protective function against predators. Some, indirect evidence suggests that eye mimicry (the similarity between the eyespot to real eyes) may be an important factor contributing to the extraordinarily wide occurrence of the eyespot pattern.

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