

Significance of butterfly eyespots as an anti-predator device in ground-based and aerial attacks

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Many butterfly genera are characterised by the presence of marginal eyespots on their wings. One hypothesis to account for an occurrence of eyespots is that these wing pattern elements are partly the outcome of visual selection by predators. *Bicyclus anynana* (Satyrinae) has underside spotting on its wings but there is also a seasonal form in which the eyespots are reduced in size or totally absent. This natural variation gives us a useful tool to test the hypothesis that marginal eyespot patterns can decoy the attacking predator by, at least sometimes, diverting attack from vital body parts to the edges of the wings. We used lizards, *Anolis carolinensis*, and pied flycatchers, *Ficedula hypoleuca*, as predators for living spotted and spotless *B. anynana*. The presence of eyespots did not increase the escape probability of resting butterflies once captured (even a form with enlarged eyespots did not add to effective deflection of attacks). There was also no evidence that eyespots influenced the location of strikes by the predators. This study thus provides no support that marginal eyespot patterns can act as an effective deflection mechanism to avoid lizard or avian predation.

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Many Lepidoptera possess eyespot patterns on their wings. Some butterflies have large, conspicuous eyespots that are concealed at rest and only exposed when the insect is disturbed by a potential predator. The sudden appearance of “a pair of eyes” frightens or confuses the attacking predator so that a prey has an opportunity to flee (Blest 1957). But when eyespots are on the ventral surface of the wings, usually towards the margins of the wings, and visible continuously in butterflies at rest, they are assumed to have a different function in avoiding predation by misdirecting the attacks of predators. Eyespots can then draw the attention of a predator towards themselves: instead of attempting to strike at the body of a prey, the predator directs its capture attempts to the marginal eyespots (Blest 1957, Wourms and Wasserman 1985, Brakefield and Reitsma 1991). In this scenario, when a predator

grabs a butterfly by its wings, it may manage to break free with its body intact, albeit having lost part of its wing tissues.

Beak marks on butterflies' wings have frequently been regarded as evidence of unsuccessful predator attacks (Bowers and Wiernasz 1979). Bengtson (1981) scored the beak mark frequencies on the wings of *Maniola jurtina* in which both sexes show variation in spot-number on the hindwings. He reported relatively higher frequencies of butterflies with such wing damage in *M. jurtina* individuals with eyespot pattern than without them when the intensity of predation was high. The opposite was true when predation pressure was low. The author suggested, nevertheless, that birds might influence spotting. Additionally, Wourms and Wasserman (1985) have provided some experimental evidence that eyespots would be advantageous. They

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painted spots (0.5 cm in diameter), stripes, or tails and combinations of these markings on the wings of dead *Pieris rapae*. The butterflies were presented to blue jays and the handling of the prey was analysed. Birds directed a greater proportion of pecks to wings bearing an eyespot than spotless ones. If wings had no eyespots, attack and handling strikes were aimed at the head of the butterfly and thus were lethal. The other wing markings used were not effective in deflection.

In some Satyrinae species, notably those of the African genus, *Bicyclus*, wet season individuals have conspicuous ventral wing eyespot and band markings while in dry season forms these markings are lacking (Brakefield and Larsen 1984) (Fig. 1). It has been hypothesised that the observed variation in eyespot pattern might be influenced by predation (Brakefield 1984, Brakefield and Larsen 1984, Brakefield and Reitsma 1991). If butterflies had visible wing markings in the dry season, they would stand out against the brown environment disrupting crypsis and making butterflies more vulnerable to visual predation. On the contrary, the wet season butterflies are considered to derive advantages from their highly visible markings. The conspicuous eyespots are thought to act as deceptive or deflective patterns for predators increasing escape probability.

The two important vertebrate predators of adult butterflies are lizards (Young 1980, Larsen 1982, Brakefield and Reitsma 1991) and birds (Dempster 1984). There are, however, conflicting results of their role as a predator for butterflies and their impact on butterfly wing markings. Brockie (1972) studied the relationship between the frequencies of the wing damages caused by lizard's attack and the number of spots in *Maniola jurtina* (Satyrinae). He found no indication that lizards would attack these phenotypes differently and thus he rejected the possibility of the importance of lizard predation in the evolution of butterflies' wing patterns. On the contrary, Brakefield and Reitsma (1991) found indications of a higher proportion of wing damage in *Bicyclus safitza* caused by lizard attacks than by birds. These dissimilar results may reflect seasonal or geographical differences in the predation pressure or in the predator species composition. Anyway, there are indications that lizards (Boyden 1976) as well as birds (Kettlewell 1955) might influence the wing colour patterns of butterflies.

There has been no empirical research to determine whether the presence of the eyespots influences the position of initial strike or, more importantly, the potential of the butterfly to escape predation. Previous fieldwork has mainly analysed the influence of wing markings by comparing the frequency of beak marks on different areas of wings (Robbins 1981, Dennis et al. 1986, Tonner et al. 1993) or on different phenotypes of the same species (Bengston 1981). Eyespots might not be the only factor affecting the observed pattern, for

example, Edmunds (1974) has pointed out that the difference in the incidence of beak marks might arise from a difference in flight ability.

To test the deflection hypothesis, we compared the survival of the spotless dry season form and spotted wet season form of *Bicyclus anynana* and examined the target of initial strike. We used two model predators: lizards (*Anolis carolinensis*) and pied flycatchers (*Ficedula hypoleuca*) that are visually hunting insectivorous predators. The live butterflies were presented to them whilst feeding on a piece of banana slice such that any possible differences in the behaviour between butterfly forms could not influence the result.

Materials and methods

Lizard predator

Anolis carolinensis is a small (snout to tail length 14.5 ± 0.5 cm, weight 2.9 ± 0.3 g), insectivorous lizard and a member of a family Iguanidae. Its natural ranges are the south-eastern United States, Bahamas, and Cuba. Wild-caught lizards were obtained from pet-shops and brought to the laboratory at Leiden University.

Lizards ($n = 16$) were kept in a group of four (3 females and 1 male) in enclosures ($32 \times 45 \times 58$ cm) which were placed in a room maintained at 25°C , 70% humidity, and under photoperiod 16h:8h light:dark. Every second day lizards were fed with buffalo worms and *B. anynana* caterpillars, which were lightly dusted with a vitamin or mineral supplement. Water was misted on to the leaves of plants daily and was also continuously available in a shallow dish.

Bird predator

Pied flycatchers (*Ficedula hypoleuca*) are small passerine birds that feed on insects and other arthropods catching them in the air, from foliage, or from the ground. The species nests in northern and central Europe and overwinters in West Africa.

We trapped the birds in Konnevesi, Central Finland and put them into illuminated cages ($65 \times 80 \times 65$ cm) where they were maintained on the diet of mealworms and water ad libitum. The experiment was conducted in June 2001 at the Konnevesi Research Station. After the experiments, we released all birds.

Bicyclus anynana

Bicyclus anynana (Satyrinae) shows variation in number, size, shape, colour composition, and position of eyespots (Brakefield and French 1999). For its natural



Fig. 1. Ventral wing surfaces of *B. anynana*, illustrating the spotless dry season form, the spotted wet season form, and the *Bigeye-comet* mutant.

range, in central Africa, an alternation of warm, wet and cool, dry seasons is characteristic. The larvae respond to high or low rearing temperatures by developing the spotted or spotless wings of the adult, respectively (Brakefield and Larsen 1984, Brakefield and Reitsma 1991). The wet season form has seven eyespots on its hindwings and two on its forewings (Fig. 1). In the dry season form these eyespots are reduced in size or totally absent, the wings being uniformly brown. Furthermore, the resting butterfly covers the posterior forewing spot with its hindwings. In addition, we used a double mutant line, *Bigeye-comet*, in which all the eyespots are larger in size than in the wet season form. Eyespots are on the underside of wings and are thus (potentially) visible when the butterfly is flying and when at rest with closed wings.

The comparisons of escape probabilities in different *B. anynana* forms

I. Experiment with lizards

Lizards ($n = 16$) were housed over night before the experiment to become familiar with the experimental cage ($94 \times 124 \times 87$ cm). The bottom of the cage was covered with green leaves of *Prunus laurocerasus* amongst which feeding butterflies were at rest. Thus, each butterfly form was equally visible (at a distance) against the background. To motivate the butterflies to feed on a banana slice, they were deprived of food for 24 hours prior to the feeding trials.

To test whether eyespots affect the escape probability of butterflies after the attack, three forms (spotless, spotted, *Bigeye-comet*) of *B. anynana* differing in eyespot pattern, were placed one at a time on the slice of banana into the cages in the presence of a lizard. Each lizard received as many butterflies as they ate during each day and thus the total number of butterflies, which lizards received, varied between 12 and 28. To minimise the possibility that lizards increased their success rate in catching butterflies with experience, the morphs were presented in random order. We counted the number of successful captures, butterflies that escaped after initially being caught, and escapes without contact. For

the statistical test, we used mean values of escape probability. On the basis of videotapes, the target of attack (body vs wings) was analysed.

II. Experiment with birds

To test whether eyespots act as decoys for an avian attack, butterflies were also introduced to pied flycatchers. The experiment was conducted in an aviary (13.3 m^2 , height 2.5 m) under lighting conditions corresponding to the natural daylight (4 pulps of Spiral light 20 W and 4 True-Lite 18 W fluorescent tubes). In the middle of the room, there was a pole (height 103 cm, diameter 10 cm) covered with leaves of *Sorbus aucubaria*. One spotless and one spotted butterfly, which were matched by weight, were placed sequentially on the slice of banana on the top of this pole. Half of the birds ($n = 10$) received first the spotless butterfly followed by the spotted one and for the other half ($n = 11$) the order was reversed. Birds were provided with a perch that was slightly higher than the pole. The experiment was video recorded to analyse the target of the attack.

Results

I. Experiment with lizards

A. carolinensis ($n = 16$) did not seem to have any difficulty in capturing, chewing, or swallowing the butterfly once they had noticed the prey. After the detection, which usually required movement of the butterfly (i.e. changing its position on the banana slice), the lizard slowly approached on the ground close to the butterflies and then jumped towards it attempting to grab it with open gape. Total number of attacks on spotless forms was 213, spotted 210, and *Bigeye-comet* 211. The proportion of attacks (per each lizard) that resulted in wing tear and escape was equal in all three forms (Friedman test: $\chi^2 = 1.654$, $df = 2$, $p = 0.437$) (Table 1). If the butterfly was caught by all its four wings, it did not survive the attack. Examples of wing damages caused by unsuccessful attacks were mostly on the hindwings (spotless 86.4%, spotted 72.3%, *Bigeye-comet* 84.2%). Furthermore, the proportion of butter-

Table 1. The fate of butterflies (% ± SE) and the proportion of initial attacks (% ± SE) that lizards (n = 16) directed to the wings in spotless, spotted, and *Bigeye-comet* butterflies. The second row in “The target”-column indicates the proportion of butterflies that were grabbed by their wings but survived.

Butterfly form	The fate			The target
	Eaten	Escaped with wing damage	Escaped without contact	Wings
Spotless	58.7 (± 2.87)	9.9 (± 2.30)	31.4 (± 2.16)	65.7 (± 6.45) 15.8 (± 4.49)
Spotted	59.8 (± 3.99)	7.3 (± 1.60)	32.9 (± 3.94)	76.1 (± 4.19) 10.7 (± 3.35)
<i>Bigeye-comet</i>	56.2 (± 4.48)	11.1 (± 2.20)	32.7 (± 3.87)	68.8 (± 4.93) 17.1 (± 3.96)

flies that survived an attack when a lizard grabbed it by the wings did not differ among the different butterfly forms used (Friedman test $\chi^2 = 2.423$, $df = 2$, $p = 0.298$).

To test whether lizards improved their capture success during the experiment, we calculated the number of unsuccessful (= butterfly escaped from lizard’s mouth) and successful attacks among the first and last ten attacks. The number of unsuccessful attacks was then divided by the total number of attacks ignoring those which resulted in escape without contact. The difference of the proportion of unsuccessful attacks among the ten first and last attacks was used as an indicator of change. The comparison indicates that the escape probability did not change (Friedman test: $\chi^2 = 0.051$, $df = 2$, $p = 0.975$). Taken together, the results provide no evidence that eyespots effectively deflect the attacking lizard, and the lizards did not learn to catch the butterflies more effectively during the experiment.

This conclusion is supported by the analyses of the target of the attacks. In a few cases the lizard blocked the view of the observer and thus the position of all strikes could not be analysed. In total, 119, 123, and 128 attacks were observed on spotless, spotted, and *Bigeye-comet* butterflies, respectively. Lizards attacked more often at the wings than the body in each butterfly phenotype (Table 1) (t-test: spotless $t = 2.428$, $p = < 0.028$; spotted $t = 6.237$, $p = 0.001$; *Bigeye-comet* $t = 3.822$, $p = 0.002$; $n = 16$). The proportions of the attacks directed to the wings did not differ significantly between the three forms (Friedman test: $\chi^2 = 2.207$, $df = 2$, $p = 0.332$) (Table 1). Thus there was no evidence that eyespots deflected the attacks towards the edges of the wings carrying these markings. The proportions of

initial strikes delivered at the wings among the ten first attacks were subtracted from the corresponding proportion among the ten final attacks. To test whether lizards changed their catching behaviour depending on butterfly form, we compared the calculated change between three butterfly forms. The result indicated that the target of attacks did not change (Friedman test: $\chi^2 = 0.974$, $df = 2$, $p = 0.614$).

The proportions of butterflies that were able to escape without injuries did not differ across the three wing pattern forms suggesting that there were no important differences in activity or behaviour (Friedman test: $\chi^2 = 0.246$, $df = 3$, $p = 0.884$).

II. Experiment with birds

Eyespots did not lead to a higher probability of escape of butterflies from the birds once captured (Wilcoxon signed-rank test: $z = -0.632$, $p = 0.527$, $n = 21$). Out of 21 attacks on each form, 8 and 6 escapes were recorded in spotless and spotted *B. anynana*, respectively (Table 2). Most of the initial strikes, which resulted in beak marks, were aimed at hindwings (spotless 5, spotted 3). Birds tended to improve their catching skills. Only five butterflies that were presented second in the pair were able to escape while the corresponding number with the first was nine.

Pied flycatchers ($n = 21$) attacked equally often the wings in both butterfly forms (8 and 8, respectively; with in five cases the bird blocking the view of the observer, Table 2). Birds preferred the wings to the body as a target for an attack independently of whether wings possessed eyespots or not (t-test: $t = 2.236$, $p = 0.041$, $n = 16$, for both forms).

Table 2. The fate of butterflies and the targets of attacks (%) by pied flycatchers (n = 16) as predators.

Butterfly form	The fate		The target	
	Eaten	Escaped with wing damage	Wings	The body
Spotless	61.9	38.1	75.0	25.0
Spotted	71.4	28.6	75.0	25.0

This was true whether butterflies were presented as the first (15 cases) or as the second (12 cases) individual in the pair. Thus, eyespot pattern did not deceive pied flycatchers to attack to the wings instead of the body.

Discussion

We did not find eyespots to be advantageous to butterflies when the attack came from the ground level or from above. In neither experiment did eyespot patterns increase the escape probability of butterflies once captured. Only a few butterflies succeeded in breaking free from the predator's grasp. With each predator, nearly all examples of wing damage resulted from attacks to hindwings. This is expected from ground-based attacks, or those from the rear of the butterfly (Young 1980). Furthermore, hindwings are fragile and the outer margins of wings break easily when grabbed (Robbins 1980, DeVries 2002), which is thus likely to help prey to survive an attack. If a predator catches the butterfly by all its four wings pinning these together, a butterfly has little chance to escape (Robbins 1980). In fact, none of these butterflies survived in the present experiment. Additionally, damage to forewings is likely to be more disadvantageous since this impairs the ability to fly (Dennis et al. 1984).

Contrary to expectation, the proportion of initial strikes aimed at wings was roughly equal irrespective of whether butterflies possessed eyespot patterns or not. Furthermore, the wings were always the most preferred targets for an attack. The absence of any decoying effect of spotting was surprising since there are indications that eyespot markings are advantageous to prey. Blest (1957) painted eyespots on mealworms and presented them to birds. He found that the highest proportion of pecks were aimed at the spots. Also Wourms and Wasserman (1985) reported that eyespots attract the pecking of birds and thus eyespots might be beneficial to butterflies.

Because of the multiple presentation of butterflies, there is a risk that predator's efficiency would have increased with experience. Lizards' capture success did not change during the experiment while birds seemed to improve slightly their success rate in catching butterflies. The change in capture efficiency was, however, totally independent of the wing pattern of a butterfly. Furthermore, there was no shift from the wings to the body as a location of attack points. It is, thus, unlikely that learning had any effect on the results.

Eyespots of *B. anynana* consist of white inner pupil surrounded by a black, and an outer gold ring, which appear to highlight the pupil. Anolis lizards have high-acuity diurnal vision (Fleishman 1992) with two foveas (Fite and Lister 1981) but their sense of odour is less well-developed (Cooper 1989). Therefore, *A. carolinensis*

utilises mainly its vision in prey detection (Fleishman 1992). The *Anolis* retina possesses four classes of cones, each of which contains a particular colour of oil droplet, with absorption maxima at about 365, 450, 495, and 565 nm (Fleishman et al. 1993). Furthermore, *A. carolinensis* has a broad field of view and has been suggested to be able to perceive prey over long distances (Fite and Lister 1981). Taken together, there are similarities between the structures of the *Anolis* and avian eye (Fite and Lister 1981). Thus eyespots on wings should be striking enough to be perceived by lizards as well as birds.

A. carolinensis is an arboreal, sit-and-wait predator (Nunez et al. 1995) which detects insects primarily from their motion (Fleishman 1992). Lizards can reach a sprinting speed of 1.2 m s^{-1} (Losos and Irschik 1996) and are capable of leaping into the air to catch flying insects (T. W. Schoener cited in Moermond 1981). Pied flycatchers catch insects in the air but prefer to snatch them from the ground or vegetation (Lundberg and Alatalo 1992). Both model predators are insectivorous but not specialised to catch butterflies. Even if, the ranges of *A. carolinensis* and pied flycatchers do not overlap with that of *B. anynana*, the use of selected species as model animals is relevant because marginal eyespot patterns are widespread in butterflies. Furthermore, there are many genera of satyrine butterflies in the neotropics with very similar wing patterning to *Bicyclus*. We emphasise here that the goal of our experiment was to test whether eyespots in general can function as an anti-predator device by deflecting at least some attacks by predators, and not only to explain their occurrence in *B. anynana*.

In our experiments, lizards and birds preyed upon butterflies which were at rest or feeding on a banana slice, and hence the possible differences in activity levels or escape efficiency of butterfly forms did not influence the results. This was indicated by the equal proportions in each form that were able to escape by flight before contact with lizards. Furthermore, the situation was natural for *B. anynana* that flies close to the ground level and feeds on fruit falls in nature. Thereby the experiment tried to imitate, as closely as possible, the field conditions and also to test Young's hypothesis. Young (1979) proposed a hypothesis to account for the presence of eyespots on the undersides of wings in *Morpho* butterflies feeding on rotten fruits on the ground and the lack of these markings on the wings of those butterflies feeding arboreally. He suggested that on the forest floor, butterflies are more likely to encounter a potential predator and thus, eyespots would give additional protection by misdirecting attacks. Frequent damage to both left and right wings suggests that butterflies are indeed more vulnerable to predation while settled on the vegetation or ground than while flying (Muysshondt and Muysshondt 1976, Shapiro 1977,

Young 1980, Larsen 1982, Dennis et al. 1986). However, we found no support for Young's hypothesis.

We suggest two possible alternative hypotheses to account for the occurrence of spotted and spotless butterfly forms. Firstly, spotting might be more effective in decoying attacks when both the butterfly and the bird are flying. A bird probably has less time to observe the prey and to decide the target of attack. Thus, eyespots might deflect attacks whilst both parties are on the wing. Secondly, in the case of *B. anynana*, the phenotypically different dry and wet season forms might reflect differences in the intensity of predation between seasons (Cott 1940). It is expected that relative predation pressure per prey individual is stronger in the dry season than in the wet season even if the total number of predators in a given area is higher in the wet season. The scarcity of alternative prey might therefore cause a strong predation pressure that favours crypsis. This is because under severe predation pressure prey animals need the most effective protection which in this case is likely to be crypsis. Spotless butterflies, which rest on brown litter, are indeed highly cryptic. In the wet season a wider variety of prey animals is available to predators that may lead to the less intense predation compared to the dry season situation. If this is true, butterflies could afford to wear more conspicuous wing patterns, which might be important, for example, in intraspecific communication. Recently, dorsal eyespot patterns have been shown to be a sexually selected trait in *B. anynana* (Breuker and Brakefield 2002) and thus, it could be possible that more conspicuous ventral eyespots would also have a sexually selected value. This hypothesis, however, has to be tested with a separate experiment. In the dry season the bare, brown leaf litter and vegetation forms a background where any colours and ornaments may stand out conspicuously, whereas in the wet season fresh, green vegetation forms a complex background where ornaments and signals are still relatively cryptic. Additionally, a pale medial band on the ventral wings of the wet season morph may function to disrupt the outline of the butterfly rendering it more cryptic (Brakefield and Larsen 1984). This kind of linkage between prey coloration and changes in predation intensity has previously been supported by field observations and experiments on guppies in which natural selection is known to favour crypsis under severe predation pressure, and when predation relaxes conspicuous coloration is favoured through sexual selection (Endler 1978, 1983). Further experiments are required to test these alternative explanations in more natural situations.

In contrast to our result, Wourms and Wasserman (1985) found a significant advantage of possessing eyespot pattern. Because of their use of dead specimens they could analyse only the point of initial strikes but not whether eyespots influence on the success of avian attacks on butterflies. Since it is the occurrence of

unsuccessful predation attempts that affects the evolution of anti-predatory traits (Vermeij 1982), spotting should enhance the escape possibility of detected and attacked butterflies compared to spotless individuals to be an effective anti-predator mechanism. Our experiment, however, demonstrated that there is no such benefit, at least under the conditions in our observation cage. Eyespots might carry a higher selective advantage when the insect encounters a naïve predator (Blest 1957), which has not yet learnt to grasp the body instead of the outer wing margins or hindwings that are apt to break allowing the butterfly to escape (DeVries 2002). This might create sufficient selection pressure to favour spotting. It is also possible that the deflective function of eyespots manifests itself only under very specific conditions that could involve background patterning, light conditions and attack distances. Thus one possible explanation for the failure to detect the selective advantage of eyespots might be the specific conditions of our experiments; although we tried to design the experiments accordingly, they might not have been favourable for sufficiently frequent expression of the deflective function of eyespots for us to be able to detect its effectiveness. However, our study provides an attempt to detect deflection of predator attacks by marginal eyespots in live butterflies, but more work is necessary to either find support under other conditions or to provide evidence for an alternative hypothesis involving some balance between crypsis and sexual selection.

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