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Anne Lyytinen

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Editors
Jukka Särkkä
Department of Biological and Environmental Science, University of Jyväskylä
Pekka Olsbo, Marja-Leena Tynkkynen
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ABSTRACT

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Insects utilise a wide variety of defence coloration including crypsis, aposematic coloration, and deflection patterns. The traditional view is that animals can maximise their cryptic coloration only on one background. I demonstrated experimentally that a compromised coloration could confer equal protection in two visually different habitats where its wearer survived altogether better than perfectly cryptic forms. Contrary to the cryptic coloration, conspicuousness is the essence of aposematic coloration and it is this character that provides the advantage of reduced predation risk through predator learning. Experiments on this intensively studied subject (and prey detection in general) have mostly ignored the fact that vision of birds, which are important predators on insects, is based on at least four colour receptors ranging from ultraviolet to red. I conducted a series of experiments to test whether UV cues alone can signal unpalatability. I did not find strong evidence that UV cues alone would function effectively as aposematic signals, but on the contrary they increased the predation risk. Our knowledge on aposematism and other defence mechanisms are largely based on experiments in butterflies. Pieridae butterflies have been regarded to exemplify the Müllerian mimicry concept. I did not, however, find support for the idea that their white coloration would signal unpalatability. Many Lepidoptera species do not rely on warning or cryptic coloration as their defence mechanism but they possess conspicuous eyespots on their wings. Eyespots are hypothesised to increase the likelihood of escape of the detected butterfly by deflecting attacks away from the body. I compared the rate of successful escapes between spotted and spotless butterflies under laboratory conditions using lizards and birds as predators. The two butterfly forms did not differ in their survival rate and thus predation hypothesis cannot solely explain the occurrence of spotting.

Key words: Aposematism; butterfly eyespots; crypsis; defence mechanisms; mimicry; ultraviolet reflection; wing patterns.

A. Lyytinen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40351 Jyväskylä, Finland

Author's address

Anne Lyytinen
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FIN-40351 Jyväskylä, Finland
e-mail: alyytine@dodo.jyu.fi

Supervisors

Professor Johanna Mappes
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FIN-40351 Jyväskylä, Finland

Academy professor Rauno V. Alatalo
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FIN-40351 Jyväskylä, Finland

Reviewers

Professor Veijo Jormalainen
Department of Biology
Section of Ecology
University of Turku
FIN-20200 Turku, Finland

Dr. Candy Rowe
Department of Psychology
Ridley Building
University of Newcastle
Newcastle upon Tyne, NE1 7RU, UK

Opponent

Professor Juha Tuomi
Department of Biology
University of Oulu
P. O. Box 333
FIN-90571 Oulu, Finland

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals. I have personally written papers II, III, IV and V and performed large part of the work. In paper I I have performed a significant proportion of the work.

I Merilaita, S., Lyytinen, A. & Mappes, J. 2001. Selection for cryptic coloration in a visually heterogeneous habitat. - Proceedings of the Royal Society of London (series B) 268: 1925-1929.

II Lyytinen, A., Alatalo, R. V., Lindström, L. & Mappes, J. 2001. Can ultraviolet cues function as aposematic signals? - Behavioral Ecology 12 (1): 65-70.

III Lyytinen, A., Lindström, L. & Mappes, J. Ultraviolet reflection and predation risk in diurnal and nocturnal Lepidoptera. (Submitted)

IV Lyytinen, A., Alatalo, R. V., Lindström, L. & Mappes, J. 1999. Are European white butterflies aposematic? - Evolutionary Ecology 13: 709-719.

V Lyytinen, A., Brakefield, P. M. & Mappes, J. Significance of butterfly eyespots as an anti-predator device in ground-based and aerial attacks. (Submitted)

1 INTRODUCTION

Insects exhibit an amazing diversity in their coloration, and this variation arises from the multiple functions of coloration. The most important function might be the avoidance of predation resulting in an array of defence strategies in which crypsis and warning coloration represent the two extreme ends of the visibility spectrum. Cryptically coloured insects gain protection by not being easily detected, while aposematic species use bold and highly visible colours to signal their unsuitability as food. Not only species but also life stages of a given species may differ in defence strategies. Usually immature stages, especially eggs and pupae, are cryptic whereas adults are conspicuously coloured (Cott 1940, Brower 1984). This difference may arise from the difference in their mobility level, since predation might be severest in immature stages because of their inability to actively escape (Dempster 1984) and furthermore a loss of even a small piece of tissue could be fatal to them (Wiklund & Sillén-Tullberg 1985). Therefore the best they can do is to try to prevent contact with predators by cryptic coloration. Additionally, cryptic coloration provides the maximum protection only if an animal is motionless. Movement is likely to attract the attention of predators and, subsequently, elicits an attack by a predator. Thus an animal is more detectable by predators when moving regardless of its colour. This means that it does indeed pay an active life stage to be aposematic. Furthermore, we cannot regard predation on adult insects as negligible (see Bowers & Wiernasz 1979, Bowers et al. 1985). Defence mechanisms have profound impact on fitness of adult insects because the longer the insect lives the closer it is its reproductive age and thus the higher reproductive potential it has (Fisher 1930). The defence strategy used by insects might also depend on population density. For example, *Schistocerca emarginata* grasshoppers bear warning coloration only if their density is high enough to allow avoidance learning by predators to occur, while they are cryptic at low local densities (Sword 1999).

Predator avoidance strategies can be divided into two categories: primary and secondary defence mechanisms (Edmunds 1974a). The primary defence includes the coloration patterns (warning coloration, crypsis) and behaviours (e.g., prey is active at a different time of day than its predator) by which prey try to avoid detection and direct contact with its predators. Secondary defence mechanisms, in contrast, come into play after discovery and attack by a predator. These two defence mechanisms are not mutually exclusive and they can be exploited by the same animals. For example, *Catocala* moths rely upon cryptic coloration of their forewings at rest, but when the predator approaches they raise their forewings to reveal the brightly coloured hindwings (Sargent 1990). This may startle the predator giving the moth an opportunity to escape.

When an animal signals its unprofitability by coloration, the colour pattern should be conspicuous, in other words it should contrast against its background (Lindström et al. 1999b). The visibility depends upon, among other things, the predator's vision (Endler 1978, 1992) because colours that the receiver does not see do not contribute to the conspicuousness (Endler 1978). In nature, prey do not face only a single predator species but a variety of predators differing in their visual abilities, learning capacities, hunting tactics and timing of foraging. This variation creates different predation pressures and hence might drive the evolution of prey coloration even into opposing directions (Endler 1978, 1988, 1991, Hazel et al. 1998). For example, red is hardly designed against red-blind mammals but most likely it functions as a warning signal to bird predators which have high-acuity colour vision. Similarly, the UV component of colours is visible to some mammals (Jacobs 1992, Tovée 1995) and diurnal birds (Bowmarker et al. 1997, Bowmarker & Hunt 1999, Cuthill et al. 2000) but not to nocturnal birds (Bowmarker & Martin 1978, Koivula et al. 1997).

Similar impacts of predator's vision can be applied to crypsis. For example, *Papilio machaon* (Papilionidae) has green and brown pupae morphs. This polymorphism is suggested to be a result of different predators relative to season (Wiklund 1975). In summer, the primary predators are birds which use visual cues in searching for prey, while in winter, non-visual predators are the main agents of mortality. Consequently, only in the summer generation does crypsis confer a selective advantage, especially to green pupae that appear more cryptic on a green background than brown ones on a brown background. In winter both cryptic and non-cryptic morphs experience equal predation.

The appearance and the relative conspicuousness (or inconspicuousness) of a given colour may vary also with ambient light (Endler 1990, 1991). Those colours matching with lighting condition appear brighter than mismatching ones (Endler 1990, 1991). For example, if the ambient light is deficient in shorter wavelengths and rich in middle wavelengths, blue colour appears relatively dull whereas green and yellow produce bright coloration. As a consequence of differences in the amount of reflected light, brightness and contrast differ between two adjacent colour patches and hence this affects the overall conspicuousness of the colour pattern (Endler 1991). Although coloration would have been tuned to correspond with the ambient light spectrum this does not, however, solely guarantee conspicuousness since visual signal does not remain unchanged on its way through the medium to the viewer's eye. Light can attenuate and degrade due to scattering from small particles in the air as a result of which distant objects appear indistinct. The degree of scattering in turn is wavelength dependent; short wavelengths scatter more than long ones

(Nassau 1980). Thus colour does not depend only on the reflectance spectrum of the object but also on colour vision of the receiver, ambient light, and the spectral transmission properties of the air (Endler 1990). To maximise conspicuousness, animals should adjust the attributes of their coloration to meet the requirements of all these factors.

It should be noted that animal coloration is a product of many selective forces (Cott 1940, Endler 1978) that may influence evolution in the same (for example see Jiggins et al. 2001) or opposite directions (Endler 1983, Brakefield 1985). For example, under severe predation, selection favours cryptic coloration in male poeciliid fishes but when predation intensity relaxes conspicuous coloration is more favoured because females prefer to mate with males bearing bright colours (Endler 1983). Taken together, given that minimising visibility is the main defence strategy of the prey animal, natural selection favours those colour patterns which are conspicuous enough to conspecifics but at the same time inconspicuous to potential predators (Endler 1991). Thus, colours represent, to some extent, a compromise between advertising an animal to its potential mate and avoiding predation (Endler 1978, 1980, 1983, 1992). There is, however, no need for compromised coloration if visual abilities of prey and predator differ because then the prey animal could possess colours which the predator does not see at all or to which it is not as sensitive as the prey itself (Endler 1978, 1991). As a result, these colours enjoy relative freedom from predation pressure.

Throughout my thesis I study how prey animals try to escape predation with their coloration. Although I focus mainly on Lepidoptera, it does not mean that similar phenomenon and attributes are limited only to this order. I do not study features of a single antipredator mechanism but the subject includes crypsis, aposematism, and one example of assumed deflection mechanism. I have adopted an experimental approach for studying arguments and assumptions concerning these defence strategies. In the experiments, birds or insectivorous lizards preyed upon insects or artificial prey items mainly under laboratory conditions.

2 DEFENCE STRATEGIES

2.1 Cryptic coloration

The purpose of cryptic coloration is to decrease the risk of predation. One way to be cryptic is to wear coloration that makes animals to match their surroundings so that they are difficult to see and thereby they could escape visual detection by predators (Cott 1940, Endler 1978). Thus in this case the degree of crypsis is dependent upon the background and as a consequence an animal is expected to be cryptic only against one background (Endler 1978). Endler (1978) specified further the concept of crypsis by introducing predation intensity, timing of predation, and predator vision into the definition. According to Endler (1978) *"a colour pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat where the prey is most vulnerable to visually hunting predators"*.

This definition considers coloration cryptic only if the coloration of an animal resembles that of the background. This is not, however, the only method to attain cryptic coloration but an animal can achieve the camouflage effect through disruptive coloration. When the coloration is a combination of matching and contrasting colours, some part of the surface stand out against the background (Cott 1940, Edmunds 1974a, Marshall & Messenger 1996, Merilaita 1998). Thus an animal fades its outline by disruptive coloration making detection by predators even more difficult. The other way to dissolve the real forms of the body is countershading that creates, for example an optical illusion of a flat surface or it softens the contours (Cott 1940, Kiltie 1988, Edmunds & Dewhirst 1994). The natural light falling down illuminates the upper parts more brightly than the under parts. Predators can use resulting shades in detecting prey, which would otherwise be cryptic on the background. By having darker colour tone on the back and lighter on the belly, an animal can diminish the effect of shade and light and blend more accurately with its surroundings.

Crypsis makes a prey unprofitable because it increases the searching time whereas more conspicuous prey is far more easily detected and thus worth more energy per time unit (Erichsen et al. 1980). As a result of this, predators should concentrate in hunting for those animals that are easier to detect in order to maximise their net energy intake. It has been experimentally demonstrated that cryptic coloration indeed reduces probability of predation (e.g., Wiklund 1975, Pietrewicz & Kamil 1977, Bond & Kamil 1998, Hazel et al. 1998). Furthermore, most palatable insect species are cryptic (Cott 1940, Endler 1978).

The fact that predators tend to improve progressively the ability to detect cryptic prey promotes the evolution of crypsis towards more and more perfect background matching (Bond & Kamil 1998). The phenomenon of improved prey search performance is called search image formation that enhances the ability to detect only one type of cryptic prey once the predator has found the first cryptic prey by chance (Tinbergen 1960, Dawkins 1971). The more cryptic the prey is the higher population density it can reach until predators achieve a search image (Bond & Kamil 1998). In addition, the effect of a search image is rather short-term (Dawkins 1971, Langley et al. 1996). For these reasons, polymorphism (i.e. occurrence of genetically different colour forms within a population) and solitary living style of prey in turn impair efficiency of search images (Edmunds 1990). In other words, cryptic coloration may be a subject to apostatic selection (Endler 1988, Bond & Kamil 1998) in which predators ignore a rare prey type and consume a commoner type more than what one could expect according to their relative abundances.

2.1.1 Cryptic coloration in a heterogeneous habitat (I)

As already noted, one determinant of crypsis depends on the resemblance between animal coloration and the background against which the animal is seen, and consequently, increase of crypsis on one background often decreases the crypsis on other, visually different background (Endler 1978). Natural background is seldom uniform but it is formed of differently coloured patches and interplay of light and shade. Furthermore, animals do have to move in their habitat and thus they at least occasionally end up to an environment where they are not optimally cryptic but rather conspicuous. Merilaita et al. (1999) developed a theoretical model according to which there could be a compromised coloration that is advantageous in two visually different habitat and whose survival is better than that of perfectly matching forms.

I set out a predation experiment to test whether this could be demonstrated in a feeding experiment. The goal was to find an answer to the question of whether cryptic coloration that compromises the requirements of two visually different backgrounds could confer better protection against visually hunting predators than coloration matching perfectly one of the two microhabitats (I). The model habitat consisted of two visually different microhabitats. I created a set of prey items, which were cryptic, highly conspicuous, or intermediate (a compromise in appearance) between these two extremes. In other words, the coloration that matched one background mismatched the other background, and vice versa. The compromised coloration matched intermediately both backgrounds. Prey items were tiny pieces of almond glued under a small paper cover bearing a black-and-white pattern. Each bird received a series of backgrounds i.e. three prey types singly on the two background types. Each combination was repeated three times. As a result each bird underwent a total of 18 trials. The searching time was used as a measure of the degree of crypsis. The longer the time was the better protection the prey enjoyed from its coloration.

The data was analysed using the model of Merilaita et al. (1999). The mean search time of each prey type on one of the two backgrounds was plotted against that on the other background producing a trade-off curve. A line, whose slope is determined by the probabilities of encountering the predator in each microhabitat, gives a set of colorations equal probability of escaping detection across the whole habitat. Because in our experiment prey was equally likely to encounter birds in every microhabitat, the slope is -1. At the origin the prey receives no protection from crypsis. Thus, the further the prey is from the origin, the better the crypsis is. The upper limit for the distance is determined by the trade-off curve. Therefore at the point where the line touches the curve, we can find the colour pattern combining crypsis in the two microhabitats in a way that yields the lowest risk of detection across the whole habitat. According to the model coloration that compromises the requirements of the two microhabitats is the best strategy when the trade-off curve is convex.

2.2 Aposematism

Predators can assess prey edibility by their coloration. Insects that are armed with spines or contain unpalatable, emetic, poisonous, or otherwise harmful substances, usually possess conspicuous coloration such as yellow, orange, red, white, or combination of these colours, while the majority of edible species has cryptic coloration (Poulton 1890, Cott 1940, Edmunds 1974a, Endler 1978). Unprofitability also includes rapid escape ability in which case costs of pursuit are high and hence prey is not worth of capture. Animals do not only use colours to advertise their unprofitability but they may also employ sounds, odours, behaviour, or a complex of warning signals (Cott 1940, Edmunds 1974a). For example, Arctiidae moths utilise pyrazine odour with either ultrasounds (Dunning et al. 1992, Dunning & Krüger 1995) or aposematic coloration (Rothschild et al. 1984) to advertise their unpalatability to bats and visually hunting predators. Pyrazines are actually employed by a wide variety of aposematic insects (Moore et al. 1990). The use of multiple signals simultaneously increases protectiveness of aposematic coloration by enhancing avoidance by predator (Avery & Nelms 1990, Marples et al. 1994, Marples & Roper 1996, Rowe & Guilford 1996, 1999a,b, Roper & Marples 1997, Rowe 1999, Lindström et al. 2001a).

Despite the fact that the conspicuousness imposes a cost in terms of higher detectability risk by predators (e.g., Gittleman & Harvey 1980, Lindström et al. 1999b, 2001b, c), aposematic coloration is of benefit to prey in avoiding attacks. This has been demonstrated in several behavioural experiments. Contrasting colours are more easily learnt than cryptic colours, and associated with unpalatability more quickly (Gittleman & Harvey 1980, Gittleman et al. 1980, Sillén-Tullberg 1985, Alatalo & Mappes 1996, Lindström et al. 1999b, 2001b, c), and this association is also retained longer (Roper & Redston 1987) and more accurately (Guilford 1986). A further essential advantage of using conspicuous colours arises from the fact that unpalatable animals employ them almost exclusively whereas most of the edible species present duller, cryptic colours (Cott 1940, Endler 1978). The distinctively dissimilar appearance of aposematic and palatable species is proposed to make the recognition task easy for predators as a result of which confusion with palatable species is avoided (Turner 1975, Guilford & Dawkins 1991, 1993). In addition to enhancing avoidance learning, typical warning colours and patterns are avoided even by inexperienced predators (Smith 1977, Schuler & Hesse 1985, Rowe & Guilford 1996). The innate avoidance is hereditary (Kovach 1978, 1983, Marples & Brakefield 1995) or acquired through social learning (Turner 1964, Avery 1996). All these features together contribute to the selective advantage of aposematic animals.

In order to effectively induce the learned avoidance, the encounters between the aposematic prey and naïve predator should occur at a high enough rate (Greenwood et al. 1989, Lindström et al. 2001c). This is because when the encounter rate is too low, predator continues to consume the aposematic prey. But if aposematic prey are common, avoidance learning can take place rapidly. For this reason selection is expected to act against rare aposematic morph. This kind of selection that favours the commoner form at the expense of the rarer one is said to be antiapostatic and aposematic animals are, therefore, expected to be monomorphic (review in Endler 1988). Avoidance learning does not, however, require a fixed absolute number of unpalatable prey items eaten and disadvantages of being rare may be balanced by benefits gained from grouping (Greenwood et al. 1989, Lindström et al. 2001c). The rare morph might also get additional advantage from neophobia since birds show reluctance to eat unfamiliar prey (Mappes & Alatalo 1997, Lindström et al. 2001b).

Besides coloration, behaviour of animals can reveal unpalatability. Birds are suggested to assess prey profitability on the basis of insect flight pattern (Srygley 1999). Typically aposematic insects move relatively slowly (see e.g., Edmunds 1974a, Chai & Srygley 1990, Srygley & Dudley 1993, Pinheiro 1996) maximising exposure of the warning coloration. Slow movement gives more time to predators to identify the detected prey and decide whether to attack or not (Endler 1978, Guilford 1986, Guilford & Dawkins 1987). This has been shown to reduce the recognition errors made by predators (Guilford 1986). Additionally, aposematic animals tend to live more often in aggregations than cryptic ones, which in turn facilitates avoidance learning (Gagliardo & Guilford 1993, Alatalo & Mappes 1996, Mappes & Alatalo 1997, Lindström et al. 1999a, 2001c, Riipi et al. 2001). The tough cuticle of insects might also give additional protection against any predator that releases the prey without lethal injuries after discovering its unpalatability (Järvi et al. 1981, Wiklund & Järvi 1982).

Only in a fraction of cases is the origin of a defence substance known (Bowers 1990). Our knowledge of them is based mostly on experiments on butterflies, which have two sources of chemicals used for defence. Insects can either synthesise defensive substances or sequester them from their larval food plant and then transfer to the adult stage (see Brower 1984, Rothschild 1985), or even gather them as adult as Danainae butterflies do (Boppré 1983). Plant-originated deterrents are so-called secondary plant compounds, which are useful for plant in protecting against herbivores. Certain invertebrate herbivores, however, have become tolerant of these chemical defences and have started to use them as a precursor to pheromone compounds (Schulz et al. 1993) and in their battle against predators. It should be noted that feeding on plants containing deterrents does not necessarily mean that the insect is unpalatable or toxic because many insects eliminate or metabolise these compounds (Rothschild 1972, Bowers 1990).

Assimilation of nasty tasting compounds from plants may lead to a palatability spectrum within an insect species, where some individuals are more unpalatable than the others depending on the concentration of deterrent substances in each host plant (e.g., Brower et al. 1968, 1972, Brower & Moffitt 1974, Ritland 1994). In an extreme case, a palatable insect mimics its own unpalatable conspecifics. This phenomenon is termed automimicry (Brower et al. 1970). Although insects would have been fed on the same plant species, variation in the concentration of defensive chemicals can be found between the sexes of a single species (e.g., Brower et al. 1972, Brower & Moffitt 1974, Brower & Glazier 1975, Brown 1984, Dussourd et al. 1988) and different body parts of an individual (Brower & Glazier 1975, Brown 1984, Dussourd et al. 1988). In addition, the ability and efficiency to accumulate these chemicals varies among different species (Dixon et al. 1978, Cohen 1985). The situation is further complicated by the fact that the sensitivity to unpalatable substances varies in different predator species (Edmunds 1974a, Fink & Brower 1981), and even experienced predators occasionally sample aposematic prey (e.g., Gitleman & Harvey 1980, Lindström et al. 2001b). Nevertheless, there is no reason to doubt the protective value of aposematism.

2.2.1 Ultraviolet vision

Birds are important predators of insects and hence have profound effect on the evolution of insects' coloration. Colour vision of birds is based on at least four colour receptors that correspond to extreme short (ultraviolet, UV), short (blue), medium (green), and long (red) wavelengths (Bowmarker et al. 1997, Bowmarker & Hunt 1999, Cuthill et al. 2000). Instead of having a distinct UV photoreceptor, birds can alternatively possess a violet cone pigment that extends its spectral sensitivity into UV range (Cuthill et al. 2000 and references therein). In avian retinae UV sensitive cones make up to a few percentages of all cone photoreceptors (Hart et al. 2000). This low proportion is partly compensated by higher sensitivity in UV range than in longer wavelengths (Kreithen & Eisner 1978, Burkhard & Maier 1989, Maier 1994). Many insects, amphibians, reptiles, fish, and even some mammals are also able to see in UV light (Jacobs 1992, Tovée 1995).

The studies on UV vision have concentrated mainly on the significance of UV colours in mate choice, especially that of birds (see Cuthill et al. 1999) and research on other potential functions for UV cones are scarce (but see Viitala et al. 1995, Koivula et al. 1997, Church et al. 1998a, Siitari et al. 1999). UV sensitivity has been overlooked by human observers in the context of protective coloration (Cuthill & Bennett 1993, Bennett et al. 1994), among other things, although UV reflecting patterns have been found in many invertebrate species. For example, some spiders (Craig & Bernard 1990) and several Lepidoptera species (e.g., Eguchi & Meyer-Rochow 1983, Brunton 1998, Church et al. 1998b) possess UV colours. The fact that many natural backgrounds, such as bark, leaves, and soil, do not reflect UV light (Endler 1993, Finger & Burkhardt 1994), gives a possibility that seemingly cryptic animals might be conspicuous. This has led, for example, Majerus et al. (2000) to reassess industrial melanism in *Biston betularia* by taking into account the whole spectrum. Church et al. (1998b) in turn proposed that UV cues might signal unpalatability but they did not present any experimental evidence to support this argument. The other plausible hypothesis is that birds might use UV cues in prey detection (Bennett & Cuthill 1994) and there are some data supporting this idea (Viitala et al. 1995, Church et al. 1998a). However, experiments that directly compare the survival of two prey types differing only in UV are lacking. Previous works on aposematism have taken into account only the human-visible range (ca. 400 - 700 nm) (see Cuthill & Bennett 1993, Bennett et al. 1994). I conducted two experiments to investigate whether UV cues could serve as an aposematic signal (II) or instead whether they attract the attention of potential predators (III).

2.2.2 UV cues as aposematic signals (II)

Because a bird's previous experience might affect its behaviour towards prey, use of natural prey animals in learning experiments is problematic. To overcome this problem, I used artificial prey items, which were slices of almond glued to a small piece of paper cover. This paper cover either reflects or absorbs UV wavelengths. To test whether the difference between these two prey types was perceptible by birds, I placed one UV-reflecting and one UV-absorbing but otherwise similar prey item on the UV-absorbing background. Each bird underwent two trials; one under UV present illumination and one under UV-deficient conditions. Because sensation of colours depends on the spectral composition of the light, we would expect UV-reflecting prey items to be more conspicuous in the UV present conditions than in the UV absent conditions. As a result, birds should eat more UV-reflecting prey items in the UV present condition.

Because birds could have an innate avoidance response to the warning colours (Schuler & Hesse 1985), or the novelty of the stimuli (Coppinger 1969) could cause their rejection, I made pairwise comparisons of birds' preferences for prey items with and without UV reflection. In the preference test, birds made a choice between one reflecting and one absorbing prey item that appeared similar in longer wavelengths.

In the avoidance learning experiment I also used a binary choice design (unpalatable vs. palatable). Each bird faced a choice of two green prey items differing visually only in the UV region. One of the prey in the pair was unpalatable. Birds underwent four trials in which they were offered sequentially six pairs of prey items. I recorded whether birds were able to learn to avoid the unpalatable prey from the palatable ones.

To test whether avoidance learning can take place under the experimental design used, a new set of birds was introduced with green palatable and red unpalatable prey items. The experimental procedure was otherwise the same as in the previous experiment.

2.2.3 UV cues and predation risk (III)

The main diurnal predators of adult Lepidoptera are birds (Dempster 1984), whereas their most important nocturnal mortality agents are bats and rodents. These two animals use different sensory modalities in prey detection. Birds are visually orientating predators while mammals use senses other than vision in searching for food. If day active predators use UV cues in prey detection, there should be increased predation risk for diurnal insects to possess UV coloration. Therefore, one can predict that UV coloration would be more common in night than in day active insects (assuming that UV does not signal unpalatability). To test this hypothesis, the occurrence of UV reflectance in Lepidoptera (assessed by the UV photographic method), was compared to the data on activity times. The study material consisted of 911 species of Lepidoptera representing 16 families whose wing patterns were classified to reflect or absorb UV light. Because of the lack of existing phylogenies I was unable to perform the comparative analysis (Harvey & Pagel 1991). Therefore I had to use taxonomic arrangements.

If the difference in UV reflection between nocturnal and diurnal Lepidoptera is, at least partly, a result of predation, there should be a disadvantage for diurnal butterflies to exhibit UV-reflecting wing patterns. To test whether UV reflection really increases the predation risk, I positioned tethered UV-reflecting (UV+) and UV-absorbing (UV-) moths in pairs in nature. Each pair consisted of one UV+ and one UV- moths that were similar in visible range (λ = 400 - 700 nm) but dissimilar in the UV region of the spectrum. I placed moths in such a way that one could see two individuals of a given pair at the same time but not the next pair. I repeated the experiment four times during daylight (40 pairs) and four times at night (40 pairs). I considered the moth to have been eaten if it had disappeared.

2.3 Mimicry

Two species can utilise same warning colour patterns to such an extent that they are indistinguishable in appearance. Traditionally mimicry is divided into Müllerian and Batesian mimicry (e.g., Turner et al. 1984, Turner 1987). The main distinction between them is that in Müllerian mimicry all co-mimics are unpalatable, whereas in Batesian mimicry only the model is unpalatable.

When two or more unpalatable species look more or less alike they are said to constitute a Müllerian mimicry complex (Müller 1879). Müller assumed that a predator eats a fixed number of unpalatable prey items before it learns to avoid them in future (but see Lindström et al. 2001c). He proposed that the imitation is advantageous to all species involved because the predators tend to generalise the aposematic signal and they have to learn only one colour pattern instead of several types. Thus, predators kill in the learning process a lower proportion of prey individuals sharing the same colour patterns than if they were completely different in appearance. This lowers the risk of being captured and thereby the cost of being conspicuous is reduced at the individual level. Furthermore, the protection gained from mimicking increases with the number of individuals involved because then the mortality per capita will be lower.

Classical examples of members of a Müllerian mimicry ring are *Heliconius erato* and *H. melpomene* (Nymphalidae), which are known to be unpalatable to birds (Pinheiro 1996) and lizards (Boyden 1976). *H. erato* and *H. melpomene* occur in the same geographical area and they both have black forewings with a red band. In addition to colour, they have similar behaviour and the flight pattern (Srygley & Ellington 1999). As these mimetic species belong to the same genus, the similar appearance might be due to common ancestral coloration. Brower (1996) rejected this alternative explanation by phylogenetical analyses which show that *H. erato* and *H. melpomene* do not share a common biogeographical history, and hence their warning signals are not similar due to common descent but have evolved independently.

According to the theory, Müllerian mimics are not expected to be polymorphic since this would increase the number of aposematic signals to be learned and as a result impede avoidance learning (e.g., Turner et al. 1984, Turner 1987). However, polymorphism does exist among Müllerian mimics (Mallet & Joron 2000). For example, *Heliconius cydno* has yellow and white colour morphs resembling *H. eleuchia* and *H. sapho,* respectively. Kapan (2001) has provided an explanation for the existence of two mimetic phenotypes. He introduced *H. cydno* into areas that were dominated either by *H. eleuchia* or *H. sapho* and found that the introduced morph that occurred in its co-mimic's range survived better than the butterflies in the absence of co-mimic. But if the density of transferred morph was high enough the difference in survival rates disappeared. In other words, selection against polymorphism relaxes when morphs become abundant. The field experiment, thus, demonstrated the mimetic advantage in polymorphic species and its dependency on relative densities (i.e. rare forms will be selected against).

In contrast to Müllerian mimicry, in Batesian mimicry a palatable species mimics an unpalatable one (Bates 1862). After a predator has learnt to avoid the model, it mistakes the mimic for unpalatable species and hence transfers the avoidance to the mimic. As a consequence, the mimic is avoided on the bases of its appearance despite it is not unpalatable or otherwise unprofitable. Batesian mimicry confers an advantage for the mimic (e.g., Sternburg et al. 1977, Turner et al. 1984) but from the model's point of a view, the resemblance is not beneficial, and indeed the mimics are parasites. The more there are mimicking individuals, the greater is the likelihood that predators encounter palatable species that would impair the avoidance (Lea & Turner 1972, Turner et al. 1984, Huheey 1988, Malcolm 1990, Speed 1993). This likelihood is lowered if palatable species imitates distinct model species. Therefore Batesian mimic species are expected to be polymorphic which is, however, relatively rare in nature. Not only the frequency of the model but also its unpalatability level affect the survival value of species in a mimicry complex (Lindström et al. 1997 and references therein). A highly unpalatable model gives better protection against predators than only a mildly unpalatable one.

The conventional views of mimicry theories and their predictions seem to be too simplistic, and it has been disputed whether definition of mimicry should be reformulated or even divided into several categories that would be Batesian, quasi-Batesian, and Müllerian mimicry (Speed 1993). The key question in the debate is how discrepancy in protection between two mimics affects their fitness, in other words, whether the mimicry relationship is mutually beneficial or parasitic. The quasi-Batesian mimicry hypothesis states that mildly unpalatable mimics can cause an increase in predation on the better-defended co-mimics and consequently dilutes the protection (Speed 1993). To decrease predator's encounter rate with the less well defended species, mimics should copy the warning signal of multiple models which would, therefore, lead to polymorphism (Speed 1993). Thus the quasi-Batesian mimicry would share certain characteristics of Batesian mimicry. The proposal of a new mimicry form has generated an avalanche of papers for (MacDougall & Dawkins 1998, Speed 1999, Speed & Turner 1999, Speed et al. 2000) and against (Joron & Mallet 1998, Mallet & Joron 2000) the quasi-Batesian hypothesis.

Although aposematism and mimicry have been theoretically studied intensively, experiments on the validity of the aposematic nature of a given insect are scarce. When tests on the palatability of an insect have been finally conducted, they have sometimes revealed an unexpected result. Viceroy butterflies (*Limenitis archippus*) are a good example. They were considered for long as the palatable mimics of the unpalatable monarch (*Danaus plexippus*) and the queen (*D. gilippus*). Palatability tests, however, proved that viceroy butterflies are actually unpalatable and, consequently, these butterfly species represent an example of Müllerian mimics, rather than Batesian mimics (Ritland & Brower 1991).

2.3.1 Pieridae and putative mimicry (IV)

It has been speculated that white coloration of Pieridae butterflies might signal unpalatability (Jones 1932, Kettlewell 1965) and that the group constitutes a Müllerian mimicry complex (Marsh & Rothschild 1974). Pieridae larvae feed on many plant species of Brassicaceae containing mustard oil glycosides that could render the adult butterflies as unpalatable (Aplin et al. 1975). The results of feeding experiments, however, are contradicting. Some papers do give support to unpalatability (Lane 1957, Marsh & Rothschild 1974), while others have failed to find strong (Kingsolver 1987) or any (Wourms & Wasserman 1985, Ley & Watt 1989) indications of unpalatability. I tested whether Pieridae butterflies are really unpalatable (IV), as it has been claimed (Jones 1932, Kettlewell 1965,

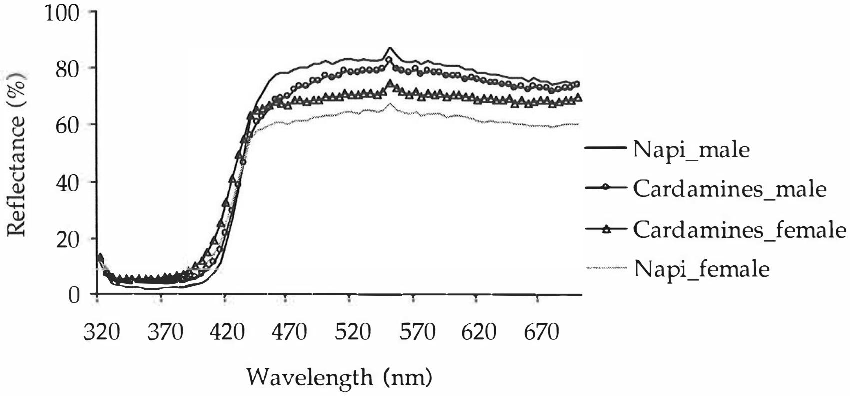

FIGURE 1 Mean spectral reflectance curves for the dorsal wings surfaces of *P. napi* and *A. cardamines*. Measurements are the means of three measurements from three individuals of each sex.

Marsh & Rothschild 1974). *Pieris napi* and *Anthocharis cardamines* exhibit similar visible and ultraviolet patterns and thus they are indistinguishable by the appearance (Fig. 1). I conducted a series of experiments to test the acceptability of these two pierid butterflies to pied flycatchers (*Ficedula hypoleuca*) in nature and their palatability to great tits (*Parus major*) in the laboratory (IV).

Firstly, I gave pied flycatchers a choice between *P. napi, A. cardamines,* and two palatable butterfly species at flycatcher nest boxes, and I ranked the order that the birds took each butterfly. The order of choice would reflect the preference differences between the butterfly species.

To compare the relative palatability of *P. napi* and *A. cardamines*, I offered them to great tits. *P. brassicae*, which has earlier been classified as unpalatable and, indeed, as the model in the putative mimicry ring (Marsh & Rothschild 1974), was also included in the test. Because the appearance of the prey could affect the behaviour of the birds, I covered the crushed butterfly with two small brown paper covers. Thus the birds that had been taught to find palatable food between the paper covers were unable to identify visually the prey. I offered a series of butterflies to birds consisting of one of the pierid butterflies, one unpalatable and one palatable butterfly. As an indicator of the level of unpalatability I used the number of beak wipes. Birds wipe their beak in order to get rid of the nasty food particle and bad taste leads to vigorous beak wiping. The behaviour of birds towards pierid butterflies was compared to reactions elicited by the known unpalatable and palatable control butterflies.

Taste is not the only possible feature that makes prey unprofitable to predators. The agility or speed of flight might render the butterfly species so difficult to catch that the energy expenditure would be higher than the energy gain. Predators might then waste their time in capturing unprofitable prey when they could for example hunt other more valuable prey, defend their territory, or seek for a mate. To test whether pied flycatchers reject more often freely flying *P. napi* or *A. cardamines* than *Leptidea sinapis*, I released singly one butterfly at a time into an outdoor cage and monitored the reaction of birds up to one hour.

2.4 Deflection and startle mechanisms

Butterfly wings often possess marginal eyespot patterns as a possible secondary defence mechanism against the predators. The deflection hypothesis states that ventral eyespots may be the target for attack directing the attention of predator from the body to the wings (Blest 1957, Young 1979, 1980, Brakefield 1984, Wourms & Wasserman 1985, Brakefield & Reitsma 1991). When a predator seizes the wings instead of the body, the butterfly might be able to escape without serious injury. It would lose a piece of its wings but it may still be capable to fly. Butterflies are suggested to be more vulnerable to predation when resting or feeding on the ground and thus eyespots would be favoured particularly in the species living near the ground level (Young 1979). This is supported by observations that eyespot patterns (Young 1979) and wing damages resulted from attacks (Muyshondt & Muyshondt 1976, Shapiro 1977, Young 1980, Larsen 1982, Dennis et al. 1986) are more common in ground-feeding than in arboreal-feeding butterflies.

In many Lycaenidae the deflection of eyespots is enhanced by a structural feature, the so-called false head (Cott 1940, Edmunds 1974a, Robbins 1980, 1981). On the outer edge of the hindwings butterfly has an allonge that resembles a head. Back and forth moving of hindwings reinforces further the illusion of the head (Robbins 1980). Thus a predator might ignore the real head and seize the false head providing the butterfly a last chance to escape (Robbins 1981). Wourms & Wasserman (1985) provided evidence that false head marking misdirects the handling strikes allowing escape by the butterfly. There is also field data on the frequency of wing damages on *Stichophthalma louisa* (Nymphalidae) that tends to support this hypothesis (Tonner 1993). The butterflies bear an eyespot on the prominent hind-tip of the hindwings. This imperfect false head had a higher proportion of beak damages than any other parts of the wing (Tonner 1993).

Another possible protection function of eyespots or other highly conspicuous wing markings is that they frighten the approaching predator away (Blest 1957). At rest some butterflies conceal eyespots but when disturbed by a potential predator, they suddenly uncover them. Paralysed with confusion the predator, which believes to see the eyes of its own predator, hesitates to attack and gives thus butterfly time to fly away unharmed. The eye-like shape elicits most effectively the fear response in birds (Blest 1957, Jones 1980). Schlenoff (1985) has provided some evidence for the existence of startle responses of bird predators. She presented artificial moths that have either uniform or brightly coloured hindwings (resembling *Catocala* moths) to blue jays and scored the behaviour of birds. She found that brightly coloured hindwings elicited the startle response in birds that eventually waned after several encounters. Conspicuousness seemed to be important in evoking of the startle behaviour.

As Sargent (1990) pointed out, we could regard the described adaptive functions of eyespots only as a hypothesis since selective advantages have not been thoroughly demonstrated. We still do not know whether the startle response or other supposed functions of eyespots increase the escape probability of butterflies in nature in that no empirical research has been done to confirm that butterflies would derive selective advantage from their eyespots. Previous fieldwork has mainly analysed the influence of wing markings by comparing the frequencies 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). Beak marks, however, do not necessarily reveal an effect of eyespots because other attributes, such as the flight ability of a butterfly, might account for the difference in the incidence of beak marks (Edmunds 1974b). Clearly this is an area needing further investigation.

2.4.1 Butterfly eyespots as a deflection mechanism (V)

African satyrine *Bicyclus anynana* has two seasonally distinct morphs that differ in wing colour patterns (Brakefield & Larsen 1984, Windig et al. 1994). Individuals of the same genotype develop into phenotypes with or without eyespots depending mainly on temperature (Brakefield & Larsen 1984, Brakefield & Reitsma 1991). Rearing larvae at 23°C or warmer produces butterflies bearing a pale band and seven eyespots on their ventral hindwings while butterflies reared at around 19°C show reduced spotting or no eyespots, the wings being uniformly brown. Wing pattern formation is sensitive to ambient temperature especially in the late larval stage and shortly after pupation (Brakefield et al. 1996, Kooi & Brakefield 1999). By timing the critical period for wing pattern induction near their emerging, butterflies can use the temperature as a reliable cue for the adult environment (Kooi & Brakefield 1999). This phenotypic plasticity is mediated by ecdysteroid hormones (Koch et al. 1996, Brakefield et al. 1998).

It is assumed that the adaptive significance of plasticity in wing patterns is to render butterflies to be cryptic (spotless) in the dry season and to produce a deflection mechanism (marginal eyespots) in the wet season (Brakefield & Larsen 1984, Brakefield & Reitsma 1991). In the dry season butterflies are effectively concealed on dead, brown leaf litter due to their brown colour and thus they could avoid visual detection. Field experiments have shown that the dry season butterflies indeed prefer to perch on brown rather than on green foliage (Brakefield & Larsen 1984). By contrast, during the wet season butterflies are more active and thus more easily perceived by predators and conspicuous eyespots may direct the capture attempts from the body to the wings enhancing escape probability.

The wing pattern variation of *B. anynana* provides a useful tool to test the advantages of marginal eyespots to butterflies in general. I studied whether eyespots affect butterfly fitness through deflection (V), which is the hypothesis suggested by many authors (Blest 1957, Young 1979, Brakefield 1984, Brakefield & Larsen 1984, Wourms & Wasserman 1985, Brakefield & Reitsma 1991). I used *Anolis carolinensis* predating on three different forms of *B. anynana* which were the spotted wet season form, the spotless dry season form, and a Bigeye-comet mutant with enlarged ventral eyespots (Fig. 2). I placed one live butterfly at a time on the slice of banana into the cage and counted the number of butterflies eaten or escaped. Additionally, I analysed the target of attack (body vs. wings) on the basis of videotapes. To compare whether eyespots are more effective to deflect avian predators, I also conducted the experiment with pied flycatchers using the spotted and spotless forms of *B. anynana*.

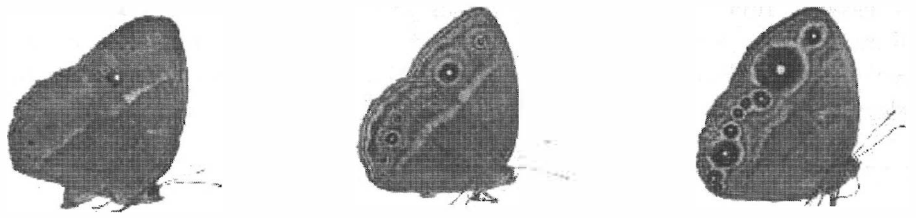

FIGURE 2 Ventral wing surfaces of *B. anynana*, illustrating the spotless dry season form, the spotted wet season form, and the Bigeye-comet mutant.

3 RESULTS AND DISCUSSION

3.1 Cryptic coloration in a heterogeneous habitat (I)

Search times for prey types increased with increasing background-matching, indicating that items that matched their background survived better than items that contrasted with their background. The most distinct form was always at a disadvantage relative to the compromised and the perfectly cryptic prey items. Although the perfect correspondence of a prey item's colour pattern with its background was the best solution in each microhabitat, the compromised prey survived best when we take into account the survival in both microhabitats. This is indicated by the shape of the trade-off curve that proved to be convex and the point of compromised colour pattern was on the line (Fig. 3). In other words, compromised colour pattern had the lowest predation risk.

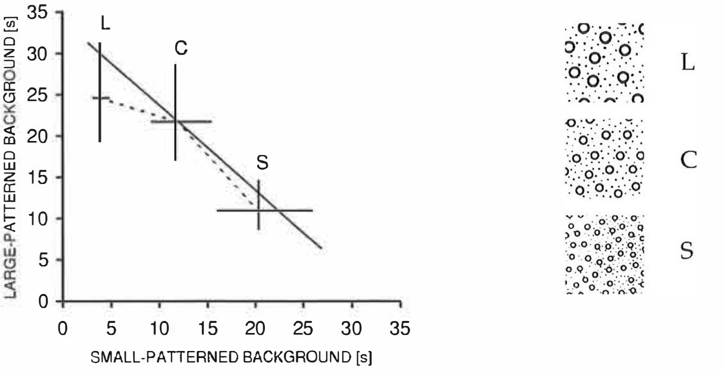

FIGURE 3 The crypsis of the three prey types on the two backgrounds measured as mean search times (s), giving the trade-off curve in crypsis between the microhabitats. Prey types: L = large patterned, C = compromised patterned, S = small patterned.

Predators are known to improve their prey search efficiency with experience (e.g., Bond & Kamil 1998). In the present experiment, each trial included cryptically and compromised coloured prey, mixed up with an equal number of conspicuous items. It is unlikely that search images would have affected search performance of birds because frequent encounters with conspicuous (Dawkins 1971) as well as with other kind of cryptic prey (Pietrewicz & Kamil 1979) are expected to interfere with search image formation.

The results indicated that a compromised pattern might be the best strategy for a prey under certain conditions. Evidence for the existence of such a system in nature is scant (for examples see Merilaita et al. 1999). This is presumably due to absence of experiments dealing with protective coloration of prey and their habitat use. One of the exceptions is provided by Shreeve (1990), who compared the degree of crypsis in *Hipparchia semele* butterflies in different microhabitats. Females appeared to be maximally cryptic only on one microhabitat, lichens, where they are resting most frequently. Males were less cryptic on lichens than females but on the other hand more cryptic on dry vegetation, litter, and live vegetation. Shreeve suggested that coloration of males, which utilise a variety of settling substrates, might be a compromise between the requirements of different microhabitats. These results together with the fact that many natural habitats are visually heterogeneous suggest that when one quantify the degree of crypsis, one should not neglect the possibility of the coloration to be compromised.

3.2 UV cues

3.2.1 UV cues as aposematic signals (II)

Great tits consumed more UV+ items in the presence of UV light than absence of UV when placed on UV-absorbing background. From this result we can conclude that birds were able to perceive the difference in the UV spectrum between prey types. In fact, the peak of the UV reflection used coincides with the peak sensitivity of the ultraviolet receptors of the passerine birds, which is at about 370 nm (Bowmarker et al. 1997, Hart et al. 2000).

If UV reflection indicates unpalatability in nature, then predators should exhibit an innate or learned aversion of these colours. There was no colour preference in the first prey item to be eaten in a simultaneous choice test when the choice was between two prey items differing only in the UV range. In other words, birds ate first equal proportions of UV+ and UV- treated prey items. Furthermore, birds did not learn effectively to avoid unpalatable prey items irrespective whether the signal was UV+ (i.e. green+UV) or UV- (i.e. green) (Fig. 4). The lower starting point for the group of birds presented with green unpalatable items than for those with green+UV unpalatable prey was not a result of more rapid avoidance learning within the first trial but more likely due to some preference for green+UV items. Although birds did not show any preference bias in the preference test for palatable items, they might have an

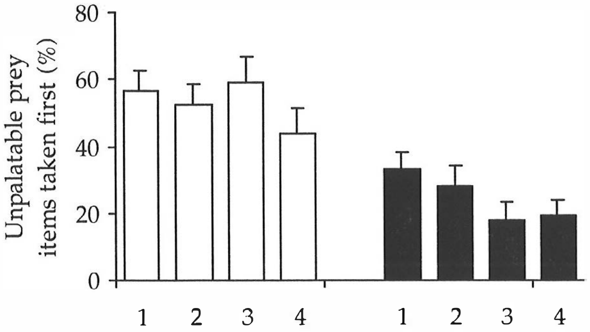

FIGURE 4 The proportion of cases (mean + SE) in which unpalatable prey items were consumed first among six presentations in the four trials of the learning experiment (n = 13). White columns = green+UV unpalatable, black columns = green unpalatable.

innate preference for green+UV items, which would arise only when prey coloration green is combined with unpalatability.

It is of course possible that birds would have been able to associate differences in UV reflection with unpalatability if they had been allowed to undergo more trials. However, the fact that birds learnt very quickly to discriminate unpalatable red from palatable green prey items under similar conditions argues against this explanation. Therefore the most plausible interpretation of the results is that the UV cues as such do not play a prominent role in aposematism at least if the great tit is the predator. Moreover, birds showed readiness to associate UV reflection with palatability, which could be assumed to interfere with any avoidance learning by bird predators.

3.2.2 UV cues and predation risk (III)

Among all Lepidoptera families, most of the night active Lepidoptera (78.6 %) possess UV reflecting wing patterns, whereas most of the day active species (69.2 %) lack any UV reflection in their wings. I am aware that species and genera are not statistically independent variables (Harvey & Pagel 1991). The observed relationship might be a result of an ancestral trait rather than a result of predation pressure. Therefore this part of the results could be considered as a suggestive. These data provide, however, evidence for the prediction that UV reflection would be more common in nocturnal than diurnal Lepidoptera.

The effect of UV reflection on predation risk was tested by a field experiment. Moths with UV wing coloration had lower survival rate than those absorbing UV light (Fig. 5). However, this was true only at daytime, while no differences could be detected when the moths were exposed to nocturnal predation. The differential survival is most likely due to the fact that the predator species composition is different by day and at night. The major potential predators of Lepidoptera are birds at daytime whereas at night bats and rodents are the most plausible mortality agents. Unlike birds, mammals do not rely on vision in searching for food. Additionally, there are indications that UV vision would be involved in prey detection by some bird species (Viitala et

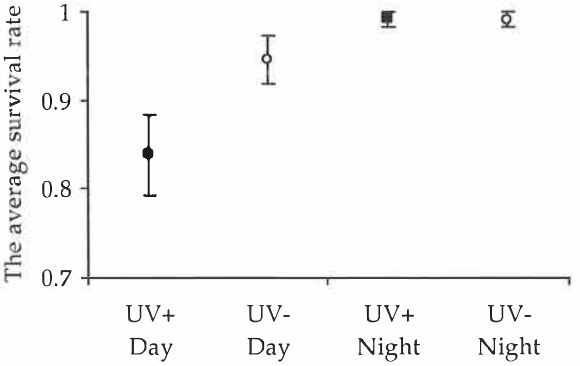

FIGURE 5 The Mayfield estimates of the hourly survival rates (± SE) for moths with UV-reflecting (UV+) and UV-absorbing (UV-) wings in the field experiments conducted in the daytime (40 pairs) and at night (40 pairs).

al. 1995, Church et al. 1998a). The higher mortality of UV+ moths by day can thus be reasonably attributed to UV sensitive predators because the coloration of the two moth types used were dissimilar only in the UV region of the spectrum. Consequently, the possession of UV wing patterns is costly only to diurnal Lepidoptera by attracting predators.

3.3 Pieridae and putative mimicry (IV)

High acceptability of *P. napi* and *A. cardamines* to pied flycatchers argues against the suggestion that these Pieridae would be aposematic. The birds did not show an aversion to *P. napi* and *A. cardamines* when the choice was between these and two palatable butterfly species (Fig. 6). A possible explanation for the absence of preference differences could be the fact that pied flycatchers could not use for example the behaviour of butterflies as a cue for unprofitability. On the other hand, the main goal of the preference test was to see whether white coloration per se is avoided. From this point of view, the result indicates that *P. napi* and *A. cardamines* do not benefit from their coloration in the form of reduced predation risk.

In addition, great tits did not find *P. napi* and *A. cardamines* particularly unpalatable. Not even *P. brassicae,* which is considered as the model in the putative mimicry ring (Marsh & Rothschild 1974), triggered the dislike behaviour. One potential explanation for this is that Pieridae species vary geographically in palatability, as monarchs do (Brower et al. 1968, 1972). The possibility thus arises that if I had used butterflies from other geographical area birds might have found them unpalatable. This, however, seems unlikely since *P. napi* butterflies collected from North America are reported to be palatable to wild Canada Jays as well (Ley & Watt 1989). Taken together, no evidence supporting the idea of that the white coloration of Pieridae signals unpalatability was found.

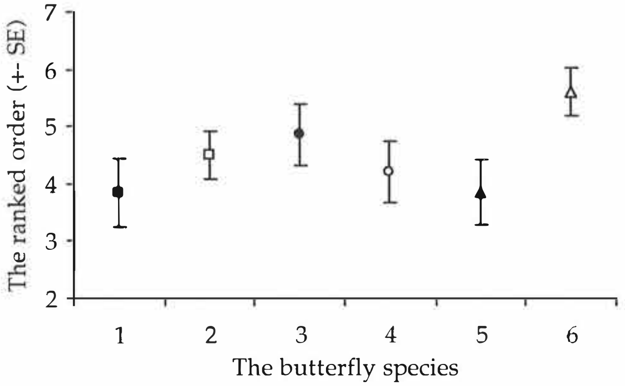

FIGURE 6 The ranked order of consumption of two control butterfly species (1, 2), *P. napi* males (3) and females (4), *A. cardamines* males (5) and females (6) in the preference experiment conducted in outdoor cages. The smaller the rank order is, the earlier the pied flycatchers (n = 20) ate the butterfly.

In outdoor cages into which free-flying butterflies were released birds showed a tendency to attack *P. napi* and *A. cardamines* at a lower rate than the control butterflies. This gave us some evidence that other characters, such as flight patterns or relatively low nutritious content, might render them unprofitable as a prey. Usually palatable butterflies fly faster and more erratically than unpalatable species (Edmunds 1974a, Chai & Srygley 1990, Srygley & Dudley 1993, Pinheiro 1996). Additionally, butterflies are able to change their flight to be more erratic in response to predator attacks and thereby predators have difficulties to predict the flight path that could enhance the escape possibilities of the prey (Humphries & Driver 1967, 1970). If predators find the prey too difficult to catch, they might learn not to attack (Gibson 1974). Furthermore, a few birds attacked and captured *P. napi* but released them seemingly unharmed. Wings of *P. napi* contain volatile odours (Hiyashi et al 1978) which are released when touched. This might lead to rejection of the butterfly. Since odours can function as warning signals (Guilford et al. 1987), enhance avoidance learning (Roper & Marples 1997), elicit a bias against colours typically associated with aposematism (Rowe & Guilford 1996, 1999), and induce aversion to conspicuous prey (Lindström et al. 2001a), it is highly possible that also *P. napi* uses its citric odour to repel its enemies.

Although I did not find any strong indication of unpalatability in Pieridae butterflies studied, they might still be shown to be Müllerian mimics. The experiment done in the outdoor cage showed that other characteristics might render them as unprofitable prey. Nevertheless, *P. napi* and *A. cardamines* are not unpalatable to avian predators.

3.4 Butterfly eyespots as a deflection mechanism (V)

Marginal eyespot patterns on wings did not enhance the butterflies' probability of being released alive once captured by lizards or birds. The proportion of attacks that resulted in wing tear and escape was equal in all butterfly forms (i.e. spotless, spotted) and this was true with both predators (Table 1). Moreover, eyespots did not decoy predators to attack wings instead of the body. The initial attacks of birds and lizards were equally likely to be directed toward wings, regardless of whether the butterfly had eyespot patterns or not. Thus I did not find any support for the importance of eyespots as an anti-predator mechanism as suggested earlier (Blest 1957, Brakefield 1984, Brakefield & Larsen 1984, Wourms & Wasserman 1985, Brakefield & Reitsma 1991).

We could regard the eyespots on *B. anynana* wings conspicuous enough to both lizards and birds because both are visually hunting predators with high-acuity vision (Fite & Lister 1981). Although *B. anynana, A. carolinensis,* and pied flycatcher do not occur in the same geographical area, the use of selected species as model animals is relevant because the goal was to study the importance of eyespots as an anti-predation mechanism in general. We can find similar ventral marginal spotting on the wings of other Satyrinae species as well. Additionally, since *A. carolinensis* and pied flycatcher are not specialised to catch butterflies, they may not be selected to improve their ability to capture butterflies and hence deceptive nature of eyespots should be at its best.

Despite the fact that butterflies are supposed to be more vulnerable to predation while resting (Muyshondt & Muyshondt 1976, Shapiro 1977, Young 1979, 1980, Larsen 1982, Dennis et al. 1986) eyespots might be more important while both the bird and the butterfly are flying. Because then the bird probably has less time available to decide its strike point in prey, it might grasp the wing. Additionally, the deflection function of eyespots perhaps manifests itself only under very specific conditions that could involve background patterning, light conditions and attack distance, for example. These aspects as well as the effect of naïve predators remain to be tested, preferably in nature.

TABLE 1 The fate of *B. anynana* butterflies attacked by lizards or by birds as predators.

	Lizards			Birds	
The form of *B. anynana*	Eaten (%)	Escaped with wing damages (%)	Escaped without contact (%)	Eaten (%)	Escaped with wing damages (%)
Spotless	58.7	9.9	31.4	61.9	38.1
Spotted	59.8	7.3	32.9	71.4	28.6
Bigeye-comet	56.2	11.1	32.7	-	-

4 CONCLUSIONS

The basic assumption in the theory of crypsis is that coloration could confer an adequate protection on a prey against potential predators only on one specific background. Therefore, the heterogeneous nature of many natural habitats has been supposed to be problematic from the prey's point of view. However, if a prey could possess coloration that renders it cryptic enough in several habitats, the prey could get rid of this constraint. My results show that this could be possible, at least under certain conditions. The cryptic colour pattern, which was a compromised solution of visual requirement of two microhabitats, did on the average better than either of cryptic forms (I). Thereby compromised coloration creates opportunities for prey to exploit two microhabitats instead of one without increased predation risk.

I did not find any strong evidence that colours based on UV reflection alone would have the potential to function as signals of unpalatability (II). Birds did not show preferences between palatable prey items differing only in UV reflection and more importantly, they did not learn effectively to avoid unpalatable prey items on the basis of differences in UV reflection. Birds had difficulties to learn to discriminate UV-reflecting unpalatable from UV-absorbing palatable prey items but the opposite task (UV+ palatable and UV- unpalatable) tended to be easier. Together these results point to the conclusion that UV cues might not deter effectively predators, instead they could be more likely to be associated with something edible. This conclusion is further supported by the experiment where UV reflection increased the probability of predation (III). Moths with UV-reflecting wings were eaten at a much higher rate than those without UV reflection. Thus UV reflection seems to invite attacks rather than to discourage predators. Additionally, more of the nocturnal than of the diurnal Lepidoptera species possess UV-reflecting wing patterns, probably because there is no negative selection by UV sensitive predators acting against UV patterns at night.

Birds did not reject *P. napi* or *A. cardamines* on sight or found them unpalatable. Therefore, it seems unlikely, at least with respect to unpalatability, that white coloration of Pieridae butterflies gives protection against visually hunting predators (IV). It is however possible that other features may make them less acceptable to predators. I found some indirect indications that the behaviour of the butterflies might render them unprofitable as prey. In outdoor cages where *P. napi* and *A. cardamines* were able to exhibit all their visual and olfactory cues, they experienced lower predation than did the control butterflies.

The marginal eyespots on butterfly wings did not seem to play a part in decoying attacks (V). The lack of difference in the survival of spotless and spotted butterflies suggests that the deflection hypothesis is not sufficient to explain the occurrence of eyespots on butterfly wings. However, it remains unclear whether these patterns are beneficial when both the prey and the predator are flying or when butterflies encounter a naïve predator. Perhaps eyespots act as an effective deflection mechanism to avoid predation under very specific conditions which are ideal only in nature. The eyespot patterns might also be a trait maintained by sexual selection (Roskam & Brakefield 1996) and may represent a trade-off between sexual selection and predation avoidance. All these points remain to be investigated.

As the results of the Pieridae experiment pointed out (III), prey animals do not take advantages of only one defence mechanism against their predators but they might utilise several means to avoid predation. Some of them might be used at greater distance (aposematic colours) while the others give protection when the enemy is at closer proximity (e.g., odour). Furthermore, advantages of many defence mechanisms are regarded to be so obvious and self-evident facts that they have not been studied watertight (Lederhouse 1990). My thesis question whether assumptions, like the white coloration of Pieridae (III) and the butterfly eyespots (V) that have been considered to improve the survival of prey function as has been assumed. The results underline the importance of testing experimentally any classical hypotheses in order to fill the gaps in our knowledge. Although insect defence coloration and colour patterns have been the subject of studies for decades, theoretical and empirical investigations might still reveal new aspects of defence mechanisms.

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YHTEENVETO

Hyönteisten väritys puolustuksessa vihollisia vastaan

Eläimet käyttävät väritystään mm. suojautuakseen saalistajilta. Useat ravinnoksi kelpaavat lajit pyrkivät sulautumaan taustaansa suojavärin, kryptisyyden, avulla kun taas pahanmakuiset lajit viestittävät räikeillä väreillä olevansa syötäväksi kelpaamattomia (aposematismi). Kokeellisesti on osoitettu pahanmakuisten eläinten hyötyvän kirkkaasta väristään, vaikka se lisääkin havaittavuutta (esim. Gittleman & Harvey 1980, Lindström et al. 1999b, 2001b, c). Saalistaja sekä oppii tehokkaammin (Gittleman & Harvey 1980, Gittleman et al. 1980, Sillén-Tullberg 1985, Alatalo & Mappes 1996, Lindström et al. 1999b, 2001b, c) että muistaa tämän assosiaation pidempään (Roper & Redston 1987) kuin jos saalis olisi kryptinen. Sekä syötävyyden että näkyvyyden kannalta kryptiset ja aposemaattiset eläimet edustavatkin kahta ääripäätä. Eräät perhoslajit eivät turvaudu kryptiseen tai aposemaattiseen väritykseen puolustusmekanisminaan, vaan niillä on siipien reunoilla silmätäpliä. Tämän kuvioinnin on oletettu harhauttavan saalistajaa kohdistamaan hyökkäyksensä siipiin, jolloin perhosella olisi mahdollisuus paeta. Väitöskirjani koostuu tutkimuksista, joissa tavoitteena on ollut kokeellisesti testata näihin puolustuskeinoihin liittyviä oletuksia ja hypoteeseja.

Endlerin (1978) määritelmän mukaan eläin voi olla kryptinen vain yhdellä taustatyypillä. Eläimet kuitenkin harvoin viettävät koko elämäänsä samalla habitaatilla, ja niinpä ne joutuvatkin aika-ajoin taustalle, jossa niiden värityksen antama suoja ei olekaan täydellinen. Merilaita et al. (1999) esittivät matemaattisen mallin, jonka mukaan kryptinen väritys voisikin olla kahden mikrohabitaatin vaatimusten kompromissi. Testasin tätä mallia kokeella, jossa linnuille esitettiin kolmenlaisia saaliita kahdella eri taustalla (I). Siten aina yksi saalistyyppi oli kryptinen toisen ollessa erittäin näkyvä; kolmas saalistyyppi oli näkyvyydeltään näiden kahden välistä. Tämä kompromissi vältti saalistuksen tehokkaammin kuin kumpikaan taustaansa täydellisesti sulautuva kryptinen saalis. Tulos osoittaa, että suojaväri, joka olisi kahden eri habitaatin vaatimusten lopputulos, olisi ainakin teoreettisesti mahdollinen.

Värien tutkimuksessa keskityttiin pitkään vain ihmissilmällä aistittavan valon spektrialueeseen (Cuthill & Bennett 1993, Bennett et al. 1994). Nykyään on kuitenkin herännyt kiinnostus ottaa tutkimuksiin mukaan sähkömagneettisen säteilyn aallonpituusalueita, joita ihminen ei kykene näköaistillaan havaitsemaan (ultraviolettivalo, 320 - 400 nm), mutta jotka ovat osa lintujen värinäköaluetta (ks. esim. Viitala et al. 1995, Church et al. 1998a,b). Käsityksemme hyönteisten kryptisyydestä ja aposemaattisuudesta saattaakin muuttua, sillä ihmissilmälle kryptinen hyönteinen voikin UV-valoa heijastavana olla hyvinkin voimakkaasti taustastaan erottuva (Church et al. 1998b). Tällaisten lajien on esitetty käyttävän vain UV-valossa näkyviä varoitussignaaleja (Church et al. 1998b). Testatakseni tätä hypoteesia tein kokeen, jossa käytin keinotekoisia saaliita (II). Jos tietty väri toimii signaalina pahanmakuisuudesta, luonnosta pyydettyjen, kokeneiden lintujen pitäisi välttää ko. värisiä saaliita. Linnuilla ei kuitenkaan havaittu preferenssieroja UV:tä heijastavien ja heijastamattomien saalistyyppien välillä. Kokeessa selvitin myös, oppivatko linnut erottamaan pahanmakuisen saaliin hyvänmakuisesta, kun saaliit eroavat väritykseltään toisistaan vain UV-alueella. Linnut eivät oppineet välttämään pahanmakuisia saaliita, vaan pikemminkin ne oppivat yhdistämään UV-heijastuksen signaalina saaliin syötävyydestä. Näin ollen kokeiden tulokset viittaavat siihen, etteivät UV-signaalit yksinään toimisi tehokkaina varoitussignaaleina.

Myös tekemäni kokeet elävillä perhosilla viittaavat siihen, että UV-signaalit eivät toimisi varoitussignaaleina vaan pikemminkin lisäävät hyönteisen riskiä tulla saalistetuksi (III). Manipuloin osan perhosista heijastamaan ja osan absorboimaan UV-valoa. Tämän jälkeen asetin perhoset luontoon ja tarkkailin niiden selviytymistä. Kokeen mukaan UV-heijastus perhosten siivissä lisäsi saaliiksi joutumisen todennäköisyyttä päivällä. Sen sijaan yöllä näiden kahden koeryhmän selviytymisessä ei havaittu eroa. Tämä osaltaan selittäisi sen, miksi linnut eivät oppineet välttämään pahanmakuista, UV-valoa heijastavaa saalista. Kiinnostavaa on, että yöaktiivisten perhosten siivissä on yleensä UV-valossa näkyviä kuviointia, mitkä puuttuvat päiväaktiivisten perhosten siivistä. Yöperhosten tärkeimpiä saalistajia ovat todennäköisesti lepakot ja jyrsijät, jotka eivät käytä saalistuksessa näköaistia vaan paikantavat saaliinsa kuulo- tai hajuaistin avulla. Siten yöaktiivisille perhosille siipien UV-heijasteet eivät aiheuta lisäkustannuksia saalistuksen muodossa.

Ilmiötä, jossa kaksi tai useampi pahanmakuista lajia muistuttavat väritykseltään toisiaan, kutsutaan Müllerin mimikryksi (Müller 1879). Pieridae heimon perhosten, jotka ovat yleisväritykseltään joko keltaisia tai valkoisia, on esitetty muodostavan mimikryryhmän (Marsh & Rothchild 1974). Aikaisemmat tutkimukset ovat antaneet viitteitä siitä, että heimoon kuuluvat lanttu- (*Pieris napi*) ja auroraperhoset (*Anthocharis cardamines*) eivät ehkä olekaan riittävän pahanmakuisia, jotta niitä voitaisiin kutsua Müllerin mimikryksi (Kingsolver 1987, Ley & Watt 1989). Testasin tätä mimikryhypoteesia sekä luonnossa että laboratoriossa (IV). Linnut valitsivat lanttu- ja auroraperhosen sekä kahden eiaposemaattisen perhosen joukosta mieluisimman saaliin. Mikäli valkoinen väritys suojaa perhosta saalistukselta, tulisi lintujen syödä valkoiset perhoset koeasetelmassa viimeisenä tai olla koskematta niihin lainkaan. Perhosten ottojärjestyksessä ei kuitenkaan havaittu eroa, ts. valkoinen väritys ei näyttäisikään suojaavan näitä perhosia. Makutestikään, jossa talitiaisten annettiin syödä perhonen, ei antanut tukea mimikryhypoteesille: linnut eivät pitäneet erityisen pahanmakuisina ko. perhoslajeja. Emme voi kuitenkaan täysin hylätä aposematismin mahdollisuutta, koska perhosten muut ominaisuudet, kuten nopea lento tai haju, voivat tehdä niistä saaliiksi kelpaamattomia. Kokeen tulokset, jossa linnut pyydystivät ulkohäkkeihin vapautettuja virna-, lanttu- ja auroraperhosia, antoivat epäsuoraa tukea tällä oletukselle. Näissä luonnollisemmissa olosuhteissa kirjosiepot söivät enemmän virnaperhosia kuin lanttu- tai auroraperhosia.

Perhosten siipien reunoilla sijaitsevien silmäkuvioiden on esitetty harhauttavan saalistajaa kohdistamaan hyökkäysiskunsa siipiin, jotka hauraina rakenteina repeytyvät helposti mahdollistaen perhosen pakenemisen saalistajan otteesta (Blest 1957, Young 1979, 1980, Brakefield 1984, Wourms & Wasserman

1985, Brakefield & Reitsma 1991). Tällöin perhonen lentäisi pois vain suhteellisen vähän vahingoittuneena. Saalistusyrityksessä vahingoittuneita siipiä on havaittu enemmän silmäkuviollisilla kuin kuviottomilla perhosilla (mm. Muyshondt & Muyshondt 1976, Shapiro 1977, Young 1980), ja tätä on pidetty osoituksena silmätäplien merkityksestä perhosen puolustusmekanismina. Oletukset silmätäplien hyödyllisyydestä perustuvatkin lähinnä juuri siipien vaurioiden (ns. beak marks) kartoittamiseen. Kokeellisesti ei ole kuitenkaan osoitettu, että silmätäplät olisivat tehokas puolustusmekanismi. Siten tutkin, vaikuttavatko silmätäplät todellakin perhosen selviytymiseen tai hyökkäyksen suuntaan (V). Käytin kokeessa mallisaalistajana hyönteisiä syöviä liskoja, *Anolis carolinensis* (Iguanidae), ja saaliina kolmea *Bicyclus anynana* (Satyrinae) muotoa. Näistä ns. sadekauden muodolla on takasiipien alapinnalla seitsemän silmätäplää, joita ei ole kuivakauden perhosilla, ja siten perhoset ovat yleisväritykseltään ruskeita. Näiden kahden muodon lisäksi käytin Bigeye comet -mutanttia, jonka siipien silmätäplät ovat kooltaan normaalia suuremmat. Hyökkäyksessä pakoonpäässeiden osuudet eivät eronneet näiden kolmen ryhmän välillä. Silmätäplät eivät myöskään ohjanneet hyökkäystä pois ruumista siipiin eivätkä täplät siten näyttäisi harhauttavan saalistajaa. Testatakseni, onko silmätäplillä enemmän merkitystä silloin, kun saalistajana ovat linnut, tein kokeen, jossa kirjosiepot saalistivat *B. anynana*'n täplällisiä ja täplättömiä muotoja. Myöskään tällöin ei selviytymisessä tai hyökkäyksen kohdistamisessa eri muotojen välillä ollut eroa.

Eräitä hyönteisten puolustusmekanismeja on pidetty niin itsestään selvinä, ettei niiden testaamiseen ole nähty aihetta (Lederhouse 1990). Väitöskirjani osoittaa ainakin joidenkin näistä olettamuksista olevan kyseenalaisia (IV, V). Lintujen on väitetty karttavan valkoisia perhosia, mutta kokeeni mukaan valkoinen väri ei olisikaan signaali pahanmakuisuudesta. Samoin vuosikymmeniä on pidetty silmätäplien ohjaavan saalistajan hyökkäykset siipiin. Näin ei kuitenkaan näyttäisi olevan.

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Original papers

I

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by

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II

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III

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IV

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V

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

by

Anne Lyytinen, Paul M. Brakefield & Johanna Mappes

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