# COLOUR PATTERNS
# IN WARNING DISPLAYS

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2012

**Colour patterns in warning displays**

Doctoral dissertation 2012

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*To my family!*

# Abstract

In aposematism a prey species use bright colours, often combined with a black contrasting pattern, to signal unprofitability as prey to potential predators. Although there are several different hypotheses about the presence of these internally contrasting patterns, there is little experimental evidence of any beneficial effects. In this thesis I have used bird predators and artificial prey signals to investigate if the contrasting internal patterns in warning displays may have evolved to increase signal efficacy, especially regarding the speed of avoidance learning. In **paper I** the relative importance of colour and pattern in avoidance learning was studied. The conclusion was that birds primarily attend to colour, not pattern, when learning the discrimination, which was further supported by the results in **paper II-IV**, all suggesting a secondary role of patterns. In **paper II** I show that predators may to some degree use patterns for discrimination, if they convey important information about prey quality. The predators showed a hierarchical way of learning warning colour components, where colour is learned to a higher degree than pattern. In **paper III** I investigate if internal contrasting patterns promote avoidance learning by increasing conspicuousness as prey-to-background contrast does. The study did not support this idea, as the presence of internal black patterns did not improve avoidance learning on a colour matching background. In **paper IV**, however, I show that the presence of many internal colour boundaries resulted in faster avoidance learning on a multi-coloured background, and predator generalization favoured more internal boundaries, while there was no effect of pattern regularity. From these studies I conclude that internal pattern contrasts may function to increase the efficacy of the warning colour, its salience, and as a means for aposematic prey to be discriminated from harmful mimics. However, the major finding is the importance of colour over pattern.

# List of papers

**I.** Aronsson, M. & Gamberale-Stille, G. 2008. Domestic chicks primarily attend to colour, not pattern, when learning an aposematic coloration. *Animal Behaviour* **75**, 417-423.

**II.** Aronsson, M. & Gamberale-Stille, G. Colour and pattern similarity in mimicry - evidence for a hierarchical discriminative learning of warning colour pattern components. *Submitted manuscript.*

**III.** Aronsson, M. & Gamberale-Stille, G. 2009. Importance of internal pattern contrast and contrast against the background in aposematic signals. *Behavioral Ecology* **20**, 1356-1362.

**IV.** Aronsson, M. & Gamberale-Stille, G. Why do aposematic prey often have contrasting internal patterns? -Evidence of benefits through predator avoidance learning and generalization. *Submitted manuscript.*

# Table of contents

“It would be highly advantageous to a caterpillar to be instantaneously and certainly recognised as unpalatable by all birds and other animals. Thus the most gaudy colours would be serviceable, and might have been gained by variation and the survival of the most easily-recognised individuals.”

*Charles Darwin, 1871*

# Introduction

Imagine yourself being a tiny little bug sitting on a plant. The most important thing for you is to live long enough to be able to reproduce and one important part of that is to avoid being predated on. There are two main strategies used by animals to increase their chances of survival. The first strategy, called crypsis, focuses on the predators not being able to detect the prey (Ruxton et al. 2004). When it comes to the other strategy (aposematism), the animals use a bright coloration to signal to potential predators that they are unprofitable as prey, due to for instance spines or toxins (Cott 1940).

Aposematic animals are often bright red, orange or yellow in combination with a black pattern (Cott 1940) causing a contrast not only against the background colour of their habitat, but also within the colour pattern itself (Fig. 1). The common view is that these bright colours have

**Figure 1.** Two examples of aposematic species, the shield bug *Graphosoma lineatum*, and the Apollo butterfly larvae, *Parnassius apollo*. Photo: Aleksandra I. Johansen & Titti Bohlin

evolved because they are easy for potential predators to learn and associate with unpalatability (Poulton 1890; Gittleman & Harvey 1980). Apart from being easily recognized and discriminated from the background (Turner 1975; Guilford & Dawkins 1991), they are also different from the cryptic prey species that the predators usually hunt, which minimizes confusion (Edmunds 1974; Turner 1975; Sherratt & Beatty 2003; Guilford 1986; 1990; Guilford & Dawkins 1991; Stevens & Ruxton 2012). Experiments have shown that predators can learn to avoid prey that are background matching in colour, but since conspicuously coloured prey are for example easier to learn and that the increased prey-to-background contrast has a positive effect on predator avoidance learning (Gittleman & Harvey 1980; Gittleman et al. 1980) it suggests that the bright colours have evolved for this purpose. There are also a number of suggested ways by which warning signals may enhance aposematic survival: 1) through enhanced neophobia (meaning reluctance to sample novel prey) (Schuler & Roper 1992); 2) dietary conservatism (Thomas et al. 2003; Lee et al. 2010) (which compared to neophobia lasts longer, Marples & Kelly 1999); 3) by reducing or preventing predators from forgetting aversive experiences (Speed 2000), and it has been thought to 4) increase signal salience since easiness to discriminate and memorize is important parts of an effective signal (Guilford & Dawkins 1991). While a cryptic species often is restricted to a certain background where it blends in and is limited in its activity since movement reveals the position, aposematic species are released from these restrictions (Merilaita & Tullberg 2005). This gives them a greater freedom to take advantage of available resources, which in turn may select for the evolution of aposematism (Speed et al. 2009). During the last decades, the research field of aposematism has increased. Although mostly studied in insects and other terrestrial arthropods, it is widespread in other invertebrate taxa (Komárek 1998) and occurs in vertebrates, like mammals (Caro 2009), amphibians, reptiles and fishes (Santos et al. 2003) as well.

### *Visual signals, predator perception & psychology*

There are several different strategies used in animal communication, both within and between species, and signals are traits that are specialized for communication (Johnstone 1997) and that benefits the sender by altering the behaviour of the receiver (Hasson 1994). For an aposematic signaller, it is important to use displays that match the sensory system of the predators (Guilford & Dawkins 1991; Endler 1992) since some animals rely more on either smell, vibrations, sound or vision (Schmidt-Nielsen 1990). In addition to that, signals vary depending on the distance and relative orientation between the sender and the receiver, all of which affect the receiver's perception of and response to the signal and hence the selection of signals (Enquist & Arak 1994).

In order to study the effect of different aposematic patterns on predators, it is important to consider the predator's perspective. Apart from their visual ability, and their ability to detect the aposematic prey's chemical defence, one also needs knowledge about the predator's ability to learn, discriminate and generalize. Early studies of how animals learn compound stimuli, consisting of two or more components, show that they foremost attend to the most salient component within the compound if it is sufficient to predict the message (Pavlov 1927; Kamin 1969). There are many situations in which a receiver benefits from the knowledge of what a signaller is trying to transmit. Since the colour pattern of, for example, an insect may appear different depending on whether it is flying or not (Kassarov 2003) a predator has to be able to recognize the prey in different situations and hence some sort of predator generalization behaviour should be of importance. Generalization is also an important part in Batesian mimicry systems, were one palatable species (the mimic) resembles an unpalatable prey species (the model). This system requires that predators generalize their avoidance behaviour such that they avoid the poorer mimics more than non-mimetic forms, and that predators discriminate by avoiding the good mimics more than they avoid poorer mimics (Shideler 1973). Another important part for a predator is to use environmental cues since the profitability (due to sequestered plant toxins) and availability (due to e.g. season or habitat) of a prey can vary depending on context making it beneficial for the predator to attack in some contexts and ignore prey in others (Hansen et al. 2010).

### *Aposematic signal design*

Aposematic animals often have bright colours that contrast not only with the background but also within the colour pattern itself, and it has been suggested that these colours give the maximum visibility against natural colours of the environment (Cott 1940). As mentioned above, it is common with red, yellow and black colours and Stevens and Ruxton (2012) have listed a number of hypotheses about why those specific colours dominate: 1) they promote detection by providing a high prey-to-background contrast (since ”many animals are thought to have red–green opponent processing mechanisms in their colour vision”); 2) they keep the signal reliable independent of habitats and light conditions (shadows make animals having colours with shorter wavelengths (blue-UV) blend in with the background); 3) they allow camouflage at distance when the yellow/red and black blur together to an average colour and hence matches the background, and, finally 4) they are easy to distinguish from profitable species. Additionally, Guilford (1986) suggests that by being conspicuous a prey may be detected and recognized as unprofitable in time for experienced predators to be able to correct recognition errors and abort the attack. Another reason for conspicuousness in warning signals could be that a bird trained to avoid, for example, a red object, will afterwards show a stronger response to a more saturated red (Gamberale-Stille & Tullberg 1999). Such biased responses could explain why some signals have evolved to be more colourful and/or distinct than others (Leimar et al. 1986).

One important component of an aposematic signal is conspicuousness and it involves features such as brightness, hue, colour intensity and prey-to-background contrast (Harvey & Paxton 1981).

There are different, not mutually exclusive, ways of increasing detectability of a colour pattern. One way is to have a colour pattern that contrasts with the prey's background (e.g. Gittleman & Harvey 1980), while another is to have contrasting colour patches within the colour pattern (Poulton 1890; Endler 1992) that vary greatly in brightness, hue and chroma (Endler 1990). Having such contrasting colour pattern elements adjacent to each other is not only used in aposematism, but also in crypsis, for instance a disruptive coloration, where colours and patterns are used to camouflage the body shape (Cott, 1940; Edmunds, 1974). In disruptive colouration the pattern is used to draw predator attention away from the body outline or other important characteristics that might increase detection (Cott 1940; Cuthill et al. 2005; Merilaita & Lind 2005; Dimitrova 2009). It has been suggested (Papageorgis 1975) and shown (Tullberg et al. 2005, Bohlin et al. 2008) that not all aposematic animals are maximized in their conspicuousness and that they rather combine crypsis at distance with aposematism when close up. This suggests that the function of a warning colour is to aid identification and association with unpalatability upon discovery, and not for increased detection as such (Gamberale-Stille et al. 2009). As mentioned above, contrasting internal patterns may also work disruptively and increase crypsis. There is, however, little experimental evidence of beneficial effects of internal contrasting patterns on warning colour efficacy, especially with regard to the speed of avoidance learning.

There are several different hypotheses for why aposematic animals often have an internally contrasting pattern. It has, for instance, been suggested that some colours and patterns are more memory stimulating (Rothschild, 1984) and that different parts of a colour pattern play different roles, where the contrasting (black) pattern attracts predator attention and the colours are remembered more accurately (Osorio et al. 1999a). Another suggestion is that pattern repetition (e.g. stripes) makes the prey individual "stand out" from the irregular background in nature and hence improves recognition (Kenward et al. 2004; Stevens & Ruxton 2012). Stevens and Ruxton (2012) also suggest that stripes and spots, by being simple patterns components and if they are easier to memorize, might aid detection and speed up avoidance learning. It has also been suggested that symmetric patterns can influence detection and the association with unpalatability (Forsman & Herrström 2004) and studies have shown that birds avoid unpalatable prey with symmetrical more than asymmetrically sized markings at the first encounter (Forsman & Merilaita 1999). Another suggestion is that symmetrical patterns in colour signals could be a way to have a strong signal independently of its position and orientation in the predator's visual field (Enquist & Arak

1994). Symmetrical colour patterns are very common in nature but an explanation for that could be that it reflects developmental constraints rather than being selected for some signalling function (Stevens & Ruxton 2012). Table 1 shows a list of these and other hypotheses for why aposematic animals often have an internally contrasting pattern.

**Table 1.** Suggested explanations for the presence of internally contrasting patterns in aposematic prey.

| ***Aposematic trait*** | ***References*** |
|---|---|
| ***A contrasting pattern*** | |
| Stimulate memorability and learning in predators | Rothschild 1984 |
| Increased signal salience by internal colour boundaries | Guilford 1990 |
| Lateral inhibition – magnifies the effect of contrast | Kenward et al. 2004 |
| Improves discrimination from palatable prey | Cott 1940; Sherratt & Beatty 2003 |
| A way for a  model to escape the negative effects of Batesian mimics; giving the predators a way to discriminate them from cheats | Fisher 1930 (in Sherrat & Beatty 2003) |
| Cryptic at distance + highly conspicuous at a shorter distance | Papageorgis 1975; Tullberg et al. 2005 |
| Facilitates the learning of a specific hue | Rowe & Guilford 2000 |
| Contrasting patterns attract the attention, other colours give specific information and are remembered more accurately | Osorio et al. 1999a |
| Aquatic animals appear differently coloured at different water depths, in such circumstances the actual pattern may be more important than the coloration | Ang & Newman 1998 |
| Decrease the cost aposematism by providing a disruptive effect | Tullberg et al. 2005; Bohlin et al. 2008 |
| ***Repetition of a pattern*** | |
| Regular patterns may stand out in a chaotic environment and hence improve recognition | Kenward et al. 2004 |
| Consistent signal - similar from all angles of attack or if partially covered, hence less likely confused with palatable prey | Guilford 1990; Guilford & Dawkins 1991 |
| Stripes - may increase visibility in daylight, while cryptic in poor light | Rev. in Ruxton 2002 |
| Stripes - might make it more difficult to single out an individual from a group | Rev. in Ruxton 2002 |
| Stripes and spots - might aid detection and speed up avoidance learning | Stevens & Ruxton 2012 |

In this thesis I have focused on the role of colour patterns in warning displays with the following questions:

**Paper I** What do birds attend to when learning a warning colour pattern?

**Paper II** Do birds learn different components of colour patterns depending on the information about prey palatability they convey?

**Paper III** Can the colour patterns of aposematic prey be explained by the effect of contrast against the background?

**Paper IV** Does an increased amount of internal pattern boundaries, pattern regularity or symmetry have positive effects on avoidance learning?

# Methods

Of the four studies presented here, three were performed at the Department of Zoology, Stockholm University, with newly hatched domestic chicks (*Gallus gallus domesticus*) (**paper I-III**, Fig. 2) and one at Tovetorp Zoological Research Station, Stockholm University, with wild caught blue tits (*Cyanistes caeruleus*) (**paper IV**, Fig. 3). All studies were experiments of predator behaviour with artificial prey and backgrounds and below I describe the methods used.

## *The predators*

In all four studies, birds have been used as predators. They are, compared to all other vertebrates, the most visually dependent (McFadden 1993), can detect small size differences and details of the stimuli and are “well

**Figure 2.** A newly hatched chick, *Gallus gallus domesticus.*

**Figure 3.** A wild caught blue tit, *Cyanistes caeruleus*.

adapted to the high-contrast properties of the visual world" (Hodos 1993). Furthermore, they have a very good colour vision and chicks have been shown to be able to notice and learn colour differences that are barely visible to humans (Osorio et al. 1999b). Being such visually dependent predators, birds are likely to have a great influence on the appearance of their prey (in this case - warning coloration).

I used male domestic chicks as predators in **paper I**, **II** and **III** (Fig. 2). Chicks are easy to hold and handle and are quite convenient for the kind of experiments I have performed. They are easily trained and they are precocial and hence can feed by themselves already as newly hatched. This gives the advantage of being able to control for their total earlier food experience before attending the experiments, which is often of interest since previous experiences may affect responses to aposematic prey. In **paper IV** I used wild caught blue tits (Fig. 3), a widespread passerine species found throughout the year in Sweden (Nilsson et al. 2008) and representing a common omnivorous avian predator in the study area. This study was performed during the winter of 2011 and the birds were trapped outside their breeding season close to the research station using mist nets and trap cages. They were kept indoors in individual cages and released at the site of capture after the experiment.

### *General procedures*

For the experiments with the chicks (paper I-III), the experimental arena (120 x 120 x 30 cm high) had a 25 cm wide runway surrounding a smaller enclosure with net walls (Fig. 4). There were 32 circular wells in which the prey-stimuli were presented, spaced uniformly along the runway. In paper I all of the wells were used, in paper II 30 wells were used while two were covered and in paper III every second well was covered leaving 16 wells for presenting prey. The smaller enclosure in the middle was used for companion chicks to reduce stress during the pre-experimental training. In all these experiments the first two days after arrival were used to train the chicks

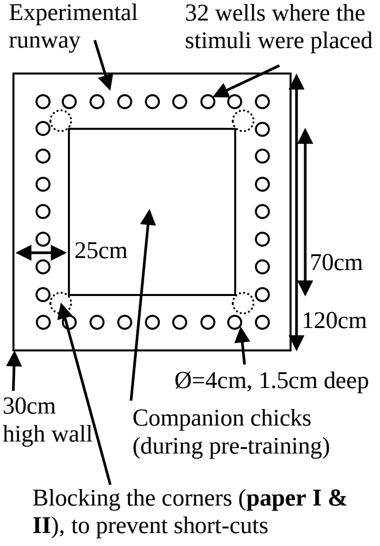



**Figure 4.** The experimental arena used in **paper I-III**.

to forage alone in the experimental arena as well as to get them accustomed to the palatable prey used in the experiment (paper III).

For the experiment with the blue tits (**paper IV**) two experimental identical rooms (229 x 240 x 190 cm) were used (Fig. 5). They had one-way-mirrors (70.5 x 45.5 cm) on two of the walls, through which the bird could be observed. A perch was placed in a corner and the experimental board (62 x 120 cm) was placed on the floor next to a water bowl. The board was painted white with an irregular multi-coloured pattern and had twelve holes (1 cm Ø), which were evenly spread out, to place mealworms in.

**Figure 5.** One of the experimental rooms used for the experiment with the blue tits in **paper IV**.

### *The prey*

In all experiments birds were trained to forage on dead mealworms (*Tenebrio molitor*) (Fig. 6) that were placed on top of (**paper I-III**) or under (**paper IV**) coloured paper. All paper stimuli were created with Adobe Illustrator CS2 12.0.1 and printed on white office paper. Although this experimental set-up is quite different from a natural foraging situation, it allows me to control for prey signal, encounter rate (important when comparing learning speed) as well as the salience of the stimuli. Using this method, presenting a paper stimulus in association with a rewarding or punishing food item, is common in the field of experimental psychology when the focus is on animal learning mechanisms, and has been frequent in aposematism and mimicry research (e.g. Terhune 1977; Osorio et al. 1999a; Gamberale-Stille & Guilford 2003; Forsman & Herrström 2004).

**Figure 6.** The prey used in the experiments were mealworms, *Tenebrio molitor*.
Photo: Aleksandra I. Johansen

# Paper I

*Domestic chicks primarily attend to colour,*
*not pattern, when learning an aposematic coloration.*

Many aposematic animals have a colour pattern that, apart from bright colours, also consists of contrasting internal patterns that contrast with each other producing internal boundaries (e.g. red or yellow coloration with a black pattern) (Cott 1940). There have been several attempts trying to explain these bright colours (e.g. Roper & Wistow 1986; Roper & Redston 1987; Lindström et al. 2001; Gamberale-Stille 2001). However, these studies have been focused on the bright colour per se and not the internal contrasting patterns.

The aim of the first study was to investigate the relative importance of colour and pattern in avoidance learning, by investigating which aspects a bird predator attends to when learning a warning colour pattern. The experimental colour patterns consisted of a bright colour and a contrasting black pattern that both predict the unpalatability of the prey. An additional aim was to investigate if birds may find one pattern more attention grabbing than another by comparing differences in discrimination learning between patterns consisting of dots and stripes. I investigated this by measuring the speed of discrimination learning in young domestic chicks, followed by a generalization test to determine what the birds had learned about the colour pattern.

In this experiment a half dead mealworm (unconditioned stimulus, US) was placed centrally on top of a paper rectangle (2.5 x 1.5 cm) on which the signal was printed (conditioned stimulus, CS). The mealworms were either palatable (frozen, cut in halves and re-frozen) or made distasteful by soaking them in a 3% solution of quinine hydrochloride for 2 h (frozen, cut in halves, soaked and re-frozen). Two types of negative stimuli were used, both with a cyan background colour and a black contrasting pattern consisting of either three black stripes or three black dots (Fig. 7). The sizes of the black areas were the same for the dots and stripes ($\approx 0.15$ $cm^2$). As positive stimulus I used a uniformly grey coloured paper rectangle, with a similar saturation as the cyan colour.

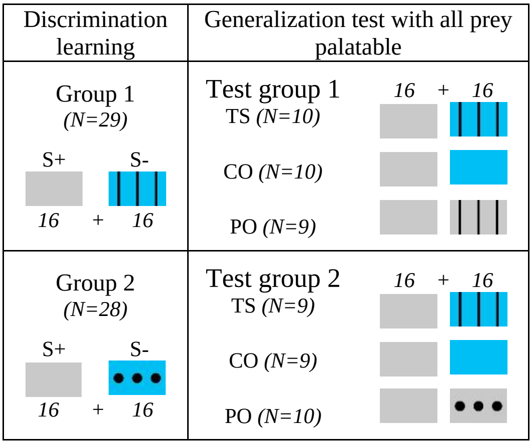



**Figure 7.** The experimental set-up in **paper I**. Two groups of birds participated in seven trials of discrimination learning with grey positive stimuli and cyan negative stimuli with either black stripes (Group 1) or dots (Group 2). Followed by a generalization test where birds in each test group received one of the three presentations: TS - “training stimulus”, CO - “colour only” or PO - “pattern only”.

## *Results paper I*

Chicks from both groups learned to discriminate between the palatable grey and the distasteful cyan with pattern and the results showed that there was no difference between the two pattern types, dots and stripes, on either learning rate or generalization behaviour.

The generalization test showed that chicks in both “colour only” and “training stimulus” significantly avoided their test prey, but “pattern only” did not (Fig. 8). There was no difference in avoidance between “colour only” and “training stimulus”. This demonstrates that the chicks generalized their learned avoidance of the “training stimulus” completely to the test stimuli with only the colour present but not to prey with only the pattern.

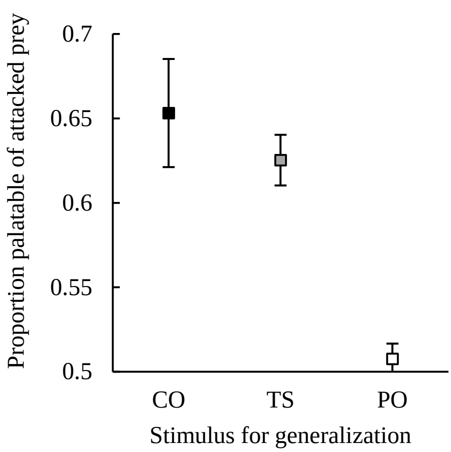



**Figure 8.** The proportion of all attacked prey that had the positive stimulus in a generalization test (mean ± SE). CO represent birds with the “colour only” presentation, TS the “training stimulus”, and PO the “pattern only”. Data from both test groups are pooled in the figure.

# Paper II

*Colour and pattern similarity in mimicry*
*- evidence for a hierarchical discriminative learning*
*of warning colour pattern components.*

In many systems in nature, there are cheaters trying to get the advantages without paying the costs, and in the case of warning signals the cheaters are the palatable mimics. In mimicry, palatable prey either mimics the visual appearance of a distasteful model as in Batesian mimicry; trying to lure the predators that they too are distasteful (Bates 1862). Or two or more defended prey species share the same warning colour pattern, as in Müllerian mimicry (Müller 1879), where they supposedly share the cost of predator education (Müller 1879; Rowland et al. 2010). How similar the mimics are to the models with regard to both colour and patterns varies (e.g. Ruxton et al. 2004). Even though the importance of colour over pattern has been repeatedly shown (Terhune 1977; Exnerová et al. 2006; **paper I**), it has also been shown that birds are able to use both colour and pattern (chicks, Vallortigara et al. 1990) as well as number of stripes and stripe colour (pigeons, Bain et al. 2007). Such qualities could be of importance for a predator when learning to discriminate between models and their mimics.

The aim of the second study was to investigate if predators may use different warning colour components for discrimination depending on the information about prey quality they convey. This was done by investigating if the presence of imperfect palatable mimics, a colour mimic or a pattern mimic, would increase the birds' attention to the existence of a pattern or the actual shape of the pattern in the negative stimuli.

The prey and the handling of the prey in this experiment were similar to that in **paper I** but with different treatment groups (Fig. 9). The chicks were divided into four groups with patterns designed to represent situations where the birds needed to attend to different parts of the colour pattern of the prey stimulus to solve the discrimination task. I used one type of negative stimulus with a cyan background colour and a pattern consisting of three black stripes. The positive stimulus varied between groups; plain grey (with a similar saturation as the cyan colour of the stimuli), plain cyan, or, cyan background colour and a pattern consisting of three black dots. The sizes of the black areas were the same for the stripes and dots ($\approx 0.15$ cm$^2$).

| Group | Distasteful model S- | Palatable mimic S+ | Palatable prey S+ |
|---|---|---|---|
| colour OR pattern *(N = 21)* | *(10)* | | *(20)* |
| colour AND pattern *(N = 21)* | *(10)* | *(10)* | *(10)* |
| pattern only *(N = 22)* | *(10)* | | *(20)* |
| pattern shape *(N = 22)* | *(10)* | *(10)* | *(10)* |

**Figure 9.** The experimental set-up for **paper II**. Four groups of chicks participated in 15 trials of discrimination learning with cyan and striped negative stimulus. The positive stimuli differed between uniformly grey, uniformly cyan and cyan with dots, depending on groups.

## *Results paper II*

Chicks in all groups, except in "pattern only", attacked the palatable prey significantly more than the unpalatable prey (Fig. 10). When comparing between the groups, the results suggest that discrimination learning was faster in the groups where colour could be used for the discrimination.

Furthermore I compared the attacks on mimics and models (the unpalatable prey) in the two mimic treatments (see Fig. 9 & 10). My results show that in the "colour AND pattern" treatment the mimic was attacked significantly less than the palatable prey and the model was attacked significantly less than both the palatable prey and the mimic. In the "pattern shape" treatment however, both the model and the mimic were attacked significantly less than the palatable prey, but there was no difference between the model and the mimic, suggesting that no pattern shape discrimination had developed.

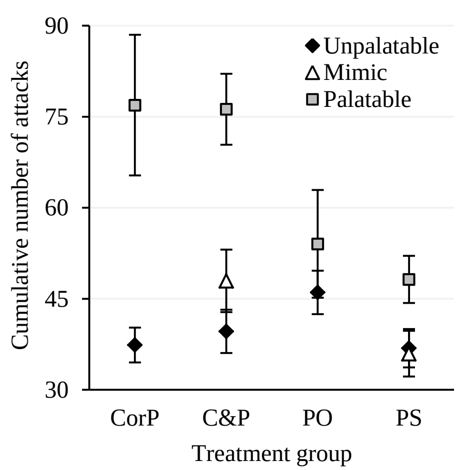



**Figure 10.** The cumulative number of attacks (mean ± 1SE) after 15 trials of discrimination learning for the different treatment groups: "colour OR pattern" (CorP), "colour AND pattern" (C&P), "pattern only" (PO) and "pattern shape" (PS).

# Paper III

*Importance of internal pattern contrast*
*and contrast against the background in aposematic signals.*

Earlier studies have shown that contrast between the prey coloration and the colour of the background increases the speed and durability of avoidance learning (Roper & Wistow 1986; Roper & Redston 1987). These effects have also been thought to explain the existence of the so common internal contrasting colour patterns (Guilford 1990). Guilford suggests that prey by producing its own internal colour boundaries of high contrast will promote conspicuousness and thus the aposematic effect. Still, to my knowledge, there is little experimental evidence for such a corresponding effect of conspicuousness generated by internal pattern contrasts.

The aim of this study was to determine if one can generalize the positive effects of conspicuousness generated by contrast against the background to include the contrast made by internal colour patterns. That is, to investigate the separate effects of prey-to-background contrast and within-prey pattern contrast on avoidance learning in domestic chicks. As well as to investigate if internal contrasting patterns can increase conspicuousness when prey are on backgrounds to which the bright colours do not contrast very much. This was done by measuring the speed of discrimination learning in young domestic chicks, followed by a generalization test.

Birds were trained to discriminate aposematic plain red or red-black striped mealworms (*Tenebrio molitor*) from palatable brown mealworms either on a red or on a brown background (Fig. 11). In this experiment all mealworms were painted and the distasteful ones were, before painting, injected with 0.02 ml of 3% solution of quinine hydrochloride. Finally, to even further increase the distastefulness of both the red non-striped and the striped mealworms, they were painted with three drops of “Stop n Grow” (Mentholatum). The paper stimuli on which the mealworms were placed were of two different colours, brown and red, and were chosen to match the colours of the painted mealworms as much as possible.

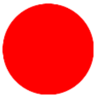
| Group *(N=15)* | Back-ground | Avoidance learning 5 trials (8 S+, 8 S-) | Generalization test (all prey palatable) |
|---|---|---|---|
| Brown/non-Striped |  | S+ S- | *8* *4* *4* |
| Brown/Striped | | S+ S- | |
| Red/non-Striped |  | S+ S- | *8* *4* *4* |
| Red/Striped | | S+ S- | |

**Figure 11.** The experimental set-up in **paper III**. Four groups of chicks participated in five trials of avoidance learning with brown palatable prey and either red non-striped or red/black striped unpalatable prey. Two groups were presented prey on brown background colour and two groups on red background colour. Followed by a generalization test where all chicks were presented all kinds of prey on their respective background colour.

## *Results paper III*

The results from the avoidance learning showed that chicks in all groups learned to discriminate palatable from unpalatable prey (Fig. 12). As seen in the figure there was an effect of background colour with faster learning on brown backgrounds, which contrasted with the red negative prey coloration. The presence or absence of a contrasting pattern did, however, have no general effect. The results from the generalization test were also in accordance with greater avoidance learning on the brown background as well as a generalization between having and not having a pattern.

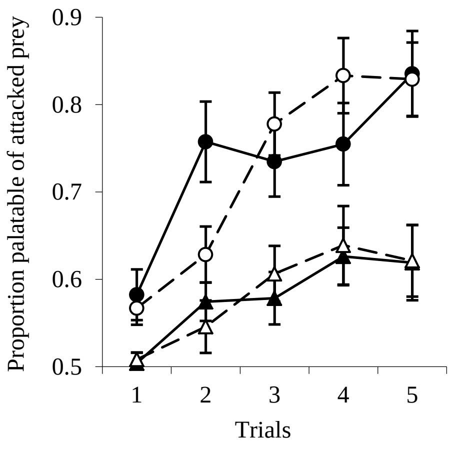



**Figure 12.** The proportion of all attacked prey that were palatable in each of 5 trials of avoidance learning for the 4 treatment groups (mean ± SE). Circles represent the brown background colour and triangles represent the red background colour. Solid lines and black symbols represent non-striped prey, and broken lines and white symbols represent striped prey.

# Paper IV

*Why do aposematic prey often have contrasting internal patterns? -Evidence of benefits through predator avoidance learning and generalization.*

In this study I used a different method to investigate if internal patterning increases the warning signal as suggested by Guilford (1990), this time with the focus on signal salience. The results may also give some information about whether pattern regularity in aposematic signals makes them “stand out” from the background and improve detection and recognition (Kenward et al. 2004), or, if predator symmetry detection also may affect how easy a predator may detect the warning signal (Curio 1976 in Delius & Nowak 1982).

The aim with this study was to test if the presences of many internal pattern boundaries, pattern regularity or symmetry have positive effects on avoidance learning on a complex multi-coloured background. Additionally the aim was to test if the presence of a bright colour might overshadow the potential effects of a contrasting pattern, since studies with domestic chicks show that they primarily learn the colour and not the pattern (**paper I & II**). This was followed by a test to investigate predator generalization behaviour to further evaluate possible selection pressures that may act on warning coloration.

As mentioned, I used a somewhat different experimental method that was more suited to the foraging behaviour of blue tits (*Cyanistes caeruleus*). Here, the mealworms were placed underneath the paper stimuli and the birds were trained to lift the paper in order to find food. Two main groups of negative stimuli were used, magenta and white, which in turn were divided into four subgroups each (Fig. 13). The colour of one of the groups was not present in the background during the experiment (magenta), while the other (white) was. Each of the four subgroups in the magenta group had a black pattern with a corresponding pattern in the white group; called regular, un-striped, irregular 1 and irregular 2. The black areas were the same for all subgroups (≈ 76.3 $cm^2$) and the stripes in the regular pattern were evenly distributed. Three types of positive stimuli were also used during the experiment; blue, brown and green.

| Groups | Discrimination learning (five trials) | | Generalization test | |
|---|---|---|---|---|
| | Subgroups | S- (6 prey) | Type 1: 2**R**+2**U**+2(**I-1**) | Type 2: 2**R**+2**U**+2(**I-2**) |
| Magenta | Regular *(MR)* | *N=13* | *N=7* | *N=6* |
| | Un-striped *(MU)* | *N=12* | *N=5* | *N=6* |
| | Irregular 1 *(MI-1)* | *N=6* | *N=6* | ----- |
| | Irregular 2 *(MI-2)* | *N=5* | ---- | *N=5* |
| White | Regular *(WR)* | *N=13* | *N=6* | *N=7* |
| | Un-striped *(WU)* | *N=12* | *N=5* | *N=7* |
| | Irregular 1 *(WI-1)* | *N=6* | *N=6* | ----- |
| | Irregular 2 *(WI-2)* | *N=6* | ----- | *N=6* |
| S+ during all trials and during the following test (2 brown + 2 green + 2 blue prey) | | | | |

**Figure 13.** The experimental set-up of **paper IV**. Two main groups of birds (magenta and white) were divided into four subgroups each (striped, un-striped and two irregular types: 1 & 2) and participated in five trials of discrimination learning followed by a generalization test.

## *Results paper IV*

Birds in all groups learned to discriminate the treatment patterns from the palatable prey and there was no difference depending on prey coloration (Fig. 14). There was, however, a significant effect of pattern suggesting differences in avoidance learning between bird groups presented with different patterns. Furher tests showed that the un-striped prey were attacked significantly more than all the other prey types.

In addition, to crudely estimate the detectability (or attractiveness) of the different stimuli, the time spent between a bird's initial landing on the experimental board until the first attack on the experimental prey in the first trial was compared. I found no significant differences between the stimuli.

The results from the generalization test showed that the birds generally attacked the previously positive prey significantly more than the experimental prey. This suggests that the birds, irrespective of treatment group, generalized more between the experimental prey than to the palatable prey. Furthermore, the results show that birds in the white group generalized similarly among the test prey, and the un-striped prey

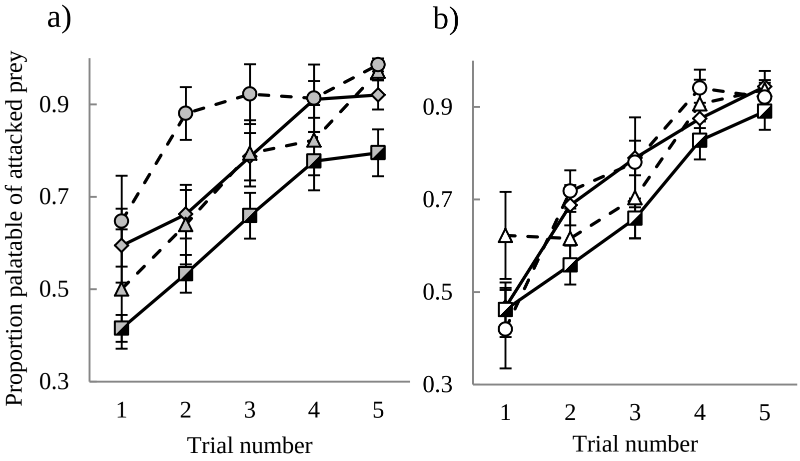



**Figure 14.** The average proportion of all attacked prey that were palatable (mean ± 1SE) in each of five trials of discrimination learning for a) the magenta colour treatments (M) and b) the white colour treatments (W). Diamonds represent striped prey (R), squares represent un-striped prey (U), triangles represent irregular type 1 (I-1) and circles represent irregular type 2 (I-2).

(WU) was attacked significantly more than both the irregular and the regular striped prey in these treatments. This was also the case for the birds trained on the magenta with irregular patterns (MI), but not for birds trained on the regular pattern (MR) or the un-striped pattern (MU).

## Discussion

The general aim of this thesis is to increase our knowledge about the function of the internally contrasting colour patterns commonly used in warning displays. As mentioned above there are several different hypotheses about the bright colours and internally contrasting patterns (Table 1) in aposematic prey species, some of which are not mutually exclusive. Previously, though, there was little experimental evidence of possible benefits of having internal contrasting patterns on warning colour efficacy, especially with regard to the speed of avoidance learning.

*What do birds attend to when learning a warning colour pattern?*

The first question addressed in the thesis concerns a quite basic, but yet important issue when it comes to understanding the function of these warning signals. With the aim of investigating the relative importance of colour and pattern in avoidance learning, I examined what the birds actually paid attention to when learning a warning colour pattern. The results from **paper I** showed that chicks primarily attend to the colour of the prey and not the pattern, which was the case in **paper II-IV** as well. In **paper I** the chicks completely generalized their learned avoidance of the negative stimuli to one with only the colour in common, while the stimuli with the pattern in common with the previously negative one was seen as completely palatable (Fig. 8). This suggests that the chicks in our experiment used colour as their primary cue when learning the discrimination task and they generalize completely between prey signals having and not having a black pattern. If both pattern and colour were important as cues of unprofitability, the expected would have been for birds in both the "colour only" and "pattern only" groups to attack at some intermediate levels, not to completely ignore the presence or absence of the pattern. When it comes to **paper II** the discrimination learning was faster in the groups where colour could be used for the discrimination (Fig. 10) and in **paper III** the chicks completely generalized their learned avoidance of the plain red or striped prey to the prey with or without stripes respectively (Fig. 12). The birds in **paper IV** also generalized a lot between the negative prey that shared the same colour, which were attacked significantly less in the test than the previously positive ones. The results from **paper I**, supported by the findings in **paper II-IV**, are in accordance with other studies, e.g. Exnerová et al. (2006, Fig. 15) and Terhune (1977), who also showed the importance of colour over pattern. One reason for these results could be that to birds, bright colours are more salient components and the pattern does not really matter, unless perhaps if they would benefit by distinguishing between prey with the same bright colour but with different patterns.

**Figure 15.** The firebug, *Pyrrhocoris apterus*, which was the aposematic species used by Exnerová et al. 2006. Photo: Titti Bohlin

*Do birds learn different components of colour patterns depending on the information about prey palatability they convey?*

In **paper II** the aim was to investigate if predators may use different warning colour components for discrimination depending on the information about prey quality they convey. Chicks were exposed to different situations where they needed to attend to different parts of the colour pattern of the prey stimulus to solve the discrimination task. The results from this experiment showed, as mentioned above, that chicks learned the discrimination task faster when colour could be used as a cue. Additionally, the results suggest a hierarchical way of learning about prey palatability, since colour was learned the most and seemed to "overshadow" the pattern which was learned to a lower degree (Fig. 10). This supports the idea that birds may attend to less salient prey stimuli only when these are needed for discrimination, as in, for instance, situations with Batesian mimics (Plowright & Owen 1980; **paper I**), which in turn may select for more accurate mimicry. It might also be that birds behave similar to humans when learning a problem; they tend to start by learning the rules, after which they learn the exceptions (e.g. Nosofsky et al. 1994). Based on that, Chittka & Osorio (2007) suggest that birds would start by learning the basic principles of warning coloration and while so they might avoid poor mimics. This in turn would suggest that in a population the proportion of well-educated predators, which have learned the "exceptions", affect the selection for perfect mimicry among prey. Being able to use pattern as well as colour could be of importance for a predator when learning to discriminate between models and their mimics (**paper I**). Birds have been shown to be able to use colour, pattern (Vallortigara et al. 1990), number of stripes and stripe colour (pigeons, Bain et al. 2007) for discrimination. In an earlier study with dragonflies Kauppinen & Mappes (2003) showed that they avoid wasp-like prey with black-yellow stripes more than uniformly coloured ones, which indicates that pattern is of importance.

Somewhat surprising are the results from the final two groups (PO & PS) in **paper II**, where the birds in the "pattern only" group, who only had the presence of the pattern on the negative stimulus, did not learn the discrimination (Fig. 10). While the birds in the "pattern shape" group learned to discriminate between the prey without the pattern and those having a pattern, they, however, did not learn to distinguish between the two pattern types. This suggests that the presence of a palatable mimic can have a positive effect on discrimination learning. It could be that the actual variation in patterns triggered the chicks' attention to the patterns, making them more aware of the patterns in general. Such positive learning effects, where a model benefits from having a palatable mimic, has until now only been theoretically described by Balogh et al. (2008). In their study learning was improved when the predators were surprised by the prey stimulus, due to variation in prey palatability, which is similar to what, in animal learning psychology, is known as "contrast effects" (Balogh et al. 2008).

*Can the colour patterns of aposematic prey be explained by the effect of contrast against the background?*

The third paper in the thesis handles one specific hypothesis put forward by Guilford (1990) and I investigate if one can explain the common colour patterns of aposematic prey, with the effect of contrast against the background (**paper III**). The results showed that there was an effect of background colour with faster learning on the ones contrasting with the negative prey coloration (Fig. 12), which are in accordance with earlier studies (e.g. Gittleman & Harvey 1980; Gittleman et al. 1980). The presence or absence of a contrasting pattern did, however, have no general effect since internal contrasts do not seem to increase conspicuousness and thereby learning speed in the same manner as prey-to background contrast has been shown to do. If internal colour patterns had increased the avoidance learning by making the prey more conspicuous, the expected result would have been that birds presented with striped unpalatable prey learned faster than birds presented with non-striped unpalatable prey. This would especially have been the case on the red background where the colour of the unpalatable prey otherwise matched the background. Hence, I found no support for the suggestion by Guilford (1990) that one can extend what is known about contrast against the background to also explain the presence of patterns by arguing that they create internal contrasts and thus a more conspicuous signal.

*Does an increased amount of internal pattern boundaries, pattern regularity or symmetry have positive effects on avoidance learning?*

In **Paper IV** the aim was to test if increased amounts of internal pattern boundaries, pattern regularity or symmetry have positive effects on avoidance learning, on a complex background, by increasing signal salience. The results from the experiment showed that birds presented negative stimuli with multiple internal colour boundaries showed faster avoidance learning than those presented with un-striped prey (Fig. 14). This indicates that many internal contrasts might produce a more salient stimulus as suggested by Guilford (1990), which in turn could be explained by the mechanism of lateral inhibition in the nervous system of the retina (Kenward et al. 2004). Simplified, this mechanism makes the eye detect changes in brightness by making the contrast even stronger. Thus it is possible that a highly contrasting internal pattern, with multiple internal boundaries, is more stimulating than one with few pattern elements. Both the experiments in **paper III** and **IV** tested whether there are any positive effects on predator avoidance learning due to internally contrasting patterns. The experiment in **paper III** tested if the presence of a black pattern can increase conspicuousness on a matching background compared to a prey with no internal contrasts, which I found no support for. While the results from **paper IV** showed that an increased amount of patterning can increase signal salience by making the prey easier to associate with unpalatability compared to a prey with fewer internal colour boundaries. It seems as though any positive effects of patterns on avoidance learning, due to an increased amount of internally contrasting boundaries, is either depending on predator species or context dependent. In a more complex environment a prey might benefit from having, for instance, multiple stripes compared to a few internal boundaries.

The results from **paper IV** showed, however, no evidence for any benefits of having a regular pattern on this multi-coloured complex background, compared to irregular. Thus no support for the idea of Kenward et al. (2004) about making the prey “stand out” from the background, as there was no significant faster learning of regular prey (within each colour treatment). This suggests that symmetry or regularity is not of great importance in avoidance learning. There might, however, be some particular pattern characteristics that could be more salient than others and therefore selected for, which is supported by the faster learning initially of one of the irregular patterns (Fig. 14a).

Additionally, the results from **paper IV** also supports the idea that animals might be able to form categories of palatable and unpalatable prey based on a few salient features (Balogh et al. 2010; Gamberale-Stille et al. 2012), in this case prey coloration. Furthermore, based on what is known from conventional discrimination learning theory, it is not surprising that birds mainly learn parts of a warning colour pattern. This since the most salient stimulus element, within a compound stimulus, should overshadow learning of other less salient elements (Pavlov 1927; Kamin 1969). Apart from in the group "colour AND pattern" in **paper II**, where colour seemed to "overshadow" the learning of the pattern, this also seemed to be the case in **paper IV**. There the birds in the white treatment, lacking a conspicuous colour, paid significantly more attention to the pattern details than the ones in the magenta treatment (Fig. 4 in **paper IV**). This suggests that the presence of the bright colour might have overshadowed the learning of the pattern to some degree.

According to the principle of background matching, the more an object matches its background, with respect to colours and pattern geometry, the harder it is to detect (Cott 1940; Stobbe et al. 2009). Based on that, together with the positive effects that have been shown in avoidance learning with regard to prey-to-background contrast (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987; **paper III**), one might assume that the opposite is true for aposematism. Hence the expected results, in **paper IV**, were a correlation between earlier detection and faster avoidance learning. When comparing the two treatment colours though, the presence of the contrasting prey colour (magenta) did not have a positive effect for discrimination learning as expected. Nor did the patterns with the most salience (MI-2) and the least salience (MU) of the magenta treatments have the shortest or the longest times until first attack. However, it was not one of the aims with the study to investigate such correlation so there is a possibility that the patterns and signals were all to easy to detect with too little variation. More research is needed to resolve this question.

## Concluding remarks

Based on earlier hypothesis and findings (some listed in Table 1), one can argue that the aposematic colour patterns used by a prey species may have evolved to protect prey at all different stages of the interaction with individual predators. Firstly, a colour pattern with internal boundaries may be cryptic at a distance (Papageorgis 1975; Tullberg et al. 2005) to minimize the risk of being detected at all, since there is a chance that the predator is inexperienced and hence attack. Having a colour pattern consisting of multiple colours (e.g. red or yellow with a black pattern) minimizes the chance of being detected, compared to having one bright colour, since the colours at distance blur together and then blend in more with the background colours of nature (Kassarov 2003; Stevens & Ruxton 2012). The second stage involves the function of the warning signal once the prey animal is first detected. Then it is important with a strong signal that is easy to learn and associate with unpalatability (Gittleman & Harvey 1980) and to discriminate from the cryptic prey species that the predators usually hunt to minimize confusion (Edmunds 1974; Turner 1975; Sherratt & Beatty 2003; Guilford 1986; 1990; Guilford & Dawkins 1991; Stevens & Ruxton 2012). By having a strong signal the prey might also give experienced predators time to correct recognition errors and hence abort the attack, giving the prey a chance to escape (Guilford 1986; 1990). Decision-time seems to be important when predators are time-limited, due to for instance the presence of a competitor (Gamberale-Stille 2000), but not with increased distance to the prey (Gamberale-Stille et al. 2009). Moreover, a strong signal may make a predator mare cautious when attacking and handling prey, thus leading to a higher survival of prey (Sillén-Tullberg 1985).

Let us say that the predator is an inexperienced one, still in the phase of learning. Then the third stage deals with how a warning signal should be designed to promote learning. As mentioned above, conspicuousness is an important part of an aposematic signal and it involves brightness, hue, colour intensity and prey-to-background contrast (Harvey & Paxton 1981). The colour of the prey seems to be of foremost importance (**paper I**), not necessarily the hue per se, but the presence of a bright colour, since it seems to overshadow learning of a contrasting internal pattern in bird predators (**paper II & IV**). Also, avoidance learning is faster when the colour of the prey can be used for discrimination (**paper II**). Prey-to-background contrast has been repeatedly shown to speed up avoidance learning (Gittleman & Harvey 1980; Gittleman et al. 1980, **paper III**) and in certain cases internal contrast, due to an increased amount of internal colour boundaries, can have a positive effect on avoidance learning as well (Guilford 1990; **paper IV**, but see **paper III**). In mimicry systems there might be a selection, driven by the predators, for increased pattern similarity, since patterns could be a way for predators to discriminate models from palatable mimics (**paper I & II**). The symmetry of a colour pattern has also been suggested to influence detection and the predators association of the prey with unpalatability (Forsman & Herrström 2004) as well as making the prey "stand out" from the background and hence improve recognition and detection (Kenward et al. 2004). However, I found no support for any benefits of having a regular compared to an irregular pattern on the multi-coloured background used in **paper IV**, rather the reverse. This suggests that symmetry or regularity is not of foremost importance in avoidance learning.

The fourth and final stage has to do with how the warning signal affects the predators after detection and learning and covers the memorability of the signal. How effective a signal is in the long run depends on how easy it is for the predators to memorize (Guilford & Dawkins 1991) and it has been suggested that some colours and patterns are more memory stimulating than others (Rothschild, 1984). Osorio et al. (1999a) argued that different parts of a colour pattern play different roles and suggested that the contrasting pattern attracts predator attention while the colours are remembered more accurately. The memorability of a signal is, for instance, important when there is a delayed-action toxin and the predator has to remember the visual image of a recently consumed prey in order to avoid attacking the same species in the future (Guilford 1990). Furthermore, Gamberale-Stille (2001) showed that prey contrast against the background may have a positive effect on prey recognition and avoidance, independently of predator viewing time. In that experiment, experienced chicks made fewer mistakes and hesitated longer before attacking aposematic prey when there was a high prey-to-background contrast (Gamberale-Stille 2001). In a recent review of the current understanding of warning signal form, Stevens and Ruxton (2012) also suggested that stripes and spots, by being simple pattern components and perhaps easier to memorize, might aid detection and speed up avoidance learning. The suggestion that patterns aid detection is contrary to what is suggested by Papageorgis (1975) who argues that the presence of a pattern makes the prey species cryptic at distance.

The main aim of this thesis was to investigate the function of colour patterns in warning displays, trying to give some answers to the question: Why do aposematic prey often have a contrasting internal pattern? The results from the experiments presented in the thesis do indeed shed some light on this question. Although birds do not primarily learn these patterns (**paper I**), they might be a way for model species to escape from the negative effects of having a mimic (**paper I**) since a contrasting pattern can be used secondarily as a cue, once the colour is learned (**paper II**). This would, in turn, suggest that imperfect Batesian mimics may be at a disadvantage from discrimination by well-educated predators. Having a contrasting pattern, with multiple internal boundaries, might also make the signal more salient and speed up predator avoidance learning, as suggested by Guilford (1990; **paper IV**). Hence, patterns containing more internals colour boundaries (e.g. stripes) may be selected for in nature. The major finding, however, that is consistent throughout the thesis, is the importance of colour over pattern (**paper I-IV**). Chicks primarily learn a bright colour rather than an equally novel conspicuous black pattern (**paper I**), showed faster discrimination learning when colour could be used as a cue (**paper II**), generalized their learned avoidance between prey types with or without pattern (**paper III**) and finally, the blue tits formed categories of palatable and unpalatable prey based on prey coloration (**paper IV**).

Although aposematism has been studied since Darwin (1871) started to ponder about the bright colours of some caterpillars, there is still a lot which remains unknown. By integrating theories about animal learning with the evolution of warning colours I hope that this thesis increases our understanding about not only the role of internal patterns in warning signals and predator-prey interactions, but also more generally about signalling systems in nature. Furthermore, I hope to have contributed to the understanding of animal behaviour and evolutionary biology.

## Svensk populärvetenskaplig sammanfattning

Tänk dig själv som en liten insekt sittandes på en buske och det viktigaste av allt är att överleva tillräckligt länge för att hinna reproducera dig. Här finns det två möjliga strategier att ta till: antingen är du kamouflerad och försöker därigenom undvika att bli upptäckt överhuvudtaget. Detta kan göras genom att efterlikna bakgrunden på olika sätt eller genom att se ut som något som inte förknippas med något ätligt (t.ex. en kvist eller fågelspillning). Den andra strategin, som den här avhandlingen handlar om, går ut på att du på något sätt signalerar till möjliga rovdjur att du av någon anledning inte är ett uppskattat byte och detta fenomen kallas aposematism. Du kanske är taggig, smakar illa, kan spreja något otrevligt i ansiktet på dem eller rentutav är dödligt giftig. Arter med dessa typer av försvar signalerar ofta detta genom att ha starka, iögonfallande färger (t.ex. röd, orange eller gul) (Cott 1940) som ger en stark kontrast mot färgerna i den naturliga bakgrunden. Denna kontrast mot bakgrunden gör att det går snabbare för rovdjur att lära sig att känna igen dem och undvika dessa djur (Roper & Wistow 1986). Utöver detta är det också vanligt att de har ett mönster (ofta svart) i färgteckningen som ger en kontrastrik effekt inom individen (t.ex. geting, *Vespula vulgaris*, och sjuprickig nyckelpiga, *Coccinella septempunctata*, Fig. 16). En arts färgteckning är därmed ofta en kompromiss mellan att inte bli upptäckt av rovdjur och mellan fördelen att vara väl synlig när det gäller att slåss för sitt territorium, att hitta partners (Krebs & Davies 1993) och för icke uppskattade byten att signallera sin oätlighet.

**Figure 16.** Sjuprickig nyckelpiga, *Coccinella septempunctata*. Photo: Aleksandra I. Johansen

Det finns ett antal hypoteser om varför dessa varningsfärgade djur har ett mönster som ger en kontrast inom färgteckningen, t.ex. att det ger djuret kamouflage på avstånd (genom formupplösning) men samtidigt är en stark signal när det väl upptäcks (Papageorgis 1975) eller att det ger en extra möjlighet för modellarter att undvika härmare (**artikel I**). Mimikry är när en ätlig art härmar utseendet av en oätlig (modellen) för att lura rovdjuren och därmed undkomma att bli uppäten (Bates 1862) eller när flera oätliga arter har samma utseende och därmed delar på kostnaden av att rovdjuren måste lära sig deras signal (Müller 1879; Rowland et al. 2010). Det finns dock inte så mycket empiriska bevis för varför dessa mönster finns och ser ut som de gör. Målet med denna avhandling var att ta reda på hur utseendet på olika varningsfärgteckningar påverkar inlärningshastigheten hos fåglar för att därigenom kunna öka förståelsen för varför färgteckningarna ser ut som de gör. Avhandlingen består av fyra olika artiklar där nykläckta kycklingar (*Gallus gallus domesticus*) (**I-III**) och viltfångade blåmesar (*Cyanistes caeruleus*) (**IV**) har använts.

**I.** *Kycklingar använder sig huvudsakligen av färg, inte mönster, när de lär sig en varningsfärgteckning.*

Målet med den första studien var att ta reda på betydelsen av färg respektive mönster när fåglar lär sig att undvika ett osmakligt byte, detta genom att undersöka vad fåglarna lär sig. Experimentbytena bestod av både en stark färg (cyan) och ett kontrastrikt mönster (svarta ränder eller prickar) där båda egenskaperna kunde användas, var för sig eller tillsammans, som ledtråd om osmaklighet (Fig. 7). En eventuell fördel med ett randigt eller prickigt mönster undersöktes också genom att jämföra inlärningshastigheterna för de båda grupperna. Kycklingarna fick sju omgångar på sig att lära sig att skilja mellan de ätliga bytena (grå) och de osmakliga bytena. Detta följdes av ett generaliseringstest för att ta reda på vad de hade lärt sig under inlärningen.

Resultatet visade att det fåglarna lärde sig var enbart färgen hos bytet medan de inte lärde sig mönstret alls. Detta var fallet oavsett vilket mönster bytet hade och det fanns inte någon skillnad i inlärningen med avseende på de olika mönstren heller. Att fåglarna koncentrerade sig på en egenskap vid inlärningen är inte förvånande enligt vad som är känt från inlärningspsykologin: om ett stimulus är sammansatt av flera delar, så kommer den starkaste delen att ”överskugga” inlärningen av andra delar inom stimulit (Pavlov 1927), såvida inte de andra delarna bidrar med någon viktig extra information.

**II.** *Färg och mönsterlikhet i mimikry – bevis för en hierarkisk inlärning av varningsfärger och mönster.*

Målet här var att dels undersöka om fåglar kan använda olika delar av en varningsfärgteckning beroende på hur mycket information om osmakligheten som kan uttydas från de olika delarna. Samt hur mycket av modellartens varningsfärgteckning som en härmare behöver för att kunna lura fåglarna och därmed förbättra sina egna överlevnadschanser. Kycklingarna delades in i fyra grupper som kunde använda sig av 1) färgen *eller* mönstret, 2) färgen *och* mönstret, 3) enbart mönstret eller 4) mönstrets utseende för att lära sig att diskriminera mellan den osmakliga och de olika ätliga bytena (Fig. 9).

Resultatet visade att kycklingarna är hierarkiska i sin inlärning då de lär sig den starkaste delen av signalen först (färgen) och därefter, men till en något lägre grad, kan lära sig mönstret (grupp 2). Chittka & Osorio (2007) föreslog att om fåglar beter sig som man vet att människor gör vid inlärning (lär sig reglerna först och sedan undantagen), så borde fåglarna först lära sig de grundläggande delarna av varningsfärgteckningen och under tiden även undvika sämre härmare. Vilket skulle kunna förklara varför kycklingarna lärt sig färgen bättre än mönstret om detta kommer i andra hand. Något förvånande är dock att när det bara var ett mönster som skiljde den osmakliga från de ätliga (grupp 3) visade det sig vara för svårt då fåglarna inte lärde sig att skilja dem åt. Däremot lärde sig fåglarna att skilja på de med mönster från de utan mönster när det fanns en ofullkomlig härmare som hade ett mönster, men dock ej med den rätta formen på mönstret (grupp 4). Något som skulle kunna bero på att variationen i mönstret gjorde kycklingarna mer medvetna om att det fanns ett mönster.

### **III.** *Vikten av kontrast inom mönstret och kontrast mot bakgrunden hos aposematiska signaler.*

Den tredje studien undersöker en hypotes av Guilford (1990) som föreslår att ett mönster inom en färgteckning skapar en intern kontrast. Som i sin tur skulle underlätta inlärningen hos rovdjuren på samma sätt som kontraster mellan bytesdjuret och dess bakgrund gör. Något som tidigare har visats påskynda inlärningen av ett osmakligt byte jämfört med ett byte vars färg saknar kontrast mot bakgrunden (t.ex. Roper & Wistow 1986). Kycklingar i fyra grupper fick under 15 omgångar lära sig att skilja mellan en brunmålad ätlig mask och antingen en rödmålad eller en röd/svart-randig osmaklig mask på en bakgrundsfärg som antingen var kontrastrik mot de osmakliga bytena (brun) eller inte (röd) (Fig. 11).

Även i detta experiment, som i ett antal tidigare (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987), så gick inlärningen snabbare i de två grupper där det var en kontrast mellan färgen på det osmakliga bytet och dess bakgrund (röd och röd/svart mot brun). Däremot fanns det inga tecken på att kontraster inom mönstret skulle ha liknande positiva effekter på inlärningen hos fåglarna. Den så vanliga förekomsten av kontrastrika mönster hos varningsfärgade djur kan därmed inte förklaras genom att enbart utvidga den positiva effekt som kontrast mellan byte och dess bakgrund visat sig ha till att också innefatta kontraster inom mönster.

**IV.** *Varför har aposematiska djur ofta en kontrastrik färgteckning? – Bevis för fördelar på grund av rovdjurens inlärnings- och generaliseringsbeteende.*

I den sista studien testades Guilfords (1990) hypotes igen, denna gång på en komplex bakgrund och med få interna kontraster jämfört med flera interna kontraster hos bytet för att se om det ökade antalet interna kontraster gav en starkare signal och därmed snabbare inlärning. Detta testades tillsammans med en idé från Kenward et al. (2004) om att ett regelbundet mönster får signalen att ”sticka ut” från oregelbundenheten i den naturliga bakgrunden och på så sätt underlätta inlärningen. Utöver detta jämfördes negativa byten med en stark färg mot vita byten för att undersöka om färgen ”överskuggade” den eventuella effekten av ett kontrastrikt mönster. Här användes viltfångade blåmesar indelade i de två färggrupperna (magenta och vit) med fyra undergrupper vardera med respektive mönster: regelbundet randig, icke-randig samt oregelbunden typ 1 & 2 (Fig. 13).

Resultatet från denna studie visade att fåglarna i alla grupperna lärde sig att skilja mellan de negativa och de positiva bytena. Några tecken på att den starka färgen hos den ena gruppen skulle ”överskugga” inlärningen av mönstret fanns ej, eftersom fåglarna i båda grupperna lärde sig lika bra. Inte heller fanns det något stöd för idén om att ett regelbundet mönster ger snabbare inlärning (Kenward et al. 2004) eftersom det inte var någon skillnad i inlärning mellan de regelbundna och de oregelbundna mönstren. Däremot fanns det en skillnad inom färggrupperna, där de med flera interna kontraster gick snabbare att lära sig, vilket stödjer Guilfords (1990) hypotes vilket då tyder på att det kan finnas en naturlig selektion för färgteckningar med fler interna kontraster, som t.ex. ränder.

……………………………………………………………………………..

För att sammanfatta så tyder mycket på att det fåglarna huvudsakligen lär sig när de ska undvika ett osmakligt varningsfärgat byte är den starka färgen på djuret och att det sker en hierarkisk inlärning. Sådan att fåglarna, vid behov för att skilja t.ex. en oätlig modellart från en ätlig härmare, sedan lär sig mönstret eller andra egenskaper. Utöver detta så verkar det även finnas en fördel i vissa situationer med ett ökat antal interna kontraster (t.ex. ränder) vilket är vanligt förekommande hos aposematiska (varningsfärgtecknade) djur.

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