# LIFE AT STAKE WHEN PLAYING HIDE AND SEEK

## CONCEALING EFFECTS OF PREY COLOURATION AND VISUAL BACKGROUNDS

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**Life at stake when playing hide and seek**

Concealing effects of prey colouration and visual backgrounds

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“I took much pleasure in watching the habits of birds,
and even made notes on the subject.”

*Charles Darwin*

# ABSTRACT

A prey animal can use different strategies to avoid becoming eaten by predators. One such widely recognised strategy is the use of body colouration to decrease the risk of becoming detected, i.e. cryptic colouration. The principles of crypsis that I have studied are background matching, disruptive colouration and distractive markings. Further, I also studied the concealing effect of the visual background habitats. I used artificial prey items and backgrounds, and blue tits (*Cyanistes caeruleus*) as predators, to investigate prey concealment. In Paper **I**, I tested if high-contrast markings in prey coloration or in the background would result in a distracting effect. I found that such markings did increase prey search time, even when the prey markings were lighter or darker than the background. In Paper **II**, I studied the use of chromatic cues by predators when searching for prey. The birds easily detected prey that chromatically deviated from its background. Interestingly, background-matching prey was more difficult to detect when the colour scheme had low ultraviolet and high shortwave reflectance compared to when the reflectance bands were even. In Paper **III**, I studied optimisation of achromatic contrast within prey colour pattern and also the effect of shape diversity of background pattern elements on prey detection. I found that all prey types were more difficult to detect on the diverse background, but the level of contrast within prey pattern did not influence search times. In Paper **IV**, I further investigated how a prey should optimise its patterning with respect to background matching. I found that prey with repeated pattern elements was equally hard to detect as prey with more variable pattern. However, prey with a spatially regular pattern (aligned pattern elements) was easier to detect than prey with a spatially irregular pattern. In this paper I also found that high complexity of element shapes in the background, made the search task more difficult.

# LIST OF PAPERS

**I.** Dimitrova, M., Stobbe, N., Schaefer, H.M. & Merilaita, S. 2009. Concealed by conspicuousness: distractive prey markings and backgrounds. *Proc. R. Soc. B* **276**, 1905-1910.

**II.** Stobbe, N., Dimitrova, M., Merilaita, S. & Schaefer, H.M. 2009. Cromaticity in the UV/blue range facilitates the search for achromatically background-matching prey in birds. *Phil. Trans. R. Soc. B* **364**, 511-517.

**III.** Dimitrova, M. & Merilaita, S. Prey concealment: visual background complexity and prey contrast distribution. In press in *Behavioral Ecology*.

**IV.** Dimitrova, M. & Merilaita, S. Avoiding detection: effects of prey pattern regularity, background matching and complexity of the habitat. *Manuscript*.

# CONTENTS

# INTRODUCTION

There is seldom harmony in nature, and animals are constantly fighting for their survival. Both predators and prey impose each other under strong selection pressures and have through evolutionary time developed adaptations that help them to survive. Predators must find and catch prey to be able to survive, whereas prey must escape predation to survive. The more efficient the predators are at catching prey, the stronger is the selection pressure on the prey to evolve strategies to escape predation and vice versa. This is a never-ending process that has often been referred to as an 'arms-race' (Dawkins & Krebs 1979).

The most obvious thing a prey can use as a defence strategy against predators is its body colours and patterning. Prey can use coloration for two main anti-predator functions: either to decrease the risk of detection and recognition by predators (i.e. camouflage), or as a post-detection defence signal (i.e. aposematic and mimetic warning coloration). In this thesis I have concentrated on prey animals and how they escape predation with help of colouration that decreases detection and/or recognition by predators (Poulton 1890; Cott 1940; Edmunds 1974; Endler 1978; Merilaita 2003; Caro 2005). Historically camouflage has constituted an important example of adaptation that has been used to advocate the theory of natural selection (e.g. Wallace 1889). The adaptive value of camouflage is determined by how predators respond to it (Cott 1940; Edmunds 1974; Endler 1978). Hence, camouflage aims to deceive predator perception.

There are several ways that have been suggested that an animal can use its body colours and patterns to improve its degree of crypsis and hence to decrease its risk of becoming detected by visually hunting predators. One way is through background matching (Wallace 1889; Thayer 1896a, b, 1902, 1909; Cott 1940; Endler 1978; Merilaita *et al*. 1999; Stevens & Merilaita 2009a), another way is through disruptive colouration (Thayer 1909; Cott 1940; Merilaita 1998; Cuthill *et al*. 2005), and a third way is through distractive markings (Thayer 1909). These three manners of achieving camouflage, investigated in this thesis, may select for different optimal appearances and, thus, be in conflict with each other: they emphasise different strategies of how to achieve camouflage and they make different predictions about how prey colouration should optimally be designed. Hopefully this thesis helps to increase our understanding of how these different strategies can shape the appearances of cryptically coloured prey.

The studies on prey concealment done so far have mainly focused on the effect of the animal colour pattern *per se* as well as on how it interacts with the visual environment. The effect of the appearance of the background *per se* on the evolution of prey camouflage has, on the other hand, received only very little attention. However, a recent study suggests that the appearance of the environment may influence the direction towards which strategy and how prey colouration evolves: in a theoretical model visual complexity of the environment hampered the detection of cryptic prey and facilitated evolution of camouflage (Merilaita 2003). Because of the huge variation that is found among natural habitats, the effect of background *per se* on the evolution of prey colouration and camouflage is a topic that clearly warrants further research. Therefore, in this thesis I have also investigated different aspects of background appearances and their effect on prey detection by visually hunting predators.

Before I start going through the different results from this thesis and to hopefully make them more understandable to a reader unfamiliar with the world of camouflage, I give a description of the various principles of camouflage that I have investigated, as well as a description of the effect of background complexity, followed by a general description of the visual perception of predators.

## *Background matching*

Camouflage through background matching is probably the most intuitive principle of concealment and was therefore one of the first to be proposed and generally accepted. Early naturalists noted that many animals have colours and patterns that help them to blend into their background (Wallace 1889; Thayer 1896a, b, 1902, 1909). According to this principle the more similar the pattern of a prey is both in colours and pattern geometry, to its visual background, the more difficult is it for a predator to detect the prey (Cott 1940; Norris & Lowe 1964; Edmunds 1974; Endler 1978).

The degree of matching between an animal and its background is presumed to depend upon several factors. One of them is the visual heterogeneity of the background, so that in a patchy habitat a coloration that matches one microhabitat is likely to visually deviate from another microhabitat (Norris & Lowe 1964; Merilaita *et al*. 1999, 2001). Another factor is the degree of exposure of prey to predators in different microhabitats. If the predator population and composition differ between microhabitats then the prey will experience different selective pressures which may drive the prey colouration in two different directions (Norris & Lowe 1964). A prey may also increase its camouflage by actively choosing a specific microhabitat (Endler 1984; Eterovick *et al.* 1997; Marshall 2000). Further, the proportion of microhabitats available and visual differences among them may affect how a prey can maximise its background matching (Merilaita *et al.* 1999, 2001).

Although the idea of background matching was proposed long time ago and several factors that may affect the degree of background matching of a prey have been proposed, surprisingly little is still known about how background matching is maximised and how natural selection should be expected to shape the appearance of a background matching prey. To further improve the understanding of background matching and to develop an analytical approach to it, Endler (1978, 1984) proposed a definition that also made it possible to quantify the degree of crypsis. It states that "*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*" (Endler 1978, 1984). This proposal assumes that all random samples of a background are equally cryptic and has been used as a basis for quantification of the degree of camouflage. However, this proposal has been found to lack generality (Merilaita *et al*. 1999, 2001; Merilaita & Lind 2005; Huston *et al*. 2007; Sherratt *et al*. 2007) and even though resemblance to the background is important for crypsis, matching a random visual sample of the background does not necessarily maximise level of camouflage (Merilaita & Lind 2005). Thus, recently background matching was described as coloration that "*generally matches the colour, lightness and pattern of one (specialist) or several (compromise) background types*" (Stevens & Merilaita 2009a). We currently know that high visual similarity between the appearances of the prey pattern and its background increases prey concealment by making it more difficult to detect by predators. However, we still cannot make precise predictions about how natural selection for background matching shapes the appearance of cryptic prey colouration in relation to the visual habitat of the prey, and we cannot tell if the resemblance of prey colouration with the background is optimised. In this thesis I have studied the importance of matching all or a subsample of shades present in the background and its effect on prey concealment (Paper **III**). I have also studied the effect of spatial distribution of matching pattern elements on crypsis, and if geometric regularity of prey pattern impairs crypsis through background matching (Paper **IV**).

### *Disruptive colouration*

In camouflage through disruptive colouration the arrangement of colour pattern is related to the body outline and shape of the prey. According to Cott (1940) it is the continuity of surface, bounded by a specific contour or outline, which chiefly enables the recognition of an object. Disruptive colouration uses pattern elements to create the appearance of false edges and boundaries and to hinder the detection or recognition of an object's, or part of an object's, true outline (Stevens & Merilaita 2009a, b). This can be achieved if disruptive colouration consists of contrasting colours that are also, at least partly. background matching. That is, some parts of the prey outline blend into the background, while other patches, placed at the body margin, highly contrast to these background matching parts and thus create false edges at the body margin that will distort the appearance of the body shape (Thayer 1909; Cott 1940; Merilaita 1998; Cuthill *et al*. 2005; Schaefer & Stobbe 2006; Stevens & Cuthill 2006; Stevens *et al*. 2006; Fraser *et al*. 2007; Cuthill & Szekely 2009).

Animals that use disruptive colouration may also seek to reduce detection through background matching (Ruxton *et al.* 2004). Therefore it is quite difficult to design experimental studies to evaluate if cryptic colouration benefits from disruptive colouration: if the degree of background matching is not controlled for, some results may be explained by differences in camouflage due to background matching and not due to the effect of disruptive colouration. As long as we know relatively little about how the degree of background matching of a colour pattern is determined, it will be difficult to properly control for. Relatively few studies have directly investigated disruptive coloration and in turn very few of these studies focused on coloration of real prey (e.g. Silberglied *et al.* 1980; Merilaita 1998; Cuthill *et al.* 2005; Merilaita & Lind 2005; Schaefer & Stobbe 2006; Stevens & Cuthill 2006; Stevens *et al.* 2006: Cuthill & Szekely 2009). Therefore, the evidence for disruptive coloration is still somewhat circumstantial, and it is not clear how important the disruptive effect is for the evolution of protective animal coloration.

There are still relatively few studies about the role of disruptive coloration in prey crypsis. Thus, future studies of the concealing effect of marginal elements, pattern variability and complexity, as well as, contrasts are needed. A prey with disruptive colouration may have some advantages compared to prey which is camouflaged by background matching alone, perhaps such prey can exploit a wider range of backgrounds without decreasing its camouflage (Merilaita *et al*. 1999). In this thesis I have studied the importance of optimisation of lightness and contrast within prey patterning and their effect on prey concealment (Paper **III**).

## *Distractive colouration*

The idea of distractive colouration and its effect on prey concealment was suggested 100 years ago (Thayer 1909), but perhaps due to the somewhat unclear description of this idea it was previously not distinguished from the principle of disruptive colouration (cf. Cott 1940). However, according to our present knowledge about optimisation of prey colouration and the different predictions we can draw from these two principles, it seems that they should be distinguished from each other and considered as separate (Stevens & Merilaita 2009a; Paper **I**).

Thayer (1909) suggested that the aim of distractive markings was to reduce "*...one form's or detail's conspicuousness by blazoning of some other detail*". He argued that these 'meaningless' markings tend to draw and hold the attention of a viewer away from informative traits that would reveal the presence of the prey, such as the body outline. These markings should highly contrast with the rest of the prey colouration to be successful in hindering detection or recognition of prey characteristics (Thayer 1909). Thus, the idea of distractive markings essentially states that a prey that has some conspicuous markings may be better concealed than a prey lacking conspicuous markings. However, it seems reasonable to assume that distractive markings only work when they are small and used in combination with background-matching coloration.

Perhaps partly due to the counter-intuitive explanation of the function of distractive markings (i.e. conspicuousness leads to inconspicuousness) there is to date only one empirical study that has found support for Thayer's proposal (Paper **I**). There exist also another study that did not find support for the function of distractive markings. Stevens *et al*. (2008) studied the predation rate from wild birds on dead mealworms pinned on trees and partly covering an artificial prey (a triangular piece of printed paper). The triangles matched the tree trunks, but half of them also had a bright spot. The bright spots did not influence the survival of the mealworms, thus Stevens *et al*. (2008) suggested that distractive markings is not an effective means of concealment. However, their experimental set-up may not have been ideal for the study of distractive markings: because of the unfamiliarity of the birds with the triangles they did not necessarily consider them as a part of the prey (i.e. the mealworm). In my thesis I present a controlled laboratory experiment that provides the first empirical evidence for the efficacy of distractive markings (Paper **I**).

### *Background appearance*

Although there is huge visual variation among natural environments in for example, contrast, lightness, spatiochromatic properties (Parraga *et al*. 2002; Frazor & Geisler 2006; Geisler 2008), the influence of background habitat *per se* on prey detection has so far received little scientific attention, as most studies have concentrated on the effect of prey patterning *per se* and how it interacts with the visual environment. However, the appearance of the background is likely to be very important because it affects how much information a predator must process to be able to detect and recognise a camouflaged prey. If the background is visually complex, there will be a lot of information that is not useful for the predator when searching for camouflaged prey. Thus, in such backgrounds a prey could receive additional help from the background appearance to avoid detection and not solely rely on its colouration. To date there is one theoretical study that points out that the visual complexity of a background may affect the detection times of camouflaged prey (Merilaita 2003). This result is further supported by some psychological experiments where the background appearance has been found to affect the search task (e.g. Gordon 1968; Farmer & Taylor 1980). There are many different aspects of the visual environment that can affect the difficulty of prey search and thus influence the detection times of camouflaged prey. In this thesis I have investigated some possible aspects of background appearances and their effect on prey detection times by avian predators (Papers **I**, **III** & **IV**).

### *Visual perception*

The factor that all camouflaged prey seek to deceive is the visual perception of predators. Overall, the degree of prey camouflage is determined by the interaction between habitat background, prey colouration as well as predator perception. Hence, the visual perception of predators is of paramount importance when studying camouflage and prey concealment. Predator's perception of prey coloration is influenced by several external factors already before it has reached the predator's eye, including the spectral properties and intensity of the ambient light, the reflectance spectrum of the prey colour pattern and the spectral transmission properties of air or water depending on if the prey is viewed in a terrestrial or an aquatic environment (Endler 1990).

Light reflected by the prey coloration and its background stimulates the photoreceptors in the retina of the predator. It is important to bear in mind that the spectral sensitivities of photoreceptors differ among taxa, and hence a given prey colour pattern is perceived differently depending on the viewer (e.g. Vorobyev *et al.* 2001a, b). For example, birds that are main predators of many insects have quite different colour vision from humans (reviewed by Bennett & Cuthill 1994; Cuthill *et al*. 2000). This is because birds have tetrachromatic vision, i.e. their colour vision is based on four types of cone cells, which all are sensitive to different wavelengths, whereas humans have trichromatic vision (Bowmaker *et al.* 1997; Osorio *et al*. 1999a, b; Vorobyev *et al.* 2001a, b). This means that we cannot rely on human colour standards when estimating the visibility of coloured stimuli to birds (Endler 1990; Bennett *et al*. 1994; Cuthill *et al*. 2000; Fleishman & Endler 2000). However, despite the difference between human and animal vision, the general properties of visual perception are fairly similar, at least among vertebrates, and therefore perceptual mechanisms known from the human visual system are useful when trying to understand and explain the concealing properties of camouflage patterns used by animals (Troscianko *et al*. 2009).

Visual perception is a hierarchical process, and there are several steps the perceptional system of the viewer must complete to be able to successfully detect and recognise an object (Mather 2009; Troscianko *et al*. 2009), in the case of this thesis a camouflaged prey. In short, there are three main stages of how an image projected on the retina is visually processed, i.e. from the time the object reaches the eye of the viewer until the object is correctly categorised and identified. At the first stage, local features of an object, such as colour, lightness and differences in them, textures, lines and edges, are processed. At the second stage, a viewer uses detected local features to detect shapes. At the third stage, objects are discriminated from the background and from each other, and they are recognized or categorised (Mather 2009; Troscianko *et al*. 2009). Thus, this stage may also lead to a predator’s decision to initiate an attack towards a target object.

Due to the complex and hierarchical nature of the processes involved in visual perception, there are several different levels and steps that prey coloration may target to deceive. If any step of visual perception is somehow tampered with, then it will be more difficult or impossible for a predator to successfully detect a prey. This suggests that there may be many different strategies of achieving concealment, and moreover, a specific prey colouration may target to hinder not just one but several steps in this hierarchical process. We cannot exclude the possibility that there may be some camouflage strategies that are still unknown to us.

In conclusion, crypsis can target various stages in predators' processing of visual information, and therefore the knowledge of visual perception is important for our understanding of prey concealment and evolution of animal camouflage. It allows us to formulate testable hypotheses about camouflage and can provide explanations for why and how specific colour patterns decrease risk of detection for prey.

## METHODS

In this thesis I present four studies on prey crypsis and concealing properties of visual backgrounds. All the studies are predation experiments that have used artificial prey items and backgrounds, and caught wild blue tits (*Cyanistes caeruleus*) as predators (Fig. 1). Below, I describe the general methods of these studies.

### *The predators*

Birds are important visually hunting predators and they are likely to impose a selection pressure that greatly influences the appearance of their prey, such as insects and other invertebrates. Blue tits (Fig. 1) are a widespread passerine species and as a partial migrant (Nilsson *et al*. 2008) they are found throughout the year in Sweden and the rest of Europe. Thus, they and other passerine birds probably impose a significant selection pressure on many camouflaged prey. Although the predation pressure on a given prey species is usually caused by several different predatory species, by only using a single species I could concentrate in finding the plausibility of a specific camouflage strategy without any confounding factors, such as differences in predator vision, search strategy, general abundance etc.

**Figure 1**. A blue tit caught in the net, eagerly waiting for its turn to participate in my experiments.

I conducted my studies during the winter (November to March) between 2005 and 2009 at Tovetorp Zoological Research Station (Stockholm University) in South-Eastern Sweden. The studies were performed with permission from the Swedish ethical board in Linköping (D.nr.: 56-06 and 62-08). The blue tits were captured with mist nets (Fig. 1) and kept indoors in individual cages with suet, sunflower seeds, peanuts and water *ad libitum*. The light:dark rhythm (with dusk and dawn) was adjusted according to the prevailing day length. After completing the experiment each blue tit was released in the area of capture.

### *Prey and backgrounds*

For all the experiments I created artificial backgrounds and prey items. The backgrounds and the prey items were made of paper: their patterning was created with the software Corel Draw 11 (Corel Corporation) and they were reproduced with a laser printer (HP LaserJet 4000 Series PS). Although I used artificial prey items they may be considered to loosely resemble small insects, such as moths or butterflies, which constitute an important part of the diet of passerine birds, such as the blue tit. The benefit of using artificial prey items and backgrounds was that I could control all aspects of their appearance (i.e. their patterning). Therefore I could pinpoint a specific question about prey camouflage or concealing properties of backgrounds, and design the backgrounds and the prey items accordingly.

When necessary, I used a spectrometer (Ocean Optics USB 2000 with a PX-2 pulsed xenon light source) to measure lightness and spectral reflectance of the backgrounds and the prey items (i.e. Papers **I**, **II** & **III**). Combined with information about the spectral sensitivity of blue tit vision (Hart *et al*. 2000), this allowed me to calibrate the printed patterns to control for that blue tits actually did experience those levels of achromatic or chromatic contrasts within a prey pattern, between prey patterns or between the prey and the background, depending on the experiment.

All printed backgrounds were A4-sized (21 x 29 $cm^2$), and they were glued to an equally-sized corrugated cardboard to constitute ‘experimental boards’. On each experimental board I made a randomly placed hole, a piece of peanut was put into the hole and then a prey item was lightly glued to cover the hole. After I had caught blue tits, I trained them to search for the artificial prey items, by teaching the blue tits to associate the printed pieces of paper of given shape (depending on experiment) with the piece of peanut they covered. The training was stepwise: first all prey items were fully visible and presented on a mismatching background. Then, the prey items were presented on a more or less matching background, so that they were camouflaged and harder to detect. After a bird had successfully completed the training sessions, they proceeded to the experiment.

### *The experiments*

All experiments were conducted in experimental cages that were made of plywood and that were lit from the ceiling (Fig. 2). All observations were made from a small window that was covered with a one-way see-through plastic sheet, and because the experimental room was always kept dark during an experiment the blue tits could not see the observer. In the experiments I measured the time it took for the blue tit to find a prey, and this was used as an estimate of prey concealment. The longer the search time was, the harder the prey item was to detect by the predators.

During the experiments the blue tits were presented with a series of experimental boards. Each series consisted of different background-prey item combinations, and each combination was repeated two or three times (depending on the experiment) for each bird. The mean search time for each background-prey item combination were then analysed.

**Figure 2.** The inside of the experimental cage.

In addition, I also performed control experiments (Paper **I**, **II** & **III**) where I investigated whether the blue tits had aversions towards any of the different prey types used in the camouflage experiments. In the control experiments the blue tits were presented with prey items in the same way as in the experiment, but on plain brown A4-sized corrugated cardboard boards thus making all prey items easy to detect. A delay before ‘attack’ would reveal if the blue tits had any aversion towards a prey. However, I found that when the prey items were fully visible the blue tits attacked immediately. Hence, I conclude that any differences in search times between the prey categories in the camouflage experiments were not caused by difference in blue tits willingness to attack, but they were caused by differences in detection times.

# RESULTS

## *Paper I. Concealed by conspicuousness: distractive prey markings and backgrounds*

In paper **I**, I have focused on a so far little studied principle of camouflage, distractive markings. The idea about distractive markings was suggested by Thayer already in 1909. Thayer (1909) suggested that highly conspicuous markings would draw and hold the attention of a predator, thus hindering detection or recognition of other, more informative prey characteristics, which could reveal a prey's presence. Perhaps due to the counterintuitive reasoning, i.e. conspicuous markings will increase prey camouflage, this principle has received little attention. Also, somewhat confusingly, it was typically integrated into the concept of disruptive coloration (cf. Cott 1940) and has only recently been acknowledged on its own.

The aim of this study was to investigate if high-contrast prey markings would decrease the risk of detection for a prey according to the idea about distractive markings. Further, I hypothesised that if distractive markings on prey make its detection difficult, then similar markings in the background should affect prey detection times as well. I specifically predicted that, if distractive markings (either in the prey patterning or in the background) are effective and increase prey detection times, they should work even when the markings do not blend in the background. However, if background matching is more important prey displayed on matching backgrounds would be harder to detect and the conspicuous markings should facilitate prey detection.

As the first study ever since Thayer (1909) suggested the idea of distractive markings, my study presents evidence that such markings in the prey patterning and also in the background can indeed increase prey detection times and hence improve prey crypsis (Fig. 3). From my experimental set-up I could not specifically pinpoint which perceptual mechanism distractive markings target. Visual attention is limited and only a certain amount of information can be processed at one time (Desimone & Duncan 1995). Brightness stimuli have been shown, in experiments with humans, to have attentional priority (Proulx & Egeth 2008) and it is possible that only the white markings, and not the black markings (Paper **I**, Fig. 1), created a distractive effect by holding the attention of the blue tits away from the 'body' shape of the prey. However, it is possible that other visual processes were involved in creating a distractive effect, such as lateral masking (i.e. peripheral perception of a visual stimulus is impaired when other stimuli/distractors are present in its adjacent surroundings; Wertheim *et al*. 2006) or other attention-driven processes.

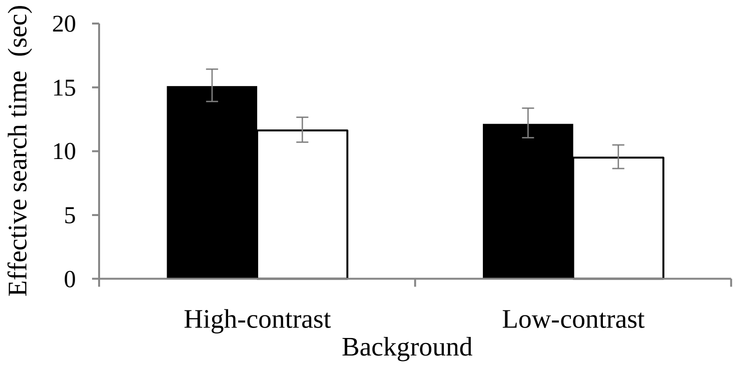


**Figure 3.** High-contrast markings in the prey colouration (black bars) and in the high-contrast background increased predator search times, thus made the prey more difficult to detect, when compared to a prey with low-contrast markings (white bars). The whiskers are back-transformed standard errors (n=33).

To conclude even though the exact mechanistic explanation for how distractive markings function is not known, my results suggest interesting possibilities about evolution of prey concealment. Also, we now know enough to consider distractive markings as a principle of camouflage on its own, distinguishable from disruptive colouration. Distractive markings may stand out from the background, but their placement should not be at the body margin or draw attention to other revealing characteristics and, as suggested by Thayer (1909), they should perhaps be quite small to be only visible at near view. Also my results hint to the possibility that prey with distractive markings can be camouflaged, not only on matching, but also on to some degree mismatching backgrounds. Hence, such markings may give prey living in visually heterogeneous habitats the possibility to use the entire habitat and still be relatively well concealed in all microhabitats. The result that all prey types were harder to detect on the high-contrast background hint to the interesting possibility that a prey can choose such backgrounds and be enough camouflaged even if it is not background matching. Perhaps this result may explain why evolution of camouflage sometimes is favoured rather than other anti-predator strategies.

### *Paper II. Cromaticity in the UV/blue range facilitates the search for achromatically background-matching prey in birds*

In Paper **II**, I have focused on the use of chromatic cues by avian predators that are searching for prey. There are different visual mechanisms a predator can use to detect the presence of the prey. Osorio *et al*. (1999a) suggested that edge detection based on achromatic cues may be one such mechanism. This assumes that predators focus on sharp achromatic discrepancies between a prey and its background. However, some studies have shown that birds and primates attend primarily to chromatic cues when searching for fruits (Sumner & Mollon 2000; Schaefer *et al*. 2006; Cazetta *et al*. 2009) and passerine birds often use chromatic cues in the UV range for intraspecific signalling (Håstad *et al*. 2005). This suggests that chromatic cues could be important for birds to attend to when searching for prey.

The aim of this study was to compare search times for prey that either matched or mismatched the background with respect to chromaticity. This was done by printing both the prey items and the backgrounds on two kinds of papers that differed in their spectral reflectance: one paper had peak reflectance in the blue part and low reflectance in the ultraviolet (UV) part of the spectrum ("chromatic paper"; here called UV-); whereas the second paper had even reflectance over the entire visual field of the blue tits ("achromatic paper"; here called UV+; see Fig. 1 in Paper **II**). More specifically, I tested if blue tits make use of chromatic information when they search for prey. If they do, then they should easily find prey that appears chromatically but not achromatically different from the background. However, when the blue tits search for background-matching prey (both with respect to chromatic and achromatic cues; for example UV+ prey on UV+ background) then the search task should be much more demanding. In addition, any asymmetries in search times between the two chromatically different, matching combinations (e.g. UV+ prey on UV+ background vs. UV- prey on UV- background) would suggest that the specific spectral properties of the prey and background pattern (and not only difference or similarity in general) do also influence the search task.

When I presented the UV+ and UV- prey items on a mismatching background, the blue tits found both prey types equally quickly (Fig. 4). These fast search times suggests that the blue tits searched for the prey items in so called 'pre-attentive' search mode, in which the whole background is scanned in parallel (Treisman & Gelade 1980). This result supports previous studies where chromatic cues have been used to search for prey items by bees and chicks (Giurfa *et al*. 1997; Giurfa & Vorobyev 1998; Osorio *et al*. 1999a; Spaethe *et al*. 2001). This confirms that colour is an important aspect of background matching (Théry & Casas 2002). Thus, if a prey does not chromatically match its background, the risk of becoming detected by avian predators would severely increase, even if it matches the background with respect to achromatic cues.

The blue tits needed a longer time to detect the matching background–prey combinations (Fig. 4). Here I suggest that the blue tits had to switch from parallel search to serial search to be able to find the prey items. In the more time-consuming serial search attention is focused on the potential targets themselves, serially identifying them as real targets or non-targets (Treisman & Gelade 1980).

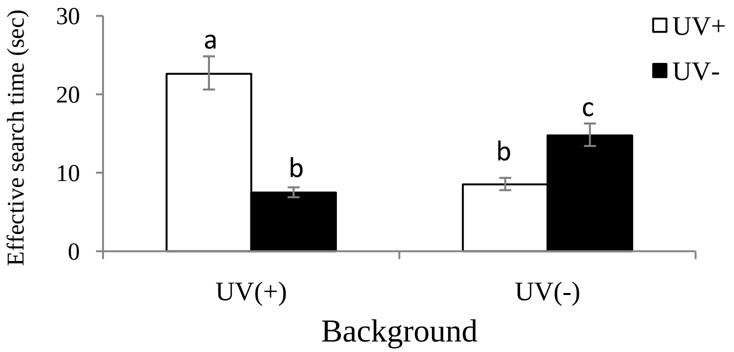


**Figure 4**. Search times of blue tits for both the UV+ prey (white bars) and the UV- prey (black bars) on both the UV+ and the UV- background. Shown are mean values and back-converted standard errors of the means (n=27). The letters above the bars denote the results of the *post hoc* comparisons so that bars with different letter differ significantly from each other (for details see Paper **II**).

In addition, I found that the search for the UV+ prey on the UV+ background was significantly longer than the search for the UV- prey on the UV- background (Fig. 4). This somewhat surprising result suggests that also the specific chromatic properties of the prey and the background influence prey search and detection. Due to the spectral properties of the papers used in this study, I cannot conclude that all differences in spectral properties will give similar results, thus in future studies other aspects of spectral dissimilarities and their effect on detection times of camouflaged prey may be interesting to investigate.

### *Paper III. Prey concealment: visual background complexity and prey contrast distribution*

In paper **III**, I have focused on two important principles of camouflage, namely background matching and disruptive coloration (Cott 1940; Edmunds 1974; Ruxton *et al.* 2004). Background matching is based on visual similarity (i.e. colour, lightness and pattern) between the prey and its background (Stevens & Merilaita 2009a). Disruptive colouration, on the other hand, emphasises the use of highly contrasting pattern elements at the body outline to break up the prey body shape, thus hindering detection or recognition of the prey (Thayer 1909; Cott 1940; Stevens & Merilaita 2009b).

The aim of this study was to investigate different predictions about optimisation of contrast within prey colouration drawn from background matching and disruptive colouration, as well as to investigate the effect of background complexity on prey detection. More specifically I looked at optimisation of lightness and contrast within prey patterning. I used prey with three different colour schemes that all matched the white-grey-and-black backgrounds: high-contrast (black-and-white), low-contrast (grey-and-white) and three-shaded (white-grey-and-black) prey. This allowed me to test if high contrast within prey pattern, predicted by disruptive coloration, makes prey difficult to detect compared to the low-contrast prey. I also tested, if it is better to match all shades that are found in the background than to only match a sub-sample of the background shades. Third, I compared the importance of spatial distribution of pattern contrast (marginal vs. central) according to predictions drawn from disruptive colouration. Finally, I compared prey search times on two backgrounds, one with a lower and one with a higher diversity of pattern element shapes.

My results did not support the prediction that prey with high-contrast patterns should be better concealed than prey with low-contrast pattern due to a stronger disruptive effect. This result is supported by a study by Stevens *et al*. (2009). However, there are several studies that have found the opposite (Cuthill *et al*. 2005; Schaefer & Stobbe 2006; Stevens *et al*. 2006). These conflicting results suggest that the effect of high-contrast markings may be context dependent (depending for example on the size of the markings) and further studies are needed to fully understand their effect on prey camouflage.

When I investigated the predictions related to background matching, I found that a prey matching a sub-sample of the background shades was equally hard to detect as a prey matching all shades in the background. This result implies that a prey does not necessary need to match all the shades present in the background habitat to achieve high degree of concealment.

I also did not find any support for the suggestion that spatial distribution of highly contrasting elements is important for prey camouflage. Both our prey items with marginal and central placement of high-contrast markings were equally hard to detect. This contrasts the result in Stevens *et al*. (2009): they found that prey with marginally placed high-contrast elements and centrally placed low-contrast elements were more difficult to detect.

Finally, I found that visual background complexity indeed has a strong effect on prey detection time independent of the appearance of the prey items. All prey items were harder to detect on the complex than on the simple background (Fig. 5). Since Merilaita (2003) suggested that background appearance *per se* may influence prey detection, my study presents the first empirical evidence for the importance of background appearance on prey detection times. In nature there is substantial variation in different visual aspects of habitats (e.g. contrast, lightness, spatiochromatic properties; Parraga *et al*. 2002; Frazor & Geisler 2006; Geisler 2008), and it is likely that there is also a substantial variation in degree of visual complexity. Thus, I suggest that prey may decrease its risk of becoming detected through a preference for visually complex habitats. In conclusion, I found that when studying evolution of prey camouflage and optimisation of prey patterning we must also consider the appearance of the background itself and its effects on predator detection times.

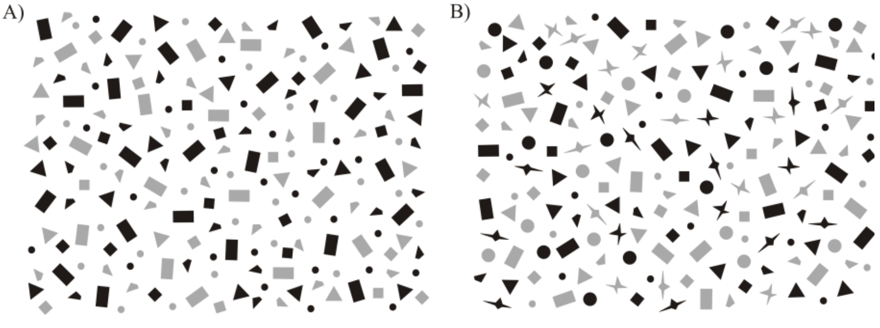


**Figure 5.** The two backgrounds, **A)** simple and **B)** diverse, differed only in the number of differently shaped pattern elements, five and eight, respectively.

### *Paper IV. Avoiding detection: effects of prey pattern regularity, background matching and complexity of the habitat*

In Paper **IV**, I again focused on background matching and selection on prey patterning. We know that several aspects of colouration and patterning (e.g. colour, lightness, size, shape and spatial distribution of pattern elements) can affect the resemblance of a prey patterning to its background. However, it is unlikely that all aspects are equally or even very important in background matching. In addition, previous studies have shown that some regular patterns, such as bilaterally symmetrical patterns tend to generally make camouflaged prey easier to detect (Cuthill *et al*. 2006; Merilaita & Lind 2006). In addition, Cott (1940) suggested that a camouflaged prey with a variable body pattern would be more difficult to detect than a camouflaged prey with an invariable body pattern. Further, due to my previous result that indicated the importance of background appearance (Paper **III**) I again focused on how visual complexity of the background affects prey detection.

This study consists of two separate experiments. The aim of the first experiment was to investigate the effect of prey pattern regularity due to repeated pattern element shapes on background matching. More specifically, I investigated if it is easier to detect a prey pattern consisting of one repeated element shape compared to more variable patterns (one completely background-matching variable prey pattern, and one partly mismatching variable prey pattern; see Fig. 1a in Paper **IV**). I presented these prey items on two backgrounds (the same ones as in study **III**), one visually simple and one visually complex, to investigate how the search task difficulty will affect prey detection.

In the second experiment, I investigated how spatial regularity of prey pattern elements affects detection of background-matching prey. More specifically, I studied if spatially regular (i.e. aligned) placement of identical pattern elements is more detrimental for crypsis than spatially irregular placement (see Fig. 2a in Paper **IV**). In addition, I tested if the complexity of the background element shapes (here defined as perimeter-to-√area ratio) influenced prey search by blue tits.

The results from the first experiment showed that a regular, background-matching prey pattern was equally easy to detect as the variable, background-matching pattern. Thus, I found no support for Cott's (1940) suggestion that increased prey pattern regularity due to repeated pattern elements would increase the probability of prey detection. Not surprisingly, I also found that a variable, mismatching prey pattern was easier to detect than a variable background-matching prey pattern. Thus, my results may be interpreted so that pattern regularity due to repeated elements incurs little extra cost for survival of cryptic prey. However, one could expect that predation may select more strongly against mismatching prey pattern element shapes for cryptic prey patterns. Still, I did not find a significant difference between the search times of the regular prey pattern and the variable, mismatching prey pattern. This latter result implies an intriguing idea about prey living in heterogeneous habitats. Namely, the mismatching pattern shape in one habitat could be background-matching in another habitat, and hence a prey with such body pattern might be able to use both habitat types without decreasing very much its camouflage. This result clearly warrants further research.

In the second experiment, prey with spatially irregular pattern elements was harder to detect than prey with spatially regular pattern (Fig. 6). This shows that also other types of spatial regularities than bilateral symmetry are important in prey concealment, and probably also for the function of anti-predator signals, such as warning colouration.

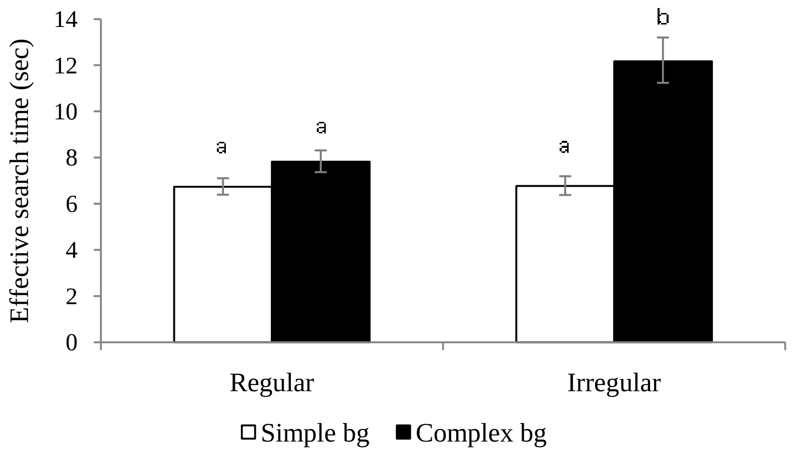


**Figure 6**. The effective search time (sec) for the spatially regular and irregular prey category on the simple background (white bars) and the complex background (black bars). The letters above the bars denote the results of the post hoc comparisons so that bars with different letters differ significantly from each other. Whiskers are back-transformed standard errors (N=35).

When considering background appearance, in the first experiment I showed that all prey items were more difficult to detect on the complex than on the simple background. In the second experiment I specifically showed that complex element shapes in the background increased prey search times. This latter result gives us one guideline to compare natural backgrounds with each other and estimate their impact on prey search. Interestingly, the effect of background complexity was dependent on the appearance of the prey (Fig. 6). The spatially regular prey patterns were equally easy to detect on both the simple and the complex background, but the spatially irregular prey pattern was significantly more difficult to detect on the complex background than on the simple background. These results suggest that different selection pressures may drive the evolution of spatial regularity of prey patterns depending on the visual complexity of the habitat the prey lives in.

To summarise, with this study I have shown that spatial regularity of prey patterning is a property that may affect the camouflage of background matching prey. Also, I showed that a specific aspect of background appearance (i.e. complexity of background element shapes) is important in determining whether a background increases the difficulty of detecting cryptic prey.

## CONCLUDING REMARKS

The work described in this thesis shows that the use of a controlled experimental set-up, i.e. laboratory experiments with artificial prey and backgrounds and trained individuals of a single predatory species, enables the investigation of very specific and detailed questions about prey concealment and optimisation of prey patterning.

In this thesis I have shown that the appearance of the background *per se* is very important to take into consideration when studying prey concealment. I have shown that a visually complex background (i.e. high diversity of element shapes and complex element shapes), as well as high achromatic contrast range of the background can make detection of prey more difficult. These results suggest the intriguing possibility that cryptic prey may evolve habitat choice behaviours that allow them to further improve their concealment simply by preferring backgrounds with characteristics that impede search. This would provide a simpler mechanism than the often suggested preference for backgrounds that match prey coloration, because it is independent of prey appearance. In addition, this result may give us further insight into how other predator avoidance strategies, such as aposematism, may evolve. For example, it could be possible that a prey in a visually complex background may pay a smaller cost associated with evolving an aposematic colouration when it lives in a visually complex background compared to a prey that lives in a visually simple background. Also, by pinpointing specific properties of the background (i.e. element complexity, achromatic contrast range), that makes it be perceived as easy or difficult by a predator, gives us some means to compare different habitats and predict which of them provides a more difficult search environment.

I have also investigated effects of different aspects of colour patterns, some of them previously unrecognised, on prey camouflage. Importantly, I have presented the first empirical evidence that high-contrast markings may indeed be effective in achieving a distractive effect and affecting predator search times. This phenomenon needs to be further studied so that we can fully understand its importance as a camouflage strategy. I hope that the findings and conclusions drawn from my studies will enhance our understanding of why animals look like they do and then they will be of help for scientist in the future to solve the optimisation of cryptic prey colour patterns.

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# KAMOUFLAGE HOS BYTESDJUR:
## EFFEKTER AV FÄRGTECKNING OCH BAKGRUND

Djur lever i en farlig värld och varje dag utspelas en ständig kamp om överlevnad. Det råder ett intrikat samspel mellan bytesdjur och rovdjur och båda har under evolutionens gång utvecklat anpassningar som hjälpt dem att överleva. Denna avhandling syftar till att bättre förstå vilka anpassningar som bytesdjur har utvecklat för att undvika att upptäckas eller kännas igen av rovdjur. I synnerhet har jag undersökt hur bytesdjur med hjälp av kamouflage optimerar sin chans för överlevnad. Kamouflage har länge erkänts som en viktig anpassning mot rovdjur och har historiskt används som ett viktigt exempel för teorin om naturligt urval som Wallace och Darwin advocerade för. Utöver bytets färgteckning har jag även undersökt hur bakgrundens utseende i sig påverkar ett bytesdjurs chans att undgå upptäckt.

Min avhandling innehåller fyra studier, där jag har studerat följande kamouflageprinciper: bakgrundsmatchning, formupplösande färgteckning, samt distraherande färgteckning. Alla experiment utfördes på Tovetorps zoologiska forskningsstation. Jag använde artificiella byten och artificiella bakgrunder, samt blåmesar (*Cyanistes caeruleus*) som rovdjur, för att studera betydelsen av bytesfärgteckning samt bakgrundens effekt. Blåmesarna tränades i att söka efter de artificiella bytena på de artificiella bakgrunderna, och motiverades genom att det under varje byte fanns en belöning i form av en liten jordnötsbit. Jag använde tiden det tog för en fågel att hitta ett byte som mått på bytets kamouflage, dvs. ju längre söktid desto bättre kamouflage.

I artikel **I** har jag undersökt om starkt kontrasterande element i bytesfärgteckningen eller i bakgrunden kan göra ett byte svårare att upptäcka. Mina resultat visar att sådana element påverkar söktiden eftersom det tog längre tid för blåmesarna att hitta bytet även när bytets färgteckning hade element som inte matchade bakgrunden. Idén om effekten av distraherande element har tidigare inte undersökts vetenskapligt, eftersom förklaringen till deras funktion är ganska kontraintuitiv. I princip handlar den om att högt iögonfallande element gör ett byte mer kamouflerad. Min studie är den första som visar att starkt kontrasterande element, både i bytesfärgteckningen men även i bakgrunden, leder till att ett byte blir svårare att upptäckas.

I artikel **II** undersökte jag hur fåglar använder färginformation när de söker efter byten. Resultaten visar att byten med färgteckning som skiljde sig från färgerna i bakgrunden var mycket lätta att hitta. Om däremot bytets färgteckning matchade bakgrundens utseende i fråga om färg, så var bytena svårare att hitta, men här fann jag skillnader i söktid beroende på de specifika färger som ingick i bytena och i bakgrunderna. Detta resultat tyder på att fåglar använder olika slags färginformation när de söker efter kamouflerade byten, samt att den specifika kompositionen av färger påverkar hur svårt ett byte är att upptäcka. I framtiden kan det vara viktigt att ytterligare studera hur olika slags färginformation används av fåglar.

I artikel **III** studerade jag optimeringen av kontraster utifrån prediktioner härledda från principerna om bakgrundsmatchning och formupplösande färgteckning. Jag undersökte hur variation i form av bakgrundselement påverkar söktiden för kamouflerade byten. Studien visar att blåmesarna fann alla byten lika snabbt oberoende av bytenas interna kontraster. Däremot var alla byten mycket svårare att upptäcka på den mer varierande bakgrunden. Detta resultat har många intressanta implikationer, bland annat så föreslår jag att byten, kan utveckla preferenser för visuellt komplexa bakgrunder för att minska upptäcktsrisken. Mina resultat visar klart att när man studerar evolution av bytesfärgteckning så måste man ta hänsyn till den visuella bakgrunden i sig och dess påverkan på rovdjurs söktid.

I artikel **IV** undersökte jag hur ett byte kunde optimera sitt kamouflage med avseende på bakgrundsmatchning. Jag fann att ett bakgrundsmatchande byte med regelbunden färgteckning (endast en elementform) var lika svårt att upptäcka som ett byte med en mer variabel färgteckning (två olika bakgrundsmatchande elementformer). Däremot, när jag undersökte den specifika placeringen av dessa element, så fann jag att om man placerade alla elementen slumpvis på bytets kropp så var detta byte svårare att hitta än när elementen placerades på en rad. Även i denna studie fann jag att den visuella komplexiteten påverkar hur lång tid det tar innan ett rovdjur hittar ett byte. Om en bakgrund innehåller elementformer som är komplexa (här definierat som kvoten av elementens omkrets delat med √arean) så påverkas blåmesarnas söktid och det tar längre tid att hitta kamouflerade byten.

Slutligen, den experimentella metoden jag använde gjorde det möjligt att ställa och undersöka specifika och detaljerade frågor gällande byteskamouflage samt optimering av ett bytes färgteckning. Resultaten i min avhandling visar klart att när vi studerar kamouflage och evolution av färgteckning så måste vi också alltid ta hänsyn till den visuella bakgrundens utseende och dess effekt på bytens upptäcktsrisk. Jag hoppas att de resultat och slutsatser som jag framfört i denna avhandling kommer att öka vår förståelse för varför djur ser ut som de gör, och att de i framtiden kommer att hjälpa andra forskare att lösa gåtan om optimering av färgteckning hos kamouflerade djur.

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