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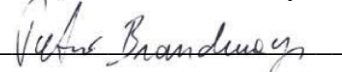
**Investigating how movement affects prey camouflage
using an insect predator**

Settore Scientifico Disciplinare BIO/05 Zoologia

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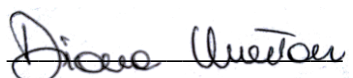
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Thesis Abstract

Patterns that help prey camouflage themselves whilst stationary prove to be ineffective once prey move. Given that motion breaks camouflage, can a moving prey ever be effectively concealed? Recent studies have found that certain patterns might help prey deceive their predators whilst moving, as in the case of ‘motion dazzle’. However, research with moving prey has been conducted using only humans or birds as predator models, and consequently, it is now known how other predator species might behave. In addition, it is important to know not just how motion affects camouflage, but also how the speed of motion can affect the efficacy of different defensive patterns.

This thesis aims to address these current gaps in the field. First, I explore the visual acuity in a group of insect predators, the praying mantids, to explore if different species vary in their visual acuity, which could impact on what they can perceive and which selective pressure they could exert on prey defensive patterns. Second, using praying mantids tracking computer-generated stimuli, I empirically investigate how cryptic and conspicuous patterns might enhance the survival of moving prey. In particular, I specifically investigate if high contrast striped prey could reduce predation risk through the visual phenomenon known as “flicker fusion effect”. I found that when prey were slow moving, all patterns were equally detectable by the mantids. However, once prey moved at faster speed, a cryptic pattern was more likely to be tracked than a more conspicuous black-and-white striped pattern suggesting that the latter was successful in inducing flicker fusion effect in praying mantids’ eyes.

This thesis starts to disentangle how pattern and speed could combine to help camouflage an animal when moving through its environment. The outcome of the study are discussed in the wider context of how animals coloration and behaviour evolved together to confer them survival advantages.

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Chapter 1: General introduction

1.1 Animal camouflage

Animals have evolved different strategies in order to increase their survival chances and reduce the cost of predation. The defensive mechanisms prey can adopt are various and, for instance, can include changes in their foraging behaviour and microhabitat use if it helps to reduce encounters with predators (e.g. Preisser & Bolnick 2008). Prey can protect themselves with harmful defences, for instance physical (e.g. Lichter-Marck et al. 2015) or chemical (e.g. Roth & Eisner 1962); or even bluffing their predator by resembling the appearance of defended species (e.g. Mappes & Alatalo 1997). Indeed, it is well established that animals' patterns have been shaped by selection to accomplish different functions and evolved to confer an adaptive advantage to both predators and their prey (Cott 1940). For instance, defended prey can gain survival advantages by advertise their would-be predators of their unprofitability and therefore reduce the chances of get injured or attacked (e.g. Wallace & Wallace 1889; Rowe & Guilford 1999; Endler & Mappes 2004; Skelhorn, Halpin, et al. 2016). Certain prey, instead, reveal their conspicuous colour pattern only once feel threat by a predators to avoid or delay its attack (e.g. Vallin et al. 2005; Olofsson, Eriksson, et al. 2012; Skelhorn, Holmes, et al. 2016). Alternatively, animals can avoid to encounter their would-be predators in the first place by camouflage themselves.

Camouflage is a widespread adaptation used by both predators and prey. Predators have adopted it to hide their presence to an approaching prey, and

therefore increase the chances that an attack is successful. Prey are camouflaged to conceal themselves, and decrease the chances of being detected or recognized by would-be predators (Endler 1978; Ruxton et al. 2004). Camouflage can be achieved through sensory modalities other than vision (Ruxton et al. 2004), including chemical (e.g. Brandmayr et al. 2006; Mizuno et al. 2014) or auditory (e.g. Olofsson, Jakobsson, et al. 2012; Igic et al. 2015). However, in my thesis, I will focus on the camouflage strategies that exploit mechanisms in visually hunting predators.

There are a number of visual camouflage strategies that have been well described and studied in the literature. *Background matching* is commonly defined as being when an animal resembles aspects of its surroundings (e.g. the colour and/or pattern); this makes prey hard to detect and distinguish from their background (Endler 1978; Cuthill et al. 2005). Alternatively, a prey can resemble a certain inedible object that is common in its surroundings: *masquerade* occurs if the predator detects the prey but does not identify it as possible prey because it is misclassified as the object that the prey resembles (Skelhorn et al. 2010; Skelhorn 2015). Another common form of camouflage is *disruptive coloration*, which consist of markings or features, generally at high contrast, which break up the body outline of the animal and create false boundaries. As a consequence, the prey makes it difficult for a predator to identify the presence of a salient visual “shape” which is often use for detection and identification (Cuthill et al. 2005; Webster et al. 2013). Similarly, prey can drive predators’ attention away from the body outline through *distractive markings* (Dimitrova et al. 2009; Olofsson et al. 2010; Olofsson, Jakobsson, et al. 2013; Merilaita & Dimitrova 2014). *Countershading* can also be used by prey to reduce their self-shadowing, improve crypsis and perhaps result less recognizable. This is where coloration gradually changes across an animal’s body from light to

dark in the opposite direction to the one of the ambient light source, effectively reducing the effect of the shadow (Rowland et al. 2008; Cuthill et al. 2016).

Whilst there has been a lot of work on the benefits and evolution of camouflage, it is interesting to note that almost all studies explore how it operates in stationary prey. Only recently have researchers started to investigate how prey with effective camouflage patterns whilst stationary will change in their detectability once they start to move (e.g. Stevens et al. 2011). Since movement breaks camouflage (e.g. Hall et al. 2013), incorporating motion into the study of defensive coloration seems to be an important and promising field for further research.

1.2 Camouflage whilst in motion

Historically, different forms of animal coloration have been classified by their function, and therefore, researchers have long discussed “defensive coloration” as those patterns that can help an animal camouflage or defend itself (e.g. Cott 1940; Endler 1978). However, it is becoming increasingly evident that visual appearance alone does not ensure an effective camouflage if it is not combined with the appropriate behaviour (e.g. Olofsson, Lovlie, et al. 2013). For example, an insect resembling the appearance of a stick should sway in the wind to help match its surrounding or else lose its ability to remain hidden (Bian et al. 2016); similarly, a prey that closely resembles its visual background should remain still in order to remain camouflaged (Ioannou & Krause 2009). Therefore, we should perhaps consider the evolution of defensive strategies rather than just colorations, since natural selection will select on both the visual appearance and the prey’s behaviour.

Indeed, movement is known to alter the efficacy of an animal's camouflage strategy: once an animal moves, motion will reveal its body outline and the animal will be more easily detected, at least if moving on its own (Hall et al. 2013). Because patterns that camouflage animals whilst stationary, e.g. background matching or disruptive coloration, become ineffective when animals move, there is increasing interest in understanding how animals try to remain hidden whilst moving.

Indeed, there is one important question that remains unanswered: can a moving animal ever be concealed? Whilst some experiments suggest that some patterns might make prey harder to catch when moving (the idea of 'dazzle coloration'; e.g. Stevens et al. 2011; Hughes et al. 2014; Hämäläinen et al. 2015), there is no evidence that moving prey become better concealed. To date, to my knowledge, there is only one strategy that could conceal animals whilst in motion, and that is the *flicker fusion effect*. The effect, which causes prey to appear different whilst moving compared to when stationary, has long been discussed in literature as a possible defensive strategy (e.g. Pough 1976; Jackson et al. 1976; Stevens 2007). Despite being discussed for over 40 years, the visual mechanism of the effect has never been fully investigated, nor has its efficacy been tested against naturally relevant predators. The mechanism behind the effect is based on the interaction of prey pattern and prey speed of motion. Indeed, in order to induce flicker fusion effect in its predator's eyes, a prey has to flee at a speed high enough so that its pattern elements cross predator's visual plane faster than what it could temporally resolve. However, whilst studies have investigated how patterned prey would appear whilst moving, extremely little is known about how animal patterns interact with the speed at which the animal moves. Only few studies have investigated how prey with variously patterned camouflage could reduce predators' attack whilst moving at different speed levels (e.g.

Blakemore & Snowden 2000; Scott-Samuel et al. 2011), although, as mentioned, prey speed could play a crucial role in help prey reduce predation risk.

The lack of a clear understanding of how speed of motion interacts with prey patterning to enhance prey survival have led to increasing confusion about whether or not certain pattern-motion combinations might help prey camouflage themselves and, more importantly, if it does occur, which mechanism(s) is (are) exploited (Kelley & Kelley 2014): possible mechanism includes reduce visibility, impair a predator's ability to accurately judge speed or trajectory of the prey, or hide prey's final resting position. Clearly, without knowing how pattern and movement might interact in putative camouflage strategies, it become hard to define them and distinguish one case from the other. For instance, I will discuss the case of the flicker fusion effect which function and mechanism has been occasionally overlapped with the one of motion dazzle (Ruxton et al. 2004; Stevens 2007).

Eventually, much uncertainty still exist on what we refers to when discussing prey camouflage whilst in motion: what is that will be camouflaged? Indeed, the animal itself can be camouflage, or its movements or both, but further investigation are needed as this field is relatively new and unexplored.

1.3 The importance of predators' perception and cognition for the evolution of prey defences

How effective a defensive strategy will be ultimately depends on the predator against which is used, and, therefore, a crucial role is played by predator' sensory ecology.

Most typically, the efficacy of prey coloration has been investigated using avian predators, since they are well-known predators of well-studied defended insects (e.g. Mappes et al. 2005; Skelhorn, Halpin, et al. 2016). Given their incredible acute colour vision (Zeigler & Bischof 1993), birds are likely to have selected for a range of colour patterns in insects, both cryptic and aposematic (studied since Kettlewell, 1955). This focus on avian predation has meant that the role of other predators, especially insect predators, has long been overlooked. This may have occurred because their visual systems are less able to resolve patterns, although they are extremely tuned to detect motion (e.g. Nordstrom et al. 2006), which is also a fundamental cue used for detection (e.g. Stevens et al. 2011). In particular, insects' visual systems, despite being constrained by a relatively small body size, have evolved to be extremely sensitive to motion and contrast, and particularly well designed to detect small targets, even whilst moving against a cluttered background (Nordström et al. 2006; Gonzalez-Bellido et al. 2016). Bird and insect predators have very different visual systems, and potentially cognitive abilities, which may have meant different selection pressures exerted by this different taxa on their prey. To confer a survival advantage, a defensive strategy needs to be effective against the whole gamut of predators that a prey might have, and therefore, it is important that we investigate how defensive strategies work against multiple predators (e.g. Endler & Mappes 2004; Ratcliffe & Nydam 2008; Mochida 2011; Nokelainen et al. 2014), include insects.

However, to date only few studies have investigate how certain target' pattern and motion combination could be detected or could elicit a predatory response in insect predators (e.g. Prete 1993; Prete et al. 2013), thus we certainly need further

study to interpret how insect' predators might have shape the evolution of prey patterns and behaviour.

1.4 Aims of the thesis

My research has explored one group of insect predator, praying mantids, in order to better understand how their visual systems and predatory decisions could select for certain defensive strategies. In particular, I have used them as a model predator to explore how the interaction of prey speed and pattern affects their predatory behaviour, to test current hypotheses about how cryptic and conspicuous patterns might enhance the survival of moving prey. My specific aims were to:

- explore the variability of visual acuity across close related species of predators and investigate whether or not they might consequently exert different selection pressure on prey patterns and movements
- investigate the interaction of prey pattern and speed, particularly test and establish whether or not prey can camouflage themselves whilst moving by induce flicker fusion effect in their predator' eyes.

Chapter 2: Unravelling the illusion of flicker fusion effect

2.1 Abstract

For over 150 years, researchers have investigated the anti-predator function of animal patterns. However, this work has mainly focussed on when prey remain still, and has only recently started to incorporate motion into the study of defensive coloration. Since motion breaks camouflage, a new challenge is to understand how prey avoid predators whilst moving around their environment, and if a moving prey can ever be camouflaged. There is a putative solution to this, in that a 'flicker fusion effect' can change the appearance of the prey in the eyes of their predators to reduce the chances of initial detection. This effect occurs when a high contrast pattern blurs at speed, changing the appearance of the prey which may help them better match their background. Despite being widely discussed in the literature, the flicker fusion effect is poorly described, there is no clear theoretical framework for testing how it might reduce predation, and the terminology describing it is, at best, rather confusing. Here these three key issues will be addressed to enable researchers formulate precise predictions about when the flicker fusion effect occurs, and test how it can reduce predation.

2.2 Introduction

Prey use an incredible array of different strategies to avoid predators (Cott 1940). These include signalling defences to predators using warning coloration

(Mappes et al. 2005; Vallin et al. 2006; Rowe & Halpin 2013), avoiding detection by predators through camouflage (Stevens & Merilaita 2009), and mimicking inedible objects in the environment to avoid being recognised (Skelhorn 2015). These defensive strategies have been largely studied in the context of how a prey's appearance enhances its survival when it is stationary. However, given that many prey need to move around their environment (e.g. to find resources and mates), or use movement as part of their defensive display, there is increasing interest in how defensive coloration and movement interact to reduce predation (Srygley 1999; Stevens et al. 2011; Olofsson, Eriksson, et al. 2012; Hall et al. 2013; Olofsson, Lovlie, et al. 2013; Skelhorn, Holmes, et al. 2016; Umbers & Mappes 2016; Bian et al. 2016). Incorporating motion into the study of defensive coloration is important since not only can it change the efficacy of a defensive strategy (Stevens et al. 2011), but also raises novel questions about how defensive strategies function and are defined (Srygley 1999; Hall et al. 2013; Skelhorn, Holmes, et al. 2016; Bian et al. 2016).

One of the major challenges for understanding the anti-predator function of colour patterns of moving prey stems from the fact that 'motion breaks camouflage' (Hall et al. 2013): if moving prey cannot conceal themselves through camouflage, what kind of patterns could help reduce predation? One possibility is that colour patterns elicit visual illusions in predators when prey are moving, making them hard to capture. For example, high contrast visible patterns could elicit 'motion dazzle', impairing predators' judgments of speed and/or trajectory of moving targets (Pough 1976; Hall et al. 2013; Von Helversen et al. 2013; Hughes et al. 2014; Kelley & Kelley 2014).

However, there is another visual illusion that has received much less attention, but which could in fact help moving prey defend and possibly conceal themselves rather than just make them tricky to catch. The 'flicker fusion effect' can cause a change in a prey's appearance if it moves sufficiently quickly that its pattern becomes blurred (Jackson et al. 1976). If that change in appearance enables prey to better match their background, it could reduce the chances that they are detected by a predator. Despite anecdotal reports by researchers of this change in appearance occurring in the wild (Pough 1976; Jackson et al. 1976), it is still not known if, or how, it might work to deter natural predators. As a consequence, the flicker fusion effect remains poorly defined and understood, despite it having the potential to be a unique way to reduce predation across a wide range of prey species (Endler 1978).

Here three main issues will be addressed. The first is to explain the psychophysics behind the illusion of flicker fusion effect so that researchers can precisely predict when it is found in nature, and what factors affect its occurrence. The second is to disentangle the putative functions of the flicker fusion effect. Enhanced concealment through background matching is not the only possible function, and here are discussed other functions suggested in the literature. Finally, it will be clarified the terminology surrounding the flicker fusion effect to avoid confusion, particularly with other strategies involving movement and coloration. The aim is to facilitate the study of the flicker fusion effect in the context of prey defences, and particularly, to highlight its potential role in enhancing concealment of moving prey.

2.3 What is the mechanism underlying the flicker fusion effect?

It was 40 years ago that Pough wrote about prey changing their appearance when in motion compared to when they were static (Pough 1976). He observed striped newborn northern water snakes (*Nerodia sipedon*) producing sudden bursts of rapid movement in response to a threat that meant that their stripes blurred together to make them appear uniformly coloured (Figure 1).

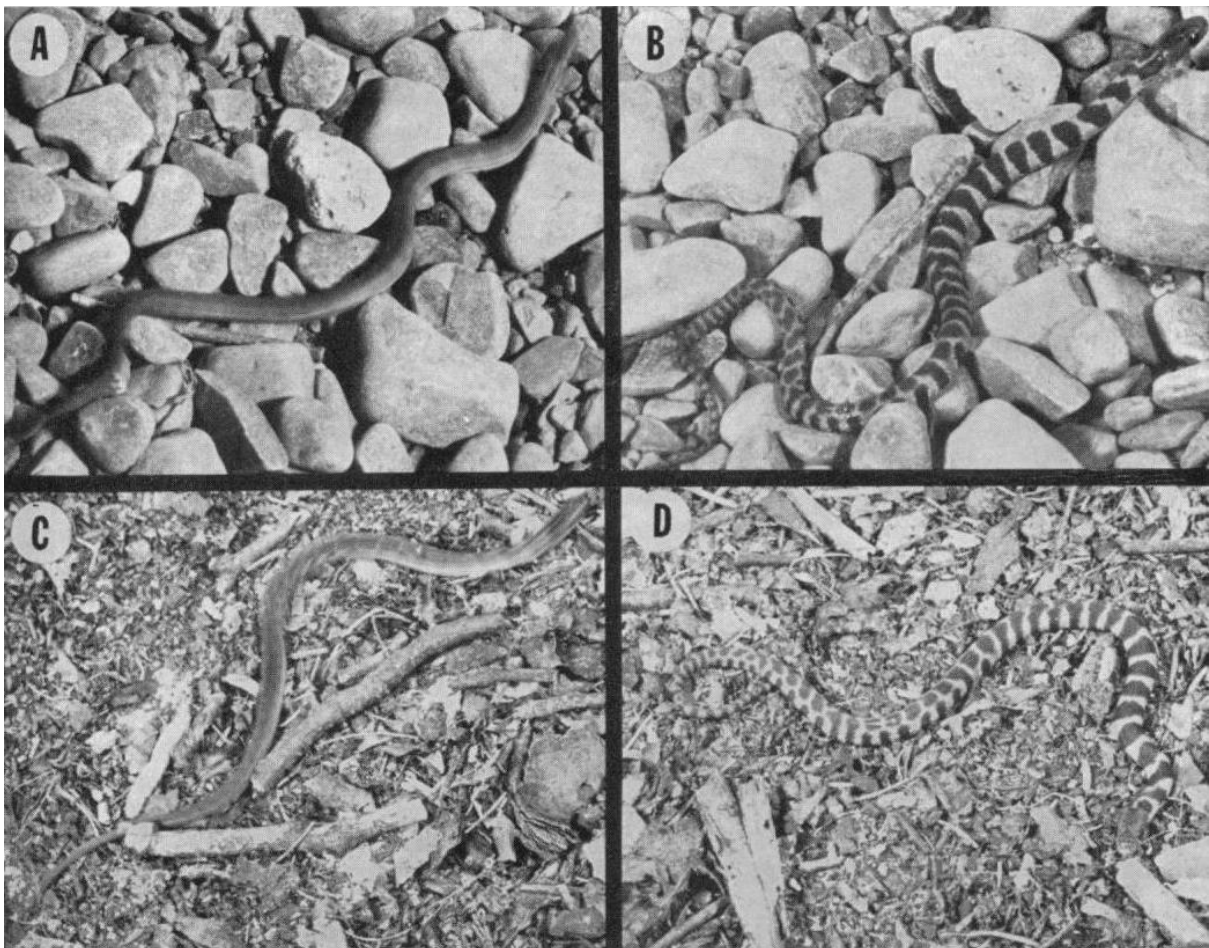


Figure 1 Newborn water snakes moving (left images) and stationary (right images) on coarse gravel (top images) and plant matter (bottom images) taken from Pough (Pough 1976)

He suggested that this change in appearance, from striped to uniform, was due to the fact that snakes' pattern elements were alternating faster than the observer's critical flicker fusion frequency (CFF), hence the name 'flicker fusion effect' (Jackson et al. 1976). The CFF is a measure of a visual system's ability to resolve rapid stimulus change, and is defined as the maximum temporal frequency at which a light can flicker before being perceived as continuous (Talbot 1834). But how does this relate to a predator's ability to resolve the stripes of a moving prey? When a striped prey moves across a predator's visual field, the pattern elements locally alternate between light and dark (Figure 2). If the prey moves fast enough, the frequency of alternation, known as the temporal frequency, will exceed the maximum frequency that the predator can temporally resolve, and the stripes will blur and no longer be perceived. The temporal frequency at which the stripes alternate depends on the stripe width and on the speed at which the prey moves, and increases as either the stripes get thinner or the speed increases.

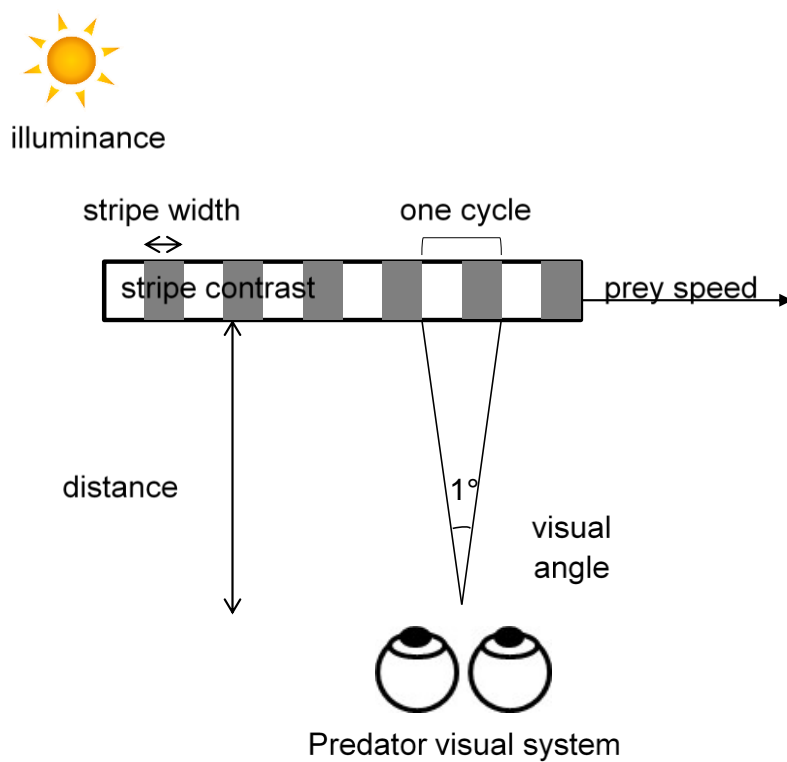


Figure 2 The perception of a moving striped prey by a visually hunting predator, and the factors that affect whether or not the predator sees a flicker fusion effect. The spatial frequency of the pattern is measured in cycles per degree, and in this example is 1 cycle per degree (one pattern cycle occurs in one degree of visual angle).

In principle, by knowing the stripe width and the speed of the prey, along with the CFF of the predator (which varies across species, see Healy et al. 2013) it should be possible to predict when the primary visual effect of blurring will occur in the eyes of a predator (Jackson et al. 1976; Titcomb et al. 2014). However, it is not quite that simple. The CFF is generally measured using a whole field flickering stimulus, which means that it is measured with a visual stimulus that has no internal pattern. In contrast, Pough's striped water-snakes represent patterned visual stimuli, which are characterized by their pattern spatial frequency: spatial frequency is the number of cycles of alternating dark and light stripes per degree of visual angle (Figure 2). For patterned stimuli, this is substantially above zero, whilst for uniform ones, it is equal to zero. Empirically, flicker fusion occurs at lower temporal frequency for patterns having higher spatial frequencies (Watson & Ahumada 2016); this means that the temporal frequency at which the stripes of a patterned prey will completely blur is not fixed, but decreases as stripe width decreases. We will call this the threshold for flicker fusion, or the TFF (shown by the red line in Figure 3). Complete blurring occurs above the TFF, although patterns will start to blur below it. The TFF is the same as the CFF only when the stimulus is uniform (i.e. where the TFF intersects the y-axis and spatial frequency is zero); the CFF is the upper limit of resolvable temporal frequency. To help visualize this, imagine a striped moving prey with a defined spatial (F_{low}) and temporal frequency (W_{low}); when slow moving, its pattern remains visible to a predator (P; Figure 3). However, if the prey has thinner stripes (1; Figure 3) with a higher spatial frequency (F_{high}), or moves faster (2; Figure 3), resulting in a higher temporal frequency (W_{high}), its stripes will alternate faster than the predator's threshold for flicker fusion (i.e. $W > TFF$). Consequently it will no

longer be possible for the predator to distinguish the pattern elements and the striped prey will appear uniform.

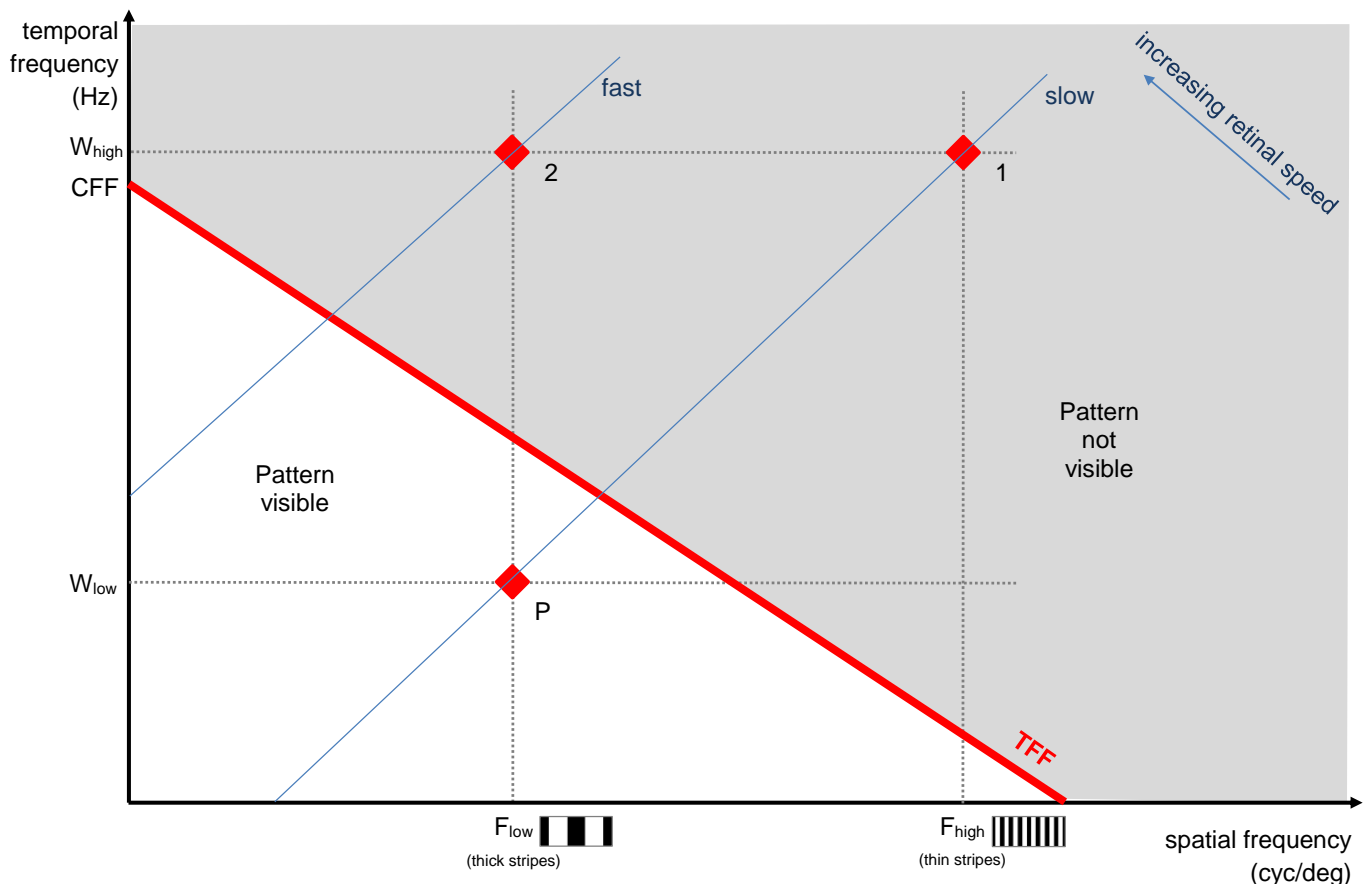


Figure 3 Visual explanation of how reducing stripe width or moving faster blurs the pattern in the eyes of a predator. Any moving prey with a particular pattern can be characterised by the spatial and temporal frequencies perceived by a predator’s retina. The blue lines are isolines for speed on the retina. The red line is the TFF for a given contrast, illumination and species (note that the CFF is the same as the TFF when it meets the y-axis, i.e. the spatial frequency is zero). When a moving prey has a spatio-temporal frequency below the TFF, its patterns can be resolved (P); however, if the prey has thinner stripes (F_{high}) or moves faster, its pattern will blur and no longer be perceived by the predator (1 and 2, respectively).

Besides the TFF, there are other factors that also influence the occurrence of the flicker fusion effect (Table 1). In particular, the viewing conditions are critical. If the prey is further away, its stripes will appear thinner to the predator, i.e. the spatial frequency increases, and the flicker fusion effect will occur at lower prey speeds. In addition, as ambient luminance decreases, the TFF also decreases because animals' eyes visually sample their environment less frequently and integrate photon capture over longer periods in order to try and gather sufficient visual information from their environment (Tyler & Hamer 1990). When animal eyes become adapted to low lighting conditions, spatial acuity can also decrease (Van Nes et al. 1967). This means that the flicker fusion effect is more likely to occur under dim compared to bright conditions (Titcomb et al. 2014), since prey do not need to be moving as fast for blurring to occur. Whilst for a given speed, finer stripes will produce faster alternation (and more likely exceed the TFF), other things being equal, the speed necessary for the flicker fusion effect will always be lower for prey patterns of lower internal contrast. The same principles discussed so far, can be applied to prey having non-striped patterns, e.g. zigzag or spotted, if the elements are repeated along the vector of motion. When the temporal frequency at which these elements alternate exceed a predator's TFF, the prey will appear uniform or even differently patterned whilst moving.

Ultimately, the speed necessary for the flicker fusion effect to occur depends upon the predator's contrast sensitivity function. Contrast sensitivity is defined as $1/\text{contrast threshold}$, where the threshold is the minimum contrast required for the predator to detect a pattern. The contrast sensitivity function describes how contrast sensitivity varies as a function of spatial and temporal frequency. The red "TFF" line in Figure 3 corresponds to a line of constant contrast sensitivity; for predators with

more sensitive vision, the TFF line will be shifted upwards and decline less steeply with spatial frequency (Watson & Ahumada 2016). And of course, flicker fusion only occurs if the predator's eyes remain stationary as the prey moves: if it tracks the prey and stabilises it on the retina, blurring will not occur.

Table 1 Factors affecting the flicker fusion effect

Factor		Impact
Viewing conditions	Distance from the prey	Increasing viewing distance increases the spatial frequency of the pattern as seen by the predator, making the flicker fusion effect more likely to occur.
	Ambient light	At lower illumination, animals integrate visual information over longer times and TFFs decrease more rapidly: the flicker fusion effect can occur at lower speeds.
Prey pattern and movement	Speed	Adequate speed is required for blurring of pattern elements to occur.
	Stripe width	Thinner stripes will blur at lower speeds as they produce more rapid temporal frequency.
	Pattern internal contrast	Low contrast patterns blur at lower speeds than high contrast ones.
	Orientation of pattern elements	Blurring occurs when elements are repeated along the vector of motion.
Predator vision	Spatio-temporal acuity	Increasing spatiotemporal acuity of the predator requires higher speeds for the flicker fusion effect to occur (in Figure 2b, TFF will shift towards higher temporal and spatial frequencies).
	Contrast sensitivity	The more sensitive the predator is to contrast at the relevant luminance level, the harder the flicker fusion effect is to achieve (in Figure 2b, TFF shifts upwards and declines more steeply).
	Fixation	If the predator tracks the prey to stabilise it on the retina, the effective speed of the prey will be reduced, weakening or abolishing the flicker fusion effect.

Given this complex interaction of factors affecting the occurrence of the flicker fusion effect, how often might it occur in the wild? To date, the evidence is limited to striped coral snake mimics (*Lampropeltis triangulum campbelli* and *L. elapsoides*), which are calculated to move fast enough when in flight for their patterns to blur in the eyes of some potential predators (raptors), particularly in dim light (Titcomb et al. 2014). Indeed, the effect may be particularly prevalent in low light intensity environments, including the deep water or forest environments. However, whilst demonstrating the feasibility of the flicker fusion effect, these calculations are likely to be conservative since they were based on predators' CFF values, and prey do not need to move as fast to blur based on the TFF. Blurring through the flicker fusion effect may be occurring more often in nature than previously thought (e.g. Titcomb et al. 2014), and occur in slower moving prey, not just those performing a rapid escape.

Although calculations for the flicker fusions effect have been made predominantly with avian predators in mind, other species of predator (e.g. insects Nityananda et al. 2015) have lower visual acuities. This means that the flicker fusion effect could be occurring more often in the eyes of these predators. Based on praying mantids' visual acuity (Nityananda et al. 2015), I calculate that a bumblebee's pattern will certainly be perceived as blurred at a typical viewing and strike distance of 5 cm (Nityananda et al. 2015) when the insect flies at 0.25 m/sec (*Bombus terrestris* maximum flying speed is 6 m/sec; Ellington 1999). Consequently, the flicker fusion effect could be more widespread than initially would appear, and not restricted to striped snakes. In the same way that UV colours were ignored for a long time because we could not see them (Bennett & Cuthill 1994), blurring through the flicker fusion effect may also have been an underappreciated feature of animal coloration because of our own visual biases.

2.4 What defensive function might the flicker fusion effect have?

The second issue to address is what anti-predator function the flicker fusion effect may have. Whilst changes in appearance caused by the flicker fusion effect have been widely assumed to be an adaptation to reduce predation (e.g. Ruxton et al. 2004; Stevens 2007), the problem is that there have been no tests with actual predators. So far, the evidence for the anti-predator function of the flicker fusion effect comes from indirect observations in snakes (Lindell & Forsman 1996; Titcomb et al. 2014). For example, the 'zigzag' morphs of *Vipera berus* appear to have a higher survival advantage compared to other morphs, but there is no evidence that this results from reduced predation, and if it does, how that occurs (Lindell & Forsman 1996). Therefore, it could be argued that the flicker fusion effect is simply the by-product of rapid movement that has been selected to escape a predator, rather than part of a defensive strategy. It is important to identify how the flicker fusion effect might work in order to conduct experiments with predators to distinguish among functional hypotheses. The following paragraph attempts to disentangle the proposed explanations to provide a theoretical framework for the future study of how the flicker fusion effect could help reduce predation (Table 2).

As already mentioned, the flicker fusion effect could help prey to become more camouflaged during movement (Endler 1978; Stevens 2007). Pough's original observations included how the uniform appearance generated by the flicker fusion effect in the escape responses of snakes made them appear to blend into their environment (Pough 1976). This could happen, for example, if prey's coloration matches the mean luminance of the background, even though it has a high contrast visual texture (e.g. stripes); such prey might be highly conspicuous when remaining still but could become camouflaged when moving fast enough for the flicker fusion

effect to occur (Endler 1978). If the flicker fusion effect does indeed improve background matching, it would be the basis for a unique form of camouflage in moving prey: rather than concealing the speed or trajectory of the prey's motion once detected (like motion dazzle; Hall et al. 2013), the flicker fusion effect would reduce the chances of initial detection.

However, it is possible that the flicker fusion effect could help prevent capture by “confusing” predators, and making it difficult for them to track and effectively capture the prey; for example, pattern blurring could cause predators to lose internal reference points (Hughes et al. 2014). The effect of blurring could also lead to additional illusory effects, such as altering prey's perceived speed due to the loss of internal contrast in the pattern or reduced contrast against the background (Thompson 1982; Blakemore & Snowden 2000; Stevens 2007). Whilst this latter idea could be considered a form of motion dazzle (Stevens 2007), the idea and study of motion dazzle has thus far relied upon the prey's pattern being visible to the predator when it is moving (Cott 1940; Scott-Samuel et al. 2011; Von Helversen et al. 2013; Hughes et al. 2014; Kelley & Kelley 2014). Therefore, if the flicker fusion effect also changes the speed and/or trajectory of prey through pattern blurring, it must be due to different perceptual mechanisms than those already proposed (e.g. Scott-Samuel et al. 2011; Kelley & Kelley 2014) and not through the pattern ‘dazzling’ predators.

A third way that the flicker fusion effect could help reduce predation is by hiding the final resting place of a moving prey, making it difficult to locate once it becomes stationary again (Pough 1976). This idea is perhaps similar to the idea of ‘flash coloration’, where an otherwise camouflaged prey suddenly reveals a conspicuous body part when it flees a predator, only to hide it again before or as it comes to rest (Cott 1940; Edmunds 2005). Although the benefits of flash coloration

are not established, it is thought that if a predator tracks the moving prey using its conspicuous coloration, it will subsequently be less able to detect cryptic features of the prey's camouflage pattern (perhaps through loss of a search image, Troscianko et al. 2013). In the case of the flicker fusion effect, when the prey suddenly becomes stationary with a cryptic pattern, the predator would continue to look for the prey based on its appearance when moving. The problem of finding the stationary cryptic prey could be further exacerbated if the predator predicts the movement of the prey along the perceived trajectory, and searches in the wrong place, either because it looks further along the path than where the prey has actually stopped (Pough 1976), or less far because of misjudging the speed (Thompson 1982).

Finally, the flicker fusion effect could simply be a way to deter predators: a novel dynamically changing appearance could elicit neophobia or an avoidance response, similar to that of warning signals (e.g. Cook & Roper 1989). Alternatively, perhaps the sudden change in coloration is a deimatic display eliciting a startle or fear response in its predators (Vallin et al. 2005; Olofsson, Eriksson, et al. 2012; Skelhorn, Holmes, et al. 2016), that gives prey an advantage to escape. In these cases, the flicker fusion effect simply performs a well-established defensive function.

I acknowledge that this may not be an exhaustive list, and of course, differences in hunting strategies or visual systems among predator species means that the flicker fusion effect could serve more than one defensive function, even for a single prey species. However, what is clear is that we need to know how it works, and particularly if it is a form of camouflage or a deterrent. I think it is particularly important to establish if it is a unique form of concealment, where blurring of an internal pattern at speed could reduce the initial detection of prey. The question of whether any pattern can reduce the detection of moving prey is one of the major

unanswered questions in the study of defensive coloration. Currently, only the flicker fusion effect offers a possible solution.

Table 2 How the flicker fusion effect might reduce predation

Function	How this is achieved
Camouflage the moving prey	The uniform colouration from blurring help prey match general features of their background, and enhance concealment.
Alter the perception of motion	The change in appearance during movement alters the prey's perceived speed or trajectory, making it difficult to capture.
Hide the final resting location	A sudden change in appearance from the moving to the static prey pattern makes it difficult for a predator to locate resting prey.
Deter predators	A sudden change in appearance caused by the flicker fusion effect may cause the attacking predator to show neophobia or hesitate, giving the prey an increased opportunity to escape.

2.5 How is confusion arising through current terminology?

To investigate the flicker fusion effect, we need to be clear about what it is we refer to when using this term. This is because the flicker fusion effect has not just been used to describe the mechanism by which the appearance of a prey's pattern changes (e.g. Lindell & Forsman 1996; Niskanen & Mappes 2005; Stevens 2007; Von Helversen et al. 2013), but has also given its name to a hypothesis (Lindell & Forsman 1996; Ruxton et al. 2004; Stevens 2007), and been used to describe a

camouflage strategy (Stevens 2007; Stevens et al. 2008; Stevens & Merilaita 2009). This has led to some confusion in the literature.

For example, some researchers refer to a 'flicker fusion hypothesis'; however, it is not clear what this is. Sometimes, it refers to the mechanism and whether or not it is possible that blurring occurs through the flicker fusion effect (Stevens 2007; Titcomb et al. 2014), whilst other times it refers to whether or not the blurring could confer a survival advantage (Lindell & Forsman 1996; Ruxton et al. 2004). Whilst this is confusing in itself, there is of course the additional problem that there are multiple functional hypotheses relating to how it might reduce predation (Table 2). The use of the term 'flicker fusion hypothesis' has the potential to lead to considerable confusion about what the hypothesis actually is, and it should be perhaps abandoned altogether.

The flicker fusion effect has also been used to describe a specific defensive strategy, 'flicker fusion camouflage' (Stevens 2007; Stevens et al. 2008), which describes the situation when the effect helps prey better match their backgrounds by making prey 'uniformly camouflaged' (Stevens et al. 2008). The problem with the use of this term is that it suggests that the function of the flicker fusion effect is to camouflage the prey, whilst several other possible functions exist (Table 2). Whilst calling motion dazzle a form of camouflage works because its only possible function is to hide the movement of the prey ('dazzle camouflage'; Scott-Samuel et al. 2011; Von Helversen et al. 2013), the same logic cannot be applied to the flicker fusion effect, because it might instead deter predators. Unless we know that patterns have evolved to elicit the flicker fusion effect to enhance concealment, I suggest that it is best not to use this term.

However, we do still need terminology that allows us to study flicker fusion, so what terminology should we be using? My view is that the flicker fusion effect should be limited to describing the visual illusion that alters the perceived pattern of a prey when it moves sufficiently quickly to exceed the predator TFF. This definition accurately describes how pattern and speed interact to produce a change in appearance in the eyes of the predator, and does not ascribe any particular function to the effect. Avoiding using flicker fusion effect in relation to any functional role reduces any implicit bias in understanding how it works. By clearly separating the mechanism (the perceptual effect) from the function (how it deters predators), the proposed terminology allows researchers to study one or the other, or both. Only once functions are better explored and identified should we start to use flicker fusion in ways that align it to particular defensive strategies.

2.6 Discussion

For a long time, the flicker fusion effect has been thought to confer a selective advantage to several snake species fleeing from putative predators. By exploring the psychophysical principles behind the effect, I hope to have highlighted how widespread the effect could be. Striped patterns in particular, but also other patterns types, common across many taxa, could blur at speed given what we know about the visual capabilities of different species of predators.

It is clear that we need more studies of the flicker fusion effect in order to understand when it occurs, and what its effect(s) are on predators. Understanding how the flicker fusion effect works is likely to be solved by a combination of approaches. Field observations will be important for establishing how the effect

might function and if it could be involved in context others than predation (e.g. signalling to mates). Nonetheless, psychophysics experiments in the lab are likely to provide valuable insights into its perceptual basis, and tests with computer-generated targets can be readily conducted with predatory species, such as birds and mantids (e.g. Ditttrich et al. 1993; Nityananda et al. 2015).

Despite these challenges to fully understand when and how it works in the wild, the study of the flicker fusion effect offers an exciting opportunity to discover new ways in which a prey's appearance and behaviour have evolved to reduce predation. Notably, the flicker fusion effect fundamentally differs from other defensive strategies involving movement and patterning, since it allows prey to look different when moving and when stationary. Crucially, it has the potential to conceal an animal during motion, reducing the chances of it being detected by a predator. Perhaps, when combined with the right pattern, motion need not always break camouflage.

Chapter 3: Introducing mantids as a predator model

3.1 Abstract

Insects have long been used to investigate the efficacy of their defensive coloration against birds. In this chapter, I will explain why more emphasis should be given to using insect predators in studies of defensive coloration. First, because insect predators are likely to prey upon the same insect species that birds prey upon: to understand why and how a defensive pattern evolved, we must take into account the whole community of predators that prey have. Moreover, insect predators might react in surprisingly different ways to prey defences compared to birds; for example, they may show reduced or no aversion to unpalatable prey, or show unique innate aversions towards different colorations or shapes. Insects also have reduced chromatic sensitivity compared to birds, which means that therefore, prey having chromatic but not brightness contrast against their background are likely to result well camouflaged against insect predators. However, insects' visual systems are exquisitely tuned for motion and small target detection, which make them incredibly precise hunters. Moreover, some species, like praying mantids, can rely on their stereopsis to make more accurate estimation of distance and perhaps better detect camouflaged prey. Investigating the efficacy of visual defensive strategies against these predators represents an important, and perhaps underestimated, opportunity to test hypotheses about how defensive strategies might evolve.

3.2 Introduction: why use insects as predator model?

In the continuous arms race between predators and prey, prey have evolved a variety of anti-predator strategies, including protecting themselves with physical defences such as spines, stings and hairs (e.g. Sugiura & Yamazaki 2014; Murphy et al. 2010), producing chemical defences (e.g. Bonacci et al. 2011; Speed et al. 2012) or even displaying startle behaviour or thanatosis (e.g. Edmunds 2005). Authors have categorized these strategies by distinguishing between “primary” and “secondary” defences: primary, or indirect, defences should help prey prevent pursuit and act before a predator could catch the prey; whilst secondary defences should increase the chances of prey survival once a predator initiates an attack (Edmunds 1974). Although this distinction is debated since it can be hard to classify every defensive strategy in this way (Ruxton et al. 2004), it is certainly true that a simple way for prey to avoid predation is by reducing their encounters with predators in the first place.

One way that prey can achieve this is through the use of camouflage patterns, which elude or deceive predators that are visually guided, by reducing the chances that they are detected or recognized as potential prey (e.g. Skelhorn 2015; Stevens & Merilaita 2009; Cuthill et al. 2005). Ever since Kettlewell’s study on peppered moth (*Biston betularia*) melanisation, insects and their incredible variation in appearance have provided researchers with powerful ground to empirically test evolutionary ideas surrounding defensive coloration (Kettlewell 1955). However, the vast majority of these studies have investigated the effectiveness of defensive coloration against avian predators (Ruxton et al. 2004). This is perhaps because birds are known predators of many vertebrate and invertebrate species, and rely almost exclusively on vision for predation (Zeigler & Bischof 1993). The role of arthropod predators in

selection in prey patterns remains poorly investigated. Here, I argue that we need more studies of arthropods in the study of the evolution of prey defences, particularly those of insects.

This is because the very same insects that birds prey upon are likely to be predated by arthropod predators too. Arthropods in general, and insects more specifically, are likely to exert an important predation pressure on their prey (e.g. Bale et al. 2008). In order to fully understand why and how some prey have specific colour patterns, it is important to look at the whole range of species that prey upon that particular species. Indeed, several studies highlight the importance of predator community heterogeneity to explain the evolution of colour patterns. For instance, predator communities are thought to drive the inter-specific variation or intra-specific polymorphism of warning signals (e.g. Nokelainen et al. 2014; Willink 2013; Valkonen et al. 2012; Mochida 2011; Ratcliffe & Nydam 2008; Endler & Mappes 2004). Indeed, prey appearance might be designed specifically to confer protection against one or few predator species, but perhaps at the expenses of the efficacy of other defences or by compromise with needs other than predator-avoidance, e.g. signalling to mates (Nokelainen et al. 2012; Endler, 1974). Alternatively, visual signalling against predators could have evolved in synergy with intraspecific communication and the same signal might be exploit by both receivers group, i.e. predators and conspecifics (e.g. Finkbeiner et al. 2014; Crothers & Cummings 2015). However, most prey species have a variety of predators, belonging to different taxa, which might respond differently to their defences (e.g. Exnerová et al. 2015; Endler & Mappes 2004). Additionally, even the nutritional state of the predator, and the prey (Barnett et al. 2007; Halpin et al. 2014), or the environmental conditions (Chatelain et al. 2013) can influence whether an individual predator will attack a prey or not.

Therefore, chances are that how effective a defensive strategy is, depends on the final predator against which that defence is used and differences between arthropods and vertebrates predators are likely to be important for the evolution of prey coloration.

One of these differences comes from having different life history strategies. In addition to showing reduced dispersal compared to most vertebrate species, insect species are characterized by being r-selected, associated with having high growth rates and rapid increases in the local population. Therefore, compared to vertebrate predators, insect predators are likely to exert a predatory pressure on their prey more circumscribed both in space and time. Moreover, insects might react differently to chemical or physical prey defences. For instance, when it comes to investigate the efficacy of aposematic coloration exhibited by unprofitable prey, we might find that some insect species might result well defended against avian species and therefore it makes sense to study their warning signals against those predators. However, the same prey species might be not as well defended against insect predators, which might find it instead profitable and which conspicuous coloration might facilitate detection. For example, a recent study found that praying mantids (*Hierodula majuscula*) showed no aversion against an aposematic, but weakly defended, stinkbug (*Tectocoris diophthalmus*), whilst birds (*Gallus gallus domesticus*) learned to avoid the bugs only after one or two encounters (Fabricant & Smith 2014). Therefore, praying mantids appear to tolerate this concentration of aldehydes and keto-aldehydes compounds (Fabricant & Smith 2014; Prudic et al. 2007). Additionally, brightly coloured aposematic milkweed bugs (*Oncopeltus fasciatus*) were found to be predated by praying mantids if no other profitable prey were available, despite containing cardenolides which can affect praying mantids

physiology, i.e. decrease juvenile growth rate (Paradise & Stamp 1993). On the other hand some prey result defended against insects but not against vertebrate predators: insect biting predators like ants and wasps are strongly deterred by the “easy bleeding” strategy of Tenthredinids sawflies larvae, which is much less effective against birds (Boevé et al. 2013; Boevé & Müller 2005). Among the sawflies family, larvae exhibit different chemical defensive strategies, and differ in their behaviour and appearance. Indeed, a recent study correlated those differences in ecological and defensive traits with the contrasted selective pressure imposed by invertebrate and avian predators on the different species of the taxa (Boevé et al. 2013). Similarly to the well-studied monarch butterfly (*Danaus plexippus*), other insect species vary for defensive coloration and behaviour during their ontogeny stages (Oberhauser & Solensky 2004), which might reflect the variation in predators they are susceptible of across their life time. Indeed, the eggs and first instar larvae of the monarch butterfly maintain a cryptic appearance whilst the caterpillars, which result unprofitable for most invertebrate and avian predators because of the toxic cardenolides they sequester from *Asclepias* plants, exhibit a bright striped black-and-yellow-and-white coloration (Oberhauser & Solensky 2004). However, assassin bugs (Reduviidae), predatory wasp (*Polistes dominulus*) and praying mantids (*Tenodera sinensis*) will prey upon monarch caterpillar regardless their toxicity, in which case caterpillar appearance does not represent an aposematic signals for these predators (Rafter et al. 2013; Oberhauser & Solensky 2004; Zalucki & Kitching 1982).

Predators might also differ for unlearned biases and prey features that can trigger an avoidance response. For instance, praying mantids do not show innate avoidance towards black-and-yellow stripes or towards red pattern, given their limited colour perception, however, they do show innate aversion to ant or ant-

mimicry morphs (Nelson et al. 2006); on the other hand, dragonflies avoid harmless flies if black-and-yellow painted or wasp shaped (Kauppinen & Mappes 2003). A similar avoidance reaction was observed in domestic chicks (*Gallus gallus domesticus*), although evidence suggest that innate avoidance or unlearned biases towards certain pattern vary also across birds species too (Exnerová et al. 2007; Roper 1990) perhaps consequences of differences in predator neophobia (Roper 1990). Specific predator' reactions towards certain prey features, e.g. innate avoidance towards certain colorations, or neophobic response of naïve predators, have been investigated in birds. However still little is known whether similar prey features would trigger the same reaction in insect predators or how willing insect predators would be to include new prey in their diet. Therefore, attention should also be directed to empirically test this interaction between insect predators and prey defences.

3.3 How do insects differ from other well-studied predator models?

When we ask whether or not a predator will spot and recognize a prey regardless its cryptic appearance, or whether it will avoid a high-contrast patterned prey that mimic a more toxic one, we are not only investigating prey's defences but also predator psychology and physiology (Skelhorn & Rowe 2016; Skelhorn, Halpin, et al. 2016; Kelley & Kelley 2014; Kazemi et al. 2014; Stevens 2007). The importance of predator psychology is evident by the amount of research exploring how and what birds learn, generalize and remember about their prey's appearance, and what factors drive their final decision on whether to attack or not a certain prey (see Skelhorn & Rowe 2016; Skelhorn et al. 2016 for review).

However, even before an animal will use the information it receives from the environment (i.e. cognition in the broadest sense; Rowe & Healy 2014), it first needs to acquire it. Indeed, when it comes to investigating the efficacy of prey appearance as an anti-predator strategy, one of the first questions surely has to be: what the predator can see (Endler 1978)? For instance, how visible would be a prey that resemble the appearance of its background? “*A visible form can only be distinguished when it is exhibited by differences of colour or tone or of light and dark shade*”, therefore a prey can become hard to recognize by reducing this differences (Cott, 1940). However, the ability to appreciate those differences in *tone* or *light and dark shades* will ultimately depend on the predator’s visual acuity, and a prey that is detected by one predator might look indistinguishable from the background to another. It is, therefore, important to establish what an insect predator can see.

Insects’ visual acuities show large variations across species. For example some cave-living species have reduced acuity, e.g. *Troglocladius* genus (Andersen et al. 2016), whilst others, such as dragonflies, show relatively high spatial resolution despite being constrained by having a tiny body (Land 1997). One striking difference between insect and avian predators is their colour vision. Birds are known for their sophisticated colour vision that drives not only their foraging strategy, but also other behaviours, such as their mate preferences and nest choices (Zeigler & Bischof 1993). Birds have four type of cones, double cones and their photoreceptors also contain oil droplets which influence the type of wavelengths available and, therefore, mediate their tetra-chromatic vision (Zeigler & Bischof 1993). In contrast, most insect species have eyes tuned for “green” and “blue” wavelengths, i.e. 560-520 and 490-450 nm (Briscoe & Chittka 2011). This means that “red” objects, though not invisible to insects, will appear monochromatically green and be harder to spot and

distinguish from a “green” background (Briscoe & Chittka 2001). However, like birds, insects can detect wavelengths that are beyond our range of visibility and extend into the ultraviolet range (400-320 nm).

Insect compound eyes also vary dramatically across species in their sensitivity and resolution power. Typically, insect eyes are roughly spherical and composed of different sampling units, called ommatidia. The diameter of the ommatidia lens and the angle between adjacent ommatidia determine the number of photons collected and the distance at which an object, such as a mate or a prey, can be resolved (Land & Nilsson 2012). The arrangements of the ommatidia is generally not uniform across the eye; different regions have become specialized for different functions, and many insects have one or more areas of larger facets and smaller interommatidial angles and, therefore, greater acuity (i.e. foveas). However, the limits of visual acuity, particularly spatial resolution, are imposed mainly by small body size in insects, and needs to be conciliate with all their visual task demands. Despite this constraint, species of *Coenosia* and *Drosophila* genus have been found to overcome their eyes size limits, and show particular retinal adaptations that confer them either greater resolution or sensitivity accordingly to their need to recognize prey with precision or adapt to dim light conditions (Gonzalez-Bellido et al. 2011). Surprisingly, despite their poor spatial resolution, some insect species have ultra-rapid vision, meaning that they sample their visual environment particularly often (Srinivasan et al. 1999). For example, tse-tse flies (*Glossina morsitans*) and locusts (*Locusta migratoria*) can perceive a light flickering up to 205 and 90 Hz respectively (Miall 1978). This might be an adaptation required for fast and/or gregarious flying and confer an important advantage when it comes to detecting an approaching moving object, whether it is a conspecific, a prey or a potential predator. In fact, one

of the striking features of the insect visual system is that it is particularly sensitive to motion, which relies mainly on luminance contrast rather than colour (Stewart et al. 2015). This makes insects incredibly precise whilst detecting and pursuing their targets (e.g. Gonzalez-Bellido et al. 2016). They can spot a prey over long distances, chase it whilst flying and succeed in capturing it in fractions of a seconds. This level of predator ability is commonly associated with eagles and other birds of prey, however, insect predators might be equally able despite their (apparently) limited visual system. Therefore the ability to resolve colour represent only one of the various visual task in which birds and insects differ. However, those very differences should encourage to further investigate and compare how dissimilar a prey might appear to an avian and to an insect predator.

3.4 The visual hunter: praying mantis

Mantodea is a fascinating Order that has been extensively investigated because mantids are one of the most voracious invertebrate predators, which can include females eating their own mates (e.g. Prokop & Maxwell 2016; Jayaweera et al. 2015). Praying mantids are opportunistic predators that, since the beginning of the Jurassic when it has been estimated that the first Mantodea appeared (Svenson & Whiting 2009), have dispersed and diversified, and today we can find them broadly distributed across all terrestrial habitats. Recently, Svenson and Whiting reconstructed the phylogeny of the order through molecular analysis demonstrating that the current classification, which includes 2366 described species, does not reflect the natural groupings for many Mantodea families, but merely their remarkable variation of morphology (Svenson & Whiting 2009). The authors

highlighted how poorly related species show similar ecomorphic specialization, which strongly correlate with ecologically diverse habitats. Hence, it is reasonable to hypothesize that variability in traits, such as eye morphology, might reflect differences in predatory strategy or prey preferences across species. Unfortunately, very little is known about mantid ecology, with field observations being rare and dated (e.g. Mitchell, 1986). More recent studies have been made under controlled laboratory conditions, e.g. Prudic et al. 2015; Paradise & Stamp 1991; Reitze & Nentwig 1991, including studies of their visual systems. Praying mantids' visual acuity has been investigated for over 30 years (Rossel 1983), and new light has been shed on how they compute the images received from each eye in order to acquire depth information, i.e. stereopsis (Nityananda et al. 2016). It is generally assumed that stereopsis evolved not only to improve depth estimation, but also to help distinguish objects from their backgrounds: this might help mantids to detect camouflaged prey, and enable them to produce rapid strikes at their prey with such precision. Therefore, testing hypothesis about the effectiveness of prey camouflage using praying mantids represent, to my opinion, an intriguing opportunity. Indeed, researchers have investigated praying mantids ability to track and strike computer generated prey stimuli that varied for their appearance and for the speed at which they moved (e.g. Prete et al. 2013; Prete et al. 2012; Prete et al. 2011). Interestingly, praying mantids response varied accordingly with some main stimulus features, i.e. size and luminance contrast against the background, and even more surprisingly the response varied across species (e.g. Prete et al. 2013). For example. *Sphodromantis lineola*, struck at stimuli in a quite large range of sizes (from 10 x 10 up to 24.5 x 62.5 degrees of visual angle), but their striking response decreased as stimuli size increased (Prete et al. 1993). On the other hand, the smaller

Euchomenella macrops struck at stimuli up to 44 degrees of visual angle and the mantis surprisingly kept striking at small stimuli even after they stop moving (Prete et al. 2012). Therefore, despite being generalist predators, praying mantids seems to compute their predatory response, i.e. strike at the prey, based on several features that the target has to match in order to be classified as a suitable prey. The differences in striking response observed across species might reflect differences in prey preferences, however differences in the kind of stimuli that elicit a tracking response, as observed in (Prete et al. 1993), might subtend differences in visual acuity. Unfortunately a comparative study investigating visual acuity across different species has never been carried out. On the other hand, in praying mantids, tracking seems to be a response strongly elicited by any moving object (Prete and Mahaffey, 1993; Nityananda et al., 2016). Moreover, those predators have been for long use in behavioural and psychophysics experiment (e.g. Rossell 1980; Prete and Mahaffey, 1993; Prete and McLean, 1996; Prete, 1999; Gonka et al., 2000; Yamawaki, 2000; Prete et al., 2002; Nityananda et al., 2015; Nityananda et al., 2016). Praying mantids are suitable candidate to expand our knowledge of how insect predators have shape the evolution of prey defences and how their selective pressure differs from the one imposed by vertebrate predators.

Chapter 4: Visual acuity variability across different species of praying mantids

4.1 Abstract

Praying mantids are voracious predators that strongly rely on vision to track and strike their prey. Intriguingly, the shape and form of their eyes are remarkably variable. I investigated if variation in eye design correspond to differences in visual acuity. To answer this question, I examined four morphologically distinct species: the African lined mantis (*Sphodromantis lineola*), the Ghost mantis (*Phyllocrania paradoxa*), the Cryptic mantis (*Sibylla pretiosa*) and the Indian flower mantis (*Creobroter gemmatus*). By observing mantids' optomotor responses, where they turn their body in response to wide-field moving stimuli, I explored the range of spatial and temporal frequencies that these species can resolve. I found that despite the differences in size and design of eyes across species, there were no significant differences in visual acuity for the range of stimuli that I tested. Because of the lack of knowledge about species' ecology, I can only speculate what could be the driving factors of such differences in eye morphology.

4.2 Introduction

Mantodea eyes design across species seems highly diverse which represent a potential testbed for evolutionary adaptation hypothesis. We can ask, what are the driving factors of such diverse eyes design? Are different shapes caused or

consequences of different visual acuity' needs? Or eyes acuity does not vary across species as it varies their design? Indeed, species having similar eyes design does not necessarily have similar visual acuity: in two *Coenosia* and *Drosophila* species having similar eyes design researchers found different architectural adaptations of their photoreceptors that match their ecological needs of catch fast moving prey or flying in low light conditions (Gonzalez-Bellido et al. 2011). Therefore, even eyes which appear to be morphologically very similar can in fact be adapted to perform very different visual functions. Similar results are suggested by a study on three praying mantids species, i.e. *Parasphendale affinis*, *Popa spurca* and *Sphodromantis lineola*, which have similarly shaped eyes but that showed different predatory behaviours towards different type of targets (Prete et al. 2013). The investigated species were presented with computer-generated targets that differed for size, contrast against the background and configuration of movements: the species showed different tracking and striking rate towards different targets, particularly differed the target size that elicit the highest striking rate (Prete et al. 2013). However, this results might not be a consequence of differences in visual acuity, but rather be a sort of "prey preference" (Prete et al. 2013). Previously, praying mantids visual acuity was investigated using behavioural experiments, only in one species, i.e. *Sphodromantis lineola*, which investigate how mantis responded to drifting gratings that varied for gratings width, contrast and speed of movement (Nityananda et al. 2015).

In this study, instead, I explored whether species having different eyes shapes could differ for visual acuity, and if so, whether this differences will be reflected in different prey preferences. Indeed, praying mantids compound eyes are composed of many units called ommatidium: in each ommatidium, there is a lens which focuses

light onto the rhabdom which is typically made of eight photoreceptor cells. Praying mantids with closed rhabdom have for each ommatidium a field of view between 0.5-3°, which offset from its neighbours view by an amount equivalent to the inter-ommatidial angle of the eye (Land & Nilsson 2012). Like other insects, praying mantis eyes have a forward-looking high acuity area called fovea, which the animal uses to centre the prey and obtain distance information through binocular triangulation (Land & Nilsson 2002). The fovea is generally characterized by smaller interommatidial angles and bigger lenses compared to other regions of the eye, which increases resolution and sensitivity (Rossel 1979). Resolution refers to how sharp detailed an image can be made and, in compound eyes, depends on the size of the angle between each ommatidium, i.e. the inter-ommatidial angle, and the size of the receptive field of each ommatidium, i.e. the acceptance angle. The sensitivity of a visual system is the number of photons a receptor needs to give a criterion response when viewing an image, which depends in compound eyes on the acceptance angles. Summarizing, the diameter of each ommatidium lens, the angles between adjacent ommatidia, and the dimensions of the rhabdom of insect compound eyes all determine an insect's ability to resolve detail in their visual environment (Land 1997).

Therefore, I selected four species of praying mantids that differed for eyes morphology and investigated their visual acuity (Figure 4): the African mantis (*Sphodromantis lineola*), the Ghost mantis (*Phyllocrania paradoxa*), the Cryptic mantis (*Sibylla pretiosa*), and the Indian flower mantis (*Creobroter gemmatus*).



Figure 4 The four praying mantids species used in this study. Top, left to right: the African mantis (*Sphodromantis lineola*) and the Ghost mantis (*Phyllocrania paradoxa*); bottom, from left to right: the Cryptic mantis (*Sibylla pretiosa*) and the Indian flower mantis (*Creobroter gemmatus*). Images are not to scale.

I investigated the range of visual stimuli that each species could resolve by presenting praying mantids with computer-generated moving stimuli. The ability to detect motion is ubiquitous across animal vision, and, along with the detection of light and dark, may be the oldest and most basic of visual capabilities (Nakayama 1985). An animal needs to explore its visual environment, estimate its own motion and the movement of external objects to make an appropriate response to each type of movement. In fact, visual cues are used to stabilize gaze on particular objects of interest, or to stabilize head movements against body movements and to estimate motion generated during locomotion (Pix et al. 2000), therefore has been suggested that the motion sensitivity of insects match their visual ecology (e.g. Nityananda et al. 2015; Gonzalez-Bellido et al. 2011; O'Carroll et al. 1996). It could be hypothesized that the chosen model species having a common ancestor, thus similar neural structures, but different eye morphology and perhaps ecology, could differ for the range of visual stimuli they can resolve, i.e. their window of visibility (Watson & Ahumada 2016).

4.3 Measures of eye morphology

In the first stage of my study, I used Scanning Electron Microscopy (SEM) to obtain images that allowed me to take measures of the eye morphology of each of the four species.

For each of my species, I took images of the eyes from one individual female to make measurements (I used only one individual per species because of time and cost constraints, however this is the procedure largely applied in previous studies e.g. Gonzalez-Bellido et al. 2011). I used females because they are more motivated to hunt, and as a consequence, their visual systems are likely to have undergone

strong selection to detect and discriminate among prey in their environments. The measurements were made on isolated mantid-heads from alcohol preserved specimen. The eyes were virtually divided into anterior, lateral and posterior region and the head was rotated in order to ensure that for each regional the image the ommatidial axis was perpendicular to the camera and there was no overlapping with other images. I measured lens diameter from high magnification scanning images (Figure 5) taken under low vacuum conditions (eSEM). For the image analysis, I used XT Docu software (v. 3.2, Soft Imaging System GmbH, Münster, Germany). For each image, ten neighbouring ommatidia were randomly chosen, and the lens diameter was measured as the distance from the centre of a lens to the centre of the adjacent lens (the protocol largely follows the one describe in Gonzalez-Bellido et al. 2011). The mean lens diameter, i.e. the mean value between the five diameters that were measured, for each region and species is indicated in Table 3.

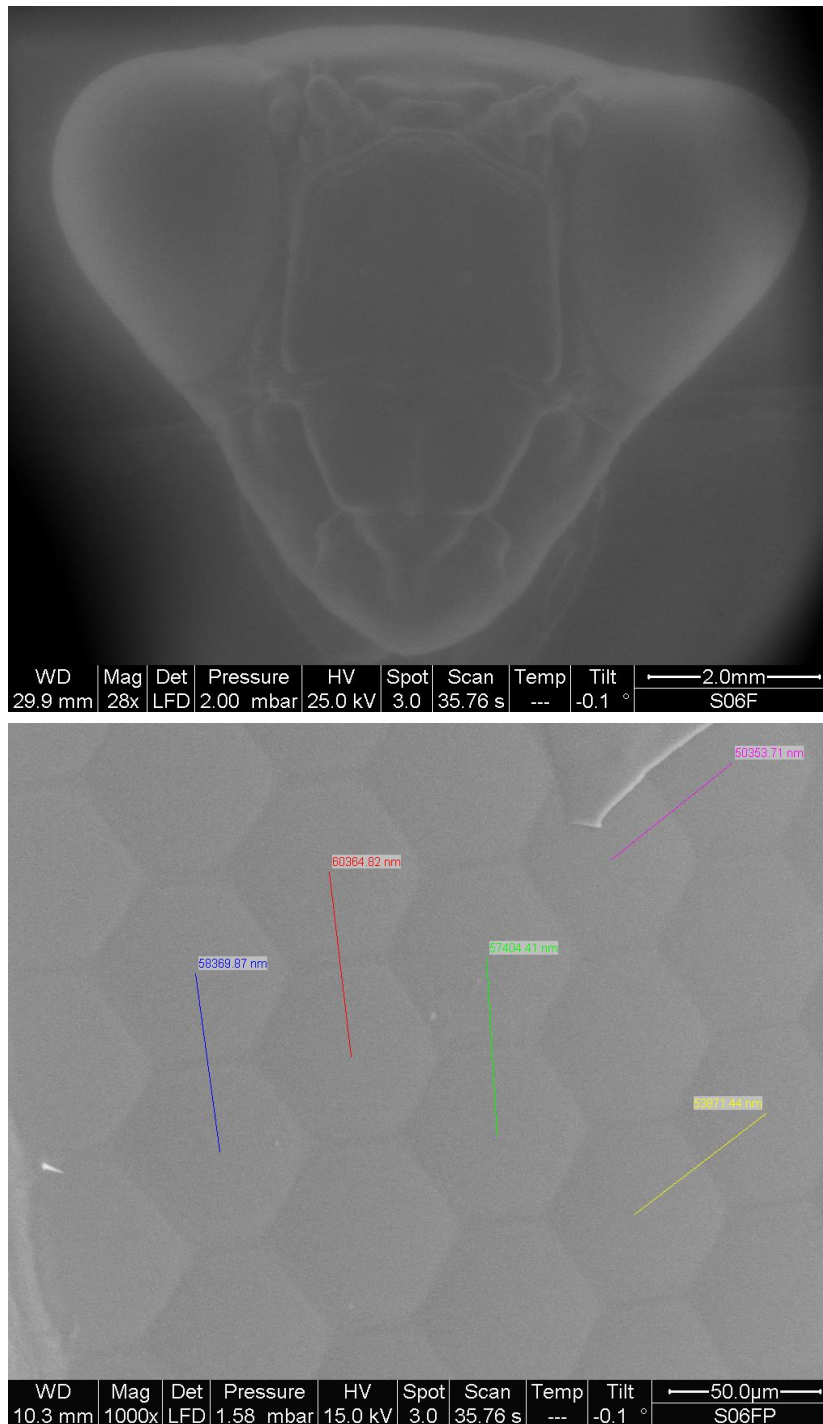


Figure 5 Example of eSEM image taken: *S. lineola* head frontal view (top) and measures of lens diameter in the posterior region (bottom).

For all species, lens diameter tended to increase from the posterior to the anterior region, results which are consistent with a previous study (Rossel 1979). In addition, the lens diameters appeared to vary across the females I measured for each species (Table 3). In particular, *Sphodromantis lineola* had larger lenses compared to the other species, which could suggest that it has higher visual acuity.

Table 3 Individual head dimensions and ommatidial diameter average measure for one female individual of each model species: *Phyllocrania paradoxa*, *Sphodromantis lineola*, *Creobroter gemmatus* and *Sibylla pretiosa*.

Species	Head measurements (mm)		Ommatidia diameter (microm)		
	width	length	frontal	lateral	posterior
<i>P. paradoxa</i>	4.4	4.8	43	39	31
<i>S. lineola</i>	7.7	6.2	63	56.5	50
<i>C. gemmatus</i>	4.7	3.6	34	33	31
<i>S. pretiosa</i>	5	3.8	44	44	37

4.4 Visual acuity using the optomotor response

I investigated the range of visual stimuli that each species could resolve using an established methodology widely used to obtain information about an animal's visual acuity, which is to study their motion detection (Srinivasan et al. 1999). Many animals respond to a moving dark-and-light grating by turning their eye, head and body in the direction of the movement. This is called 'optomotor response' and is an innate compensatory movement to avoid falling: when viewing the movement of a wide-field image over the retina, the animal responds accordingly to stabilise its

position relative to the environment (Srinivasan et al. 1999; Poggio & Reichardt 1976). Following a well-established protocol (Nityananda et al. 2015), I presented praying mantids with computer-generated full-screen moving grating stimuli and observed whether or not the animals were performing the compensatory movement. I observed a robust response across all individuals, but no significant differences between species groups.

4.4.1 Subjects

Mantids were acquired from a UK breeder at adult stage or at 4-5th instar, and raised to adulthood. All animals were housed in individual plastic boxes (17cm L x 17cm W x 19cm H), perforated to facilitate ventilation. The boxes were stored in an insect housing facility where the temperature was maintained at 25 C on a 12:12 light/dark cycle. Mantids were fed a single cricket (*Grylloides sigillatus*, 18–25mm) twice a week, and boxes were cleaned and sprayed with a fine mist of water weekly.

4.4.2 Experimental set-up

The experimental set-up consisted of a metal stand holding a Perspex perch (5cm x 5cm). The viewing platform was a piece of plastic net wrapped around a piece of cardboard and clamped 10 cm away from a computer screen (Samsung 21" colour monitor, resolution 1920px x 1200px, refresh rate 60 Hz). A Kinobo USB B3 HD webcam observing camera (Point Set Digital Ltd, Edinburgh, Scotland) was placed above the screen and focussed only on the animal. This camera was connected to a Lenovo ThinkPad laptop used by the experimenter to observe

animals' responses and record behaviour in real time blind to the stimuli being shown on the screen. A second camera was placed behind the viewing platform to record the experiment (Figure 6). To avoid visual distraction for the animal, the experimental set-up was enclosed. All experiments were run in the dark, with the only light coming from the computer screen in front of the mantis.

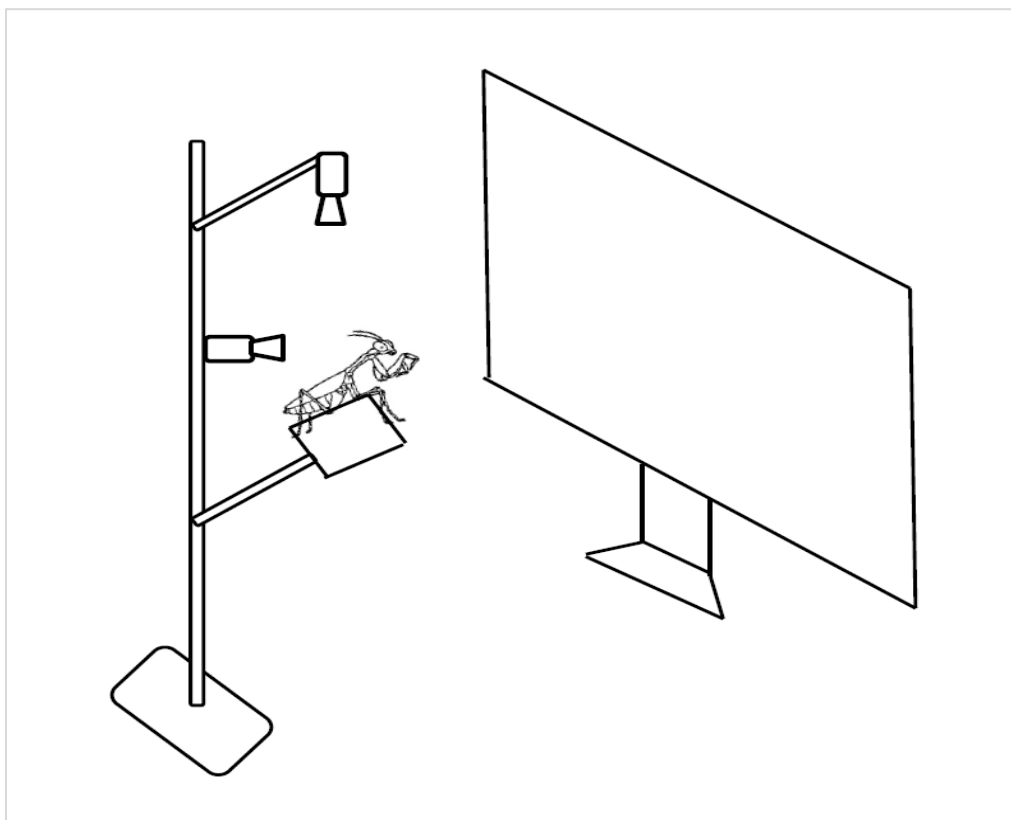


Figure 6 The experimental set-up where each individual praying mantis was free to move on a viewing platform placed 10 cm away from the screen where the visual stimuli were presented. The observing camera was placed above the animal, whilst the recording camera was placed behind the animal.

4.4.3 Computer-generated visual stimuli

Visual stimuli were programmed and rendered using Psychophysics Toolbox 3 for Matlab (Mathworks). By manipulating the width of the bars and the speed at which they moved along the screen, I could test a relevant range of spatio-temporal frequencies (Nityananda et al. 2015), where spatial frequency describes the number of cycles of alternating dark-and-light bars per degree of visual angle (measured in cycle/degree), whilst temporal frequency describe how often the bars alternate in each point the screen space (measured in Hz). The grating could have four level of internal contrast between the dark-and-light bars, in order to explore how the spatio-temporal acuity of the species varied with contrast level. I tested six different spatial frequencies (0.007, 0.010, 0.016, 0.03, 0.06, 0.12 cycles/deg) and ten temporal frequencies (0.03, 0.06, 0.125, 0.25, 0.5, 1, 2, 4, 8, 16 Hz), and choose to to test 30 spatio-temporal combinations. Every spatio-temporal frequency combination was tested at four possible contrast levels: 0.25, 0.5, 0.75 and 1, resulting in 120 test conditions. The contrast level was defined as Michelson contrast, i.e. the amplitude of the luminance grating divided by its mean luminance. The direction of motion of the grating also varied, with half of the gratings moving from left to right and half from right to left, balanced across presentations. Every experiment began with an alignment stimulus being presented on the screen, consisting of a black fly-shaped bug stimulus (luminance 0) spiralling at a decreasing speed from the edge to the centre of the screen on a plain grey (luminance 0.5) background (described in more detail in Nityananda et al. 2015). Once aligned, a mantid was presented with a test stimulus presentation. Each animal received 240 stimulus presentations in total; two presentations in each of the 120 conditions in different directions of travel. The order of the presentations was randomised for each mantid.

4.4.4 Experimental procedure

The behavioural experiment protocol largely followed that of Nityananda et al. (2015). An individual mantis was placed on the viewing platform at a viewing distance of 7 cm (eye to screen) and allowed to acclimatise for 15 minutes. After this period of acclimation, the alignment stimulus was displayed on the screen in order to ensure that the animal was responsive and looking towards the centre of the screen. Once the mantid's gaze was centrally aligned, a stimulus presentation was rendered on the screen for 5 secs. Once a stimulus presentation was completed, the alignment stimulus was shown again and the procedure repeated until all test stimuli had been presented. The response of the subject was scored by the experimenter as either: (i) compensatory movement to the left; (ii) compensatory movement to the right; or (iii) no compensatory movement. Compensatory movement was defined as being when the animal turned its head, prothorax or whole body in response to the moving grating (Figure 7). If the mantid left the viewing platform or stopped responding to the alignment stimulus for any reason, it was returned to its housing box for 30 minutes after which the mantis was replaced on the platform. This intervention made the mantid more responsive to stimuli being presented on the screen.

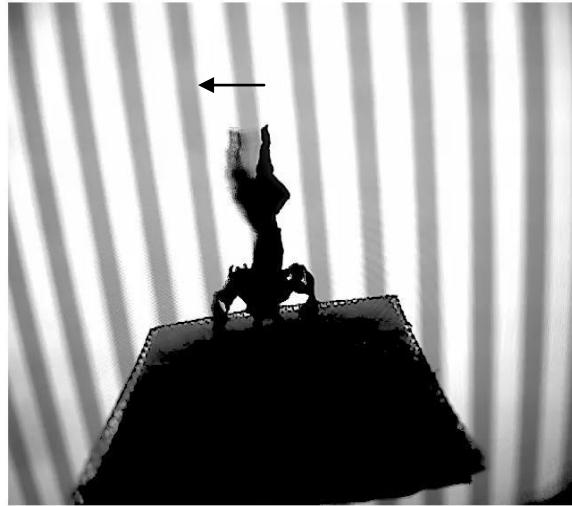


Figure 7 Long exposure frame showing mantids in the experimental set-up exhibiting the compensatory movement: *P. paradoxa* (left) and *S. pretiosa* (right); the arrows indicate gratings' direction of motion.

4.4.5 Data analysis

A total of 32 animals were tested with: *Sphodromantis lineola* (N=9, 7 females and 2 males); *Phyllocrania paradoxa* (N=7, 4 females and 3 males); *Sibylla pretiosa* (N=11, 4 females and 7 males); *Creobroter gemmatus* (N=5, 2 females and 3 males). This gave a total of 7680 stimulus presentations to be analysed. Mantids' responses were coded blind to the stimulus being shown on the screen. They were scored according to whether the mantis showed correct compensatory movement (i.e. in the same direction as the grating) or did not perform any optomotor response. No mantid ever performed the compensatory response in the opposite direction to moving grating. For each species, the responses for each point in the contrast sensitivity space were pooled across all individuals. Therefore, for every condition, I obtained for each species the number of optomotor response performed or not performed by all the individual tested.

I wanted to test if any observed differences in response to a certain condition between species were significantly higher than what was expected by chance, i.e. that the responses were not affected by species. I performed a Chi-squared test of independence with variables organized in a contingency table. The Chi-squared test allowed me to overcome the differences in the numbers of individuals tested across the four species. The analyses were coded and run using Anaconda 2.2 version for Python. Each table, built having condition in each row, contained the number of individual belonging to each species that performed the optomotor response and the ones that did not. Therefore, the table was built as [counts of C=0 in the four species; counts of C=1 in the four species] per row, i.e. per condition, being C the mantis optomotor response binary coded, such that [No response=0, Response=1]. For instance to test the case where, for a specific tested condition, *S. lineola* had counts

[7, 2] given by the sum of all individuals response, *P. paradoxa* counts were [5, 2], *S.pretiosa* had counts [5, 6], *C. gemmatus* had [2, 3], the resulting matrix tested would have be [7, 5, 5, 2; 2, 2, 6, 3]. In this way, I evaluated 120 conditions to look at whether the counts of C=0 and C=1 were randomly distributed across the species or showed some dependency, i.e. the effect of species group. Because of the multiple comparison computed, results were Bonferroni corrected.

4.4.6 Results

All species consistently performed the compensatory responses to stimuli presented within the parameter space. To visualize the responses that each species exhibited to each condition tested, I plotted the probability of performing optomotor response at every combination of spatial and temporal frequency (x and y axis) at every contrast level for each species (Figures 8 and 9). Although species appeared to differ in the parameter combinations that they were most likely to respond to, the Chi-squared test failed to find significant differences of mantis response across species, except for one visual condition. Indeed, out of these 240 p-values, i.e. 120 condition times 2 direction of motion, that were computed, 120 failed the statistical computation for low statistical power (i.e. due to small sample size), whilst 30 comparison were significant and the remaining 90 were not significant. However, when using the Bonferroni correction to control for multiple testing, only for one tested condition the response of the mantis remained significantly affected by species group, i.e. contrast=0.25, spatial frequency=0.12238, temporal frequency=8.0 and direction leftwards, which showed a Bonferroni-corrected p-value of 0.049. Indeed, this result would be probably be lost with an increased sample size,

as it is unlikely that the animals have different responses toward grating moving in opposite direction and the model did not find any differences between species response for the same contrast, spatio-temporal frequency grating condition but with gratings moving in the other direction. Moreover, if differences in visual acuity exist across species they would be exhibited for more than one combination of spatio-temporal frequency and contrast levels.

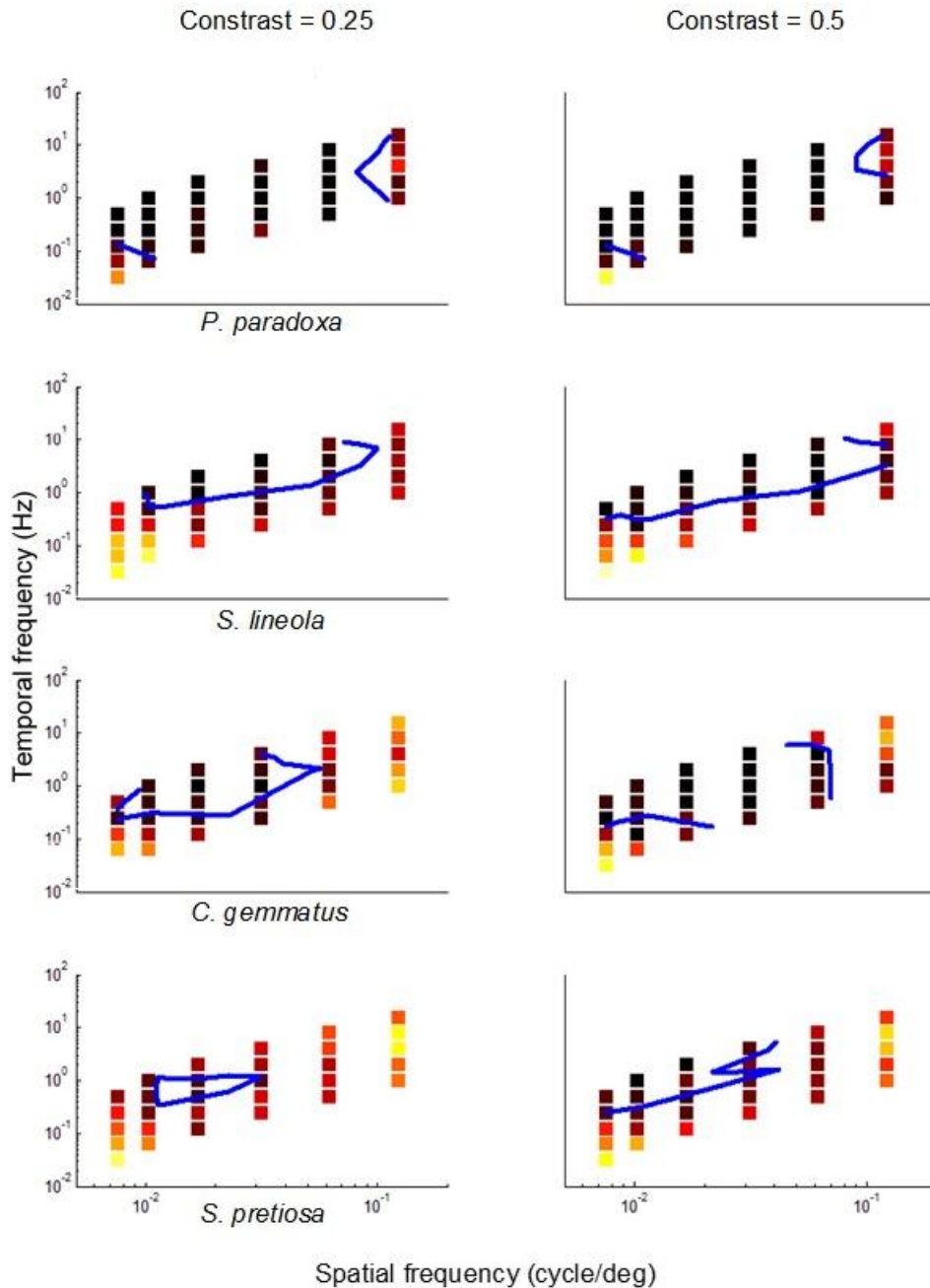


Figure 8 Probability of praying mantids showing optomotor responses towards gratings of different contrast ratio and varying in temporal and spatial frequencies. The temporal frequencies (Hz) and the spatial frequencies (cycle/deg) are indicated on the y and x axes respectively, on a logarithmic scale. The contrast ratios are indicated above the column: 0.25 (left) and 0.5 (right). Squares indicate the probability of response for a certain species, on a chromatic scale increasing values from light to dark colours. The blue line defines the area of $\geq 85\%$ probability of response. Each row shows the results for a certain species, from the top: *Phyllocrania paradoxa*, *Sphodromantis lineola*, *Creobroter gemmatus* and *Sibylla pretiosa*.

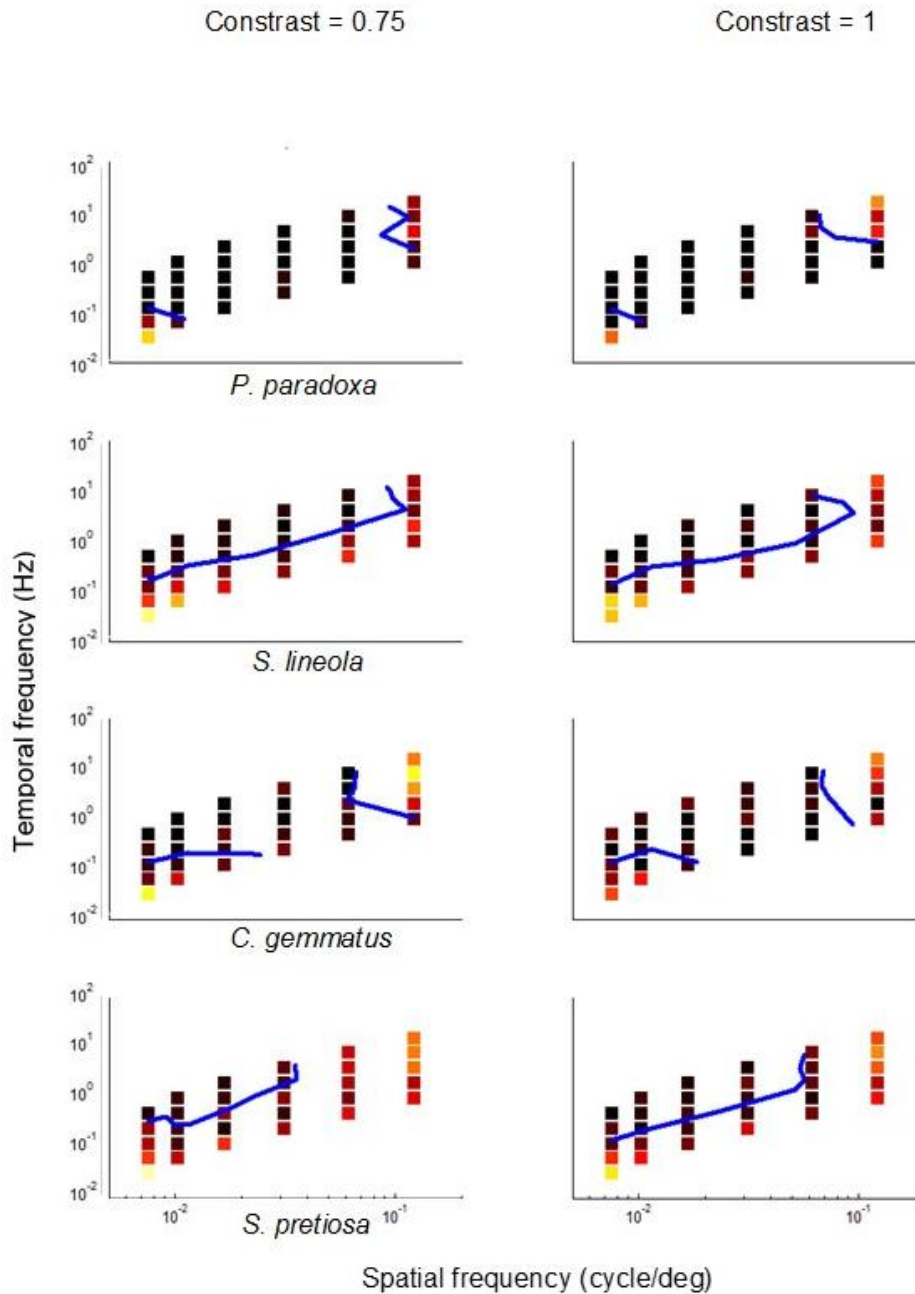


Figure 9 Probability of praying mantids showing optomotor responses towards gratings of different contrast ratio and varying in temporal and spatial frequencies. The temporal frequencies (Hz) and the spatial frequencies (cycle/deg) are indicated on the y and x axes respectively, on a logarithmic scale. The contrast ratios are indicated above the column: 0.75 (left) and 1 (right). Squares indicate the probability of response for a certain species, on a chromatic scale increasing values from light to dark colours. The blue line defines the area of $\geq 85\%$ probability of response. Each row shows the results for a certain species, from the top: *Phyllocrania paradoxa*, *Sphodromantis lineola*, *Creobroter gemmatus* and *Sibylla pretiosa*.

4.5 Discussion

My results show that praying mantids species with morphologically different eyes do not differ in their ability to resolve moving wide-field gratings in the range of spatio-temporal frequencies and contrast levels tested. Indeed, the behaviour performed by the individuals of a group species in response to a certain condition did not relate to its species group and did not differ from the response exhibited by other species.

This is the first study that compared the visual acuities of morphologically different species for a comprehensive range of contrast and spatio-temporal frequency moving gratings. To date, mantids' sensitivities were only similarly investigated only for one species, *Sphodromantis lineola* (Nityananda et al. 2015). On the other hand, there are a number of studies investigating which visual prey-like stimuli can elicit mantids predatory behaviour in different species (e.g. Prete and Mahaffey, 1993; Prete et al. 2002, Prete et al., 2011). These studies did, in fact, find that the probability that an individual strikes at a moving erratic disk varied between species depending on the size, speed and contrast of the stimulus (Prete et al. 2013, Prete et al. 2011). However, those differences are likely to reflect prey preferences across species, rather than visual acuity intended as ability to resolve a certain pattern. One can hypothesize that prey preference can be cause or consequences behind differences in eyes morphology, but, at least based on my data, those differences in eyes shape do not reflect differences in visual acuity. The visual acuity of a species is thought to have evolved to meet the ecological needs of individuals, and to reflect the pressure of various driving factors: (i) the animal's visual environment, e.g. cryptic or with low or high visual noise; (ii) prey that the animal

preys upon and needs to detect, e.g. cryptic or conspicuous prey; (iii) predation strategy, e.g. ambush-static or cursorial-stalking; (iv) predators pressure and animal defensive strategy against them (e.g. Nityananda et al., 2015; Farnier et al., 2015; Gonzalez-Bellido et al., 2011; O'Carroll et al., 1996; Lythgoe 1979). Additionally, an insect's visual system is size-constrained and exposed to a strong optimization evolutionary pressure (Gonzalez-Bellido et al., 2016). Because the species differed in their eyes design and lens diameter, which is a key determinant of visual acuity in compound eyes (Land & Nilsson 2012), one can speculate that their vision might be optimized and tuned to different ranges of stimuli. However, I found that my model species did not differ in acuity towards the vast majority of the tested conditions. Therefore, the differences in eyes design observed across species must be the results of others driving factors, whilst their visual acuity could perhaps be neuro-physiologically constrained. For instance, it has been found that, in insect species, the neuron physiology of target tracking systems is strikingly similar even across phylogenetically distant species displaying different hunting behaviours, suggesting little or no plasticity in its arrangement (Gonzalez-Bellido et al., 2016). Perhaps different eye designs across species reflect different camouflage strategies and are the result of geographic variation in mantis' predator community composition and behaviour, as observed in other taxa (e.g. Willink et al., 2014; Ratcliffe and Nydam, 2008; Endler and Mappes, 2004). Mantis's lineages exhibit extremely variable morphology, the convergence in ecomorphic specialization between disparate groups are likely to reflect geographical isolation and similarity in species habitat (Svenson and Whiting, 2009). Unfortunately, little is known about the ecology of praying mantids. However, I observed different behaviours in my four species which might reflect differences in hunting strategies. The African lined mantis (*S. lineola*) is

commonly found in the open habitat of the Sub-Saharan regions of Africa, and despite being commonly known to be a sit-and-wait ambush predator (Prete, 1999), it can actively explore its surrounding and run after prey (personal observation). Similar behaviour, typical of a cursorial predators, was observed for the cryptic mantis (*S. pretiosa*) and the Indian flower mantis (*C. gemmatus*). On the other hand, no active prey approach was observed for the ghost mantis (*P. paradoxa*), which were generally found hanging upside-down in their housing boxes swinging like a leaf and waiting for the prey to be at the right distance before making a strike (personal observation). Interestingly, I observed the ghost mantis performing the thanatosis when approached by the experimenter whilst the other species often react, to what it seems to them to be a threat, with a startle display and exhibit their coloured inner forelegs and opening their wings. This differences in the observed behaviour, despite not supported by observation in the field unfortunately, might reflect differences in defensive strategy between the species. Some species might have specialized to be camouflage and blend in their background, e.g. the ghost mantis, whilst other might have opted for a more active defensive strategy. Therefore, the eyes might have been shaped by defensive needs rather than to serve specific visual task, e.g. detect the “preferred” prey. Further investigations are needed to better understand which selective pressures and behavioural habits shaped the intriguing variation of praying mantids eye design.

Chapter 5: The flicker fusion effect can enhance the concealment of moving prey

5.1 Abstract

How colour patterns have evolved to help prey avoid being detected by visually hunting predators has long fascinated evolutionary biologists. Recent studies suggest that those strategies that confer anti-predator advantages whilst prey are stationary, are ineffective when prey move: 'movement breaks camouflage'. Therefore, there is increasing interest in whether or not moving prey can ever be camouflaged or which pattern a prey should have to help maximise concealment. To date, the only putative, and yet untested, mechanism through which prey could better match their background and conceal themselves whilst moving is through the flicker fusion effect. Using praying mantids tracking computer-generated prey, I show that high contrast stripes can blur at speed and help to conceal striped prey when moving. For the first time, my results demonstrate that the flicker fusion effect can have an antipredator function and uniquely reduce predator detection rate of otherwise conspicuous moving prey.

5.2 Introduction

The flicker fusion effect is a mechanism by which striped prey can differ in appearance to their predators when moving compared to when they are stationary. The original idea was based on observations of snakes, which flee sufficiently quickly that the stripes of their pattern appear to blur into a uniform colour, at least to

human eyes (Pough 1976). There have been numerous hypotheses by which the sudden change in appearance could help prey defend themselves, for example, by impairing predators' abilities to track them along their path, by helping prey blend into the background, or by being a deterrent to predators (see Chapter 2 for a review). However, despite the long existence of these ideas in the literature, supporting evidence is limited to human observations and calculations of whether or not prey move fast enough for flicker fusion to occur for avian and mammalian predators (Jackson et al. 1976; Titcomb et al. 2014). Perhaps surprisingly, we still don't know if and how the flicker fusion effect can change predators' responses towards patterned prey (Chapter 2).

Flicker fusion is predicted to occur in a predator's eyes when a patterned prey crosses its visual field with sufficient speed that the repeating elements of its patterns (e.g. stripes) alternate faster than the predator can temporally resolve. At this point, the prey's pattern blurs and it will appear uniform (Pough 1976; Jackson et al. 1976). The frequency at which the alternation of the pattern elements can no longer be resolved by a predator is not fixed (Watson & Ahumada 2016), and will depend not only on a predator's visual system and the environmental conditions (see Chapter 2), but also on the pattern features themselves. In the case of a striped prey, prey with thinner stripes do not need to move as quickly as prey with wider stripes in order to achieve the frequency of alternation at which blurring occurs. The frequency at which the stripes alternate whilst crossing a predator's visual field, i.e. pattern temporal frequency, depends on the number of stripes within a given degree of predator visual angle, i.e. pattern spatial frequency, and of course on the speed at which the prey moves (see Chapter 2 for a detailed explanation). Therefore, at any given speed, thinner stripes (i.e. a striped pattern with higher spatial frequency) will

produce a higher temporal frequency compared to wider stripes (i.e. a striped pattern with lower spatial frequency). If the loss of patterning and appearing uniform helps prey to better match features of their background, predators should find it harder to detect and/or track their prey, perhaps because of the loss of internal references (e.g. Hughes et al. 2014) and/ or because a uniform patterned prey will not trigger predators' small target motion detectors as a much as patterned one (e.g. Nordström et al. 2006). If this was the case, flicker fusion would be the only way by which prey could become better concealed when they move (see also Chapter 2).

Despite it being theoretically possible, whether concealment through the flicker fusion effect does occur has yet to be empirically established. Here, for the first time, I investigated whether or not prey with high contrast stripes could become better concealed through the flicker fusion effect. I presented African praying mantids (*Sphodromantis lineola*) with computer-generated prey targets. The speeds and patterns of these prey targets were designed and manipulated based on what is known about praying mantids spatial and temporal acuities (Chapter 4; Nityananda et al. 2015). In addition, their tracking behaviour towards computer-generated targets is a reliable proxy of prey detection (e.g. Prete 1993; Nityananda et al. 2015) and can be used as a measure of how visible a prey is to the predator. Because praying mantids use luminance as a cue for detection (e.g. Prete et al. 1990; Prete 1993), the striped prey were isoluminant with the backgrounds against which they were presented. This laboratory system allows fine control over stimulus presentation whilst using the behaviour of a real predator to measure how different patterns can reduce detection and enhance survival.

I specifically tested the two general principles underlying the flicker fusion effect to show that it can occur in the eyes of a predator to promote prey survival.

The first is that the occurrence of the effect depends upon the interaction between the spatial frequency of the stripes and the prey's travel speed: high spatial frequency patterns (thin stripes) should be harder to resolve and blur at lower travel speeds than low spatial frequency patterns (wide stripes). The second is that there can be a camouflage advantage due to the blurring of pattern elements into a uniform appearance.

5.3 Methods

5.3.1 Subjects

I used twelve adult female African praying mantids (*Sphodromantis lineola*), acquired from a UK breeder. Mantises were housed individually in plastic boxes (17cm L x 17cm W x 19cm H) which were perforated to facilitate ventilation, and stored in an insect housing facility at 25°C on a 12:12 light/dark cycle. Mantises were fed a single cricket (*Gryllodes sigillatus*, 18-25mm) twice a week, and the individual boxes were cleaned and sprayed with a fine mist of water weekly.

5.3.2 Experimental set-up

The experimental set-up was housed in an unlit laboratory. It consisted of a metal stand holding a Perspex perch (5 cm x 5 cm), from which the mantids hung upside-down, and which was clamped 4 cm away from a CRT screen to ensure that each mantis had a viewing distance from the screen of 2.5 cm (Figure 10). The CRT screen (Hewlett-Packard 21" colour monitor P1130) was 40.4 cm x 30.2 cm, with pixel dimensions of 1600 px x 1200 px, and subtended a visual angle of 165.9

degrees at the viewing distance of the mantis. The CRT monitor was gamma corrected (Gamma = 2.0), had a mean luminance of 51.4 cd/m² and its refresh rate was 85 Hz (mantids are reported to not perceived flicker above 50 Hz; Prete and Kral 2004). The set-up was enclosed to avoid mantises being visually distracted by the experimenter or by other movements in the experimental room. Two cameras Kinobo USB B3 HD Webcam (Point Set Digital Ltd, Edinburgh, Scotland) were placed above the screen. One of these was an observation camera, which was connected to a second computer (DELL OptiPlex 9010) and positioned so that the observer could score response behaviours blind to the stimuli presented on the screen. The second camera had a broader field of view and was used to record the experiments. All experiments were run in the dark, with the only light coming from the computer screen in front of the mantis.

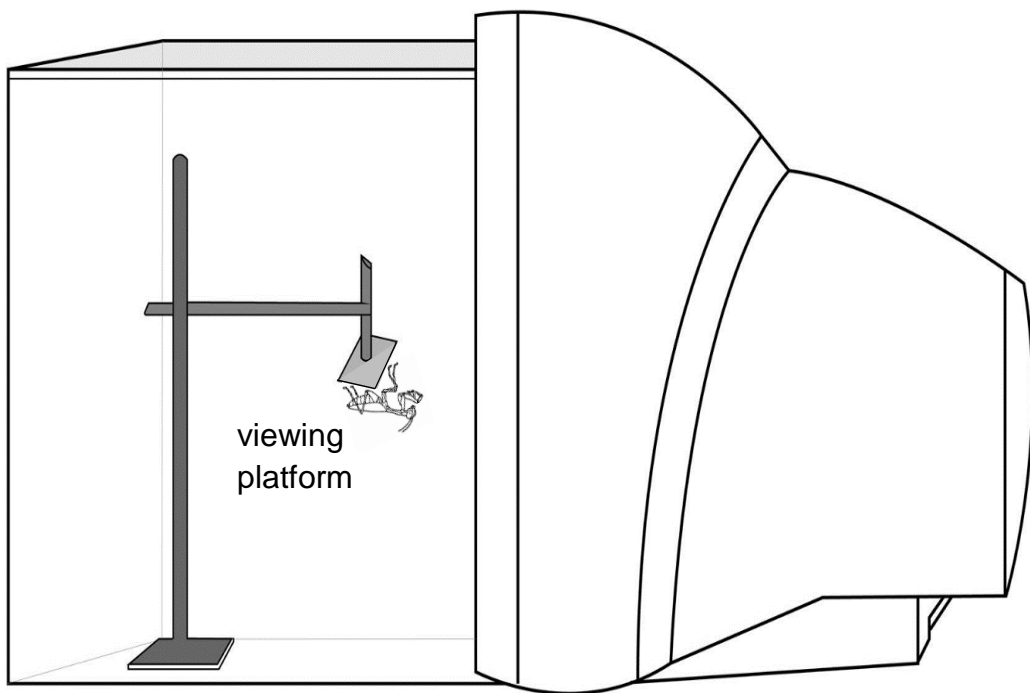


Figure 10 The experimental set-up where mantids were holding upside-down on a viewing platform placed in front of a CRT screen.

5.3.3 Computer-generated prey

Computer-generated prey were programmed and rendered using Psychophysics Toolbox 3 for Matlab (Mathworks). In order to test the principles underlying the flicker fusion effect, I presented four different prey types to the mantids (Figure 11): uniform black prey (luminance of 0); uniform grey prey (luminance of 0.5); wide-striped prey; and, thin-striped prey (all striped prey mean luminance of 0.5). The pattern of the two striped prey was a black-and-white square-wave grating that was perpendicular to the vector of movement. The two prey types had different numbers of wave cycles: the wide-striped prey had two wave cycles and the thin-striped prey had eight cycles. To ensure that the leading and rear edges of the striped prey had the same luminance regardless of their stripe width, and that the entire length of the prey could be discerned, the patterns of both striped prey types were shifted so that both vertical edges were black (i.e. the start and end of the pattern was a half-width black stripe; see Figure 11). Both striped prey types had a mean luminance of 0.5. The uniform grey prey had the same mean luminance as the striped prey, and was important for testing if blurring was occurring (more detail below). The inclusion of uniform black prey ensured that mantids' behaviour towards prey with lower mean luminance was due to the prey being hard to see, rather than the mantids not being responsive (black prey that have a high contrast to the background elicit strong tracking and predatory behaviour from mantids; e.g. (Prete et al. 2002). All prey were the same size (1.6×1.0 cm; or 64×30 pixels).

The prey were tested on two different backgrounds: textured and uniform grey (Figure 11). Both backgrounds had the same mean luminance (0.5), which matched the mean luminance of the uniform grey and striped prey. Prey stimuli and background contrast levels are defined as Michelson contrast. Textured

backgrounds were generated (uniquely for each prey presentation) in MatLab, and had luminance levels in the range 0 to 1 and a $1/f$ spatial frequency spectrum resembling that of natural backgrounds. Natural image statistics were used to capture the spatial features of natural scenes, and allowed all four prey types to be visible when moving. The uniform background allowed me to test if blurring was occurring: if the stripes of the patterned prey blurred, they would not be visible on the grey background.

In each prey presentation, a prey target moved across one of these two backgrounds at one of two different speeds: 259 and 501 pixel/sec, which corresponded to 74 and 145 degree/sec, respectively.

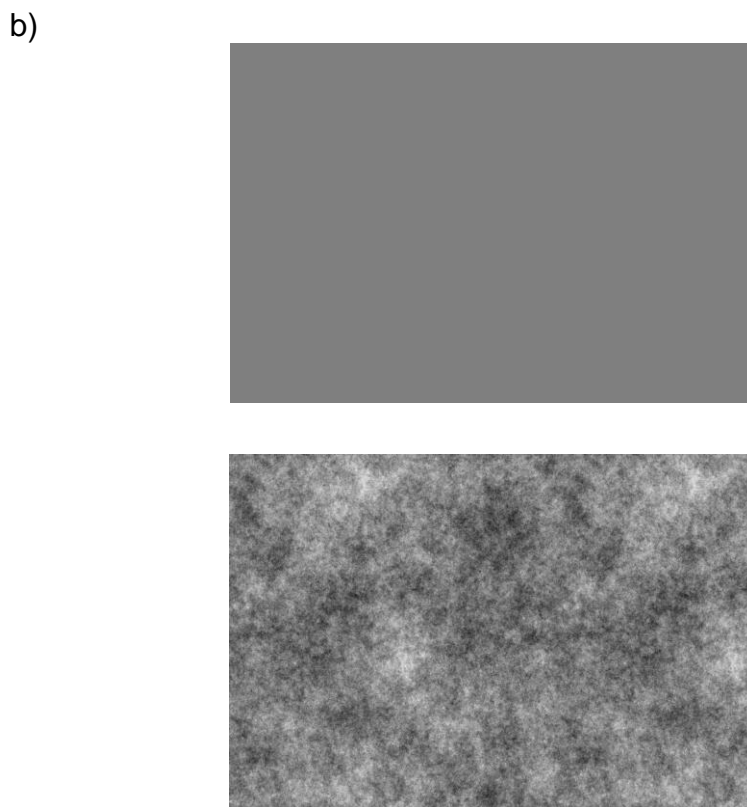


Figure 11 Visual stimuli tested were a) four types of prey, from the top-left: black, grey, wide-striped and thin-striped prey. Prey were moving against b) two types of background: uniform grey (top) and textured (bottom).

In order to investigate the flicker fusion effect, I needed to design the visual stimuli such that they were placed at known points in the mantids' spatio-temporal acuity space (see detail below, Fig.12). This was because the visibility of the stripes is predicted to vary across this space. As already mentioned, the temporal frequency (TF) at which stripes will alternate whilst crossing a predator's visual field, depends on pattern spatial frequency (SF) and on the speed at which prey moves, following the equation:

$$TF [Hz] = Speed[px/sec] \times SF[cycle/px] \quad \text{Eq.1}$$

At the distance at which mantids viewed the prey stimuli, wide-striped and thin-striped prey had spatial frequency of 0.05 and 0.2 cycle/deg respectively. The resulting temporal frequency that the striped prey produced whilst moving at the slow and fast speed can then be calculated (Table 5).

Table 4 Temporal frequency of the striped prey tested

Prey	Speed (deg/sec)	Speed (px/sec)	SF (cycle/deg)	SF (cycle/px)	TF (Hz)
wide-striped	75	259	0.05	1/32	8.1
wide-striped	145	501	0.05	1/32	15.7
thin-striped	75	259	0.2	1/8	32.4
thin-striped	145	501	0.2	1/8	62.6

Based on published data on the optomotor response for *S. lineola* (Nityananda et al. 2015), I could estimate when a mantid would likely resolve a pattern having specific spatial and temporal frequencies. For increasing spatial or temporal frequencies, the minimum contrast between pattern elements needed also increase in order for an observer to be able to resolve the pattern, i.e. the contrast threshold increases. In Figure 12, the contours are the contrast threshold isolines for

each combination of spatial-temporal frequency (x and y axis respectively), At the very centre, where the spatio-temporal frequencies are ideal for mantids vision, it is sufficient that a pattern has an internal contrast of 0.02 between its elements for mantids to be able to resolve it. Moving away from this central point, the minimum contrast that mantids will detect increases. By testing prey having patterns with maximum internal contrast (i.e. black-and-white stripes), I expected mantids to be able to resolve the pattern when spatio-temporal features lay within the isoline where the contrast threshold is equal to 1 (Figure 12). Therefore, I predict that the wide-striped pattern would be easier for mantids to resolve compared to the thin-striped pattern, regardless of speed (the wide-striped prey lie well within the contour, and their stripes are likely to be resolved even at lower internal contrast). Crucially, I expected mantids to be able to resolve the thin-stripes at the lower speed, but be unable to resolve this pattern when the thin-striped prey moved at the higher speed, since this lies outside the mantids' temporal acuity. For this reason, I predicted that the thin-striped prey should appear uniform grey whilst fast moving, and therefore be detected at the same rate as uniform grey prey, and be wholly undetectable against the uniform grey background.

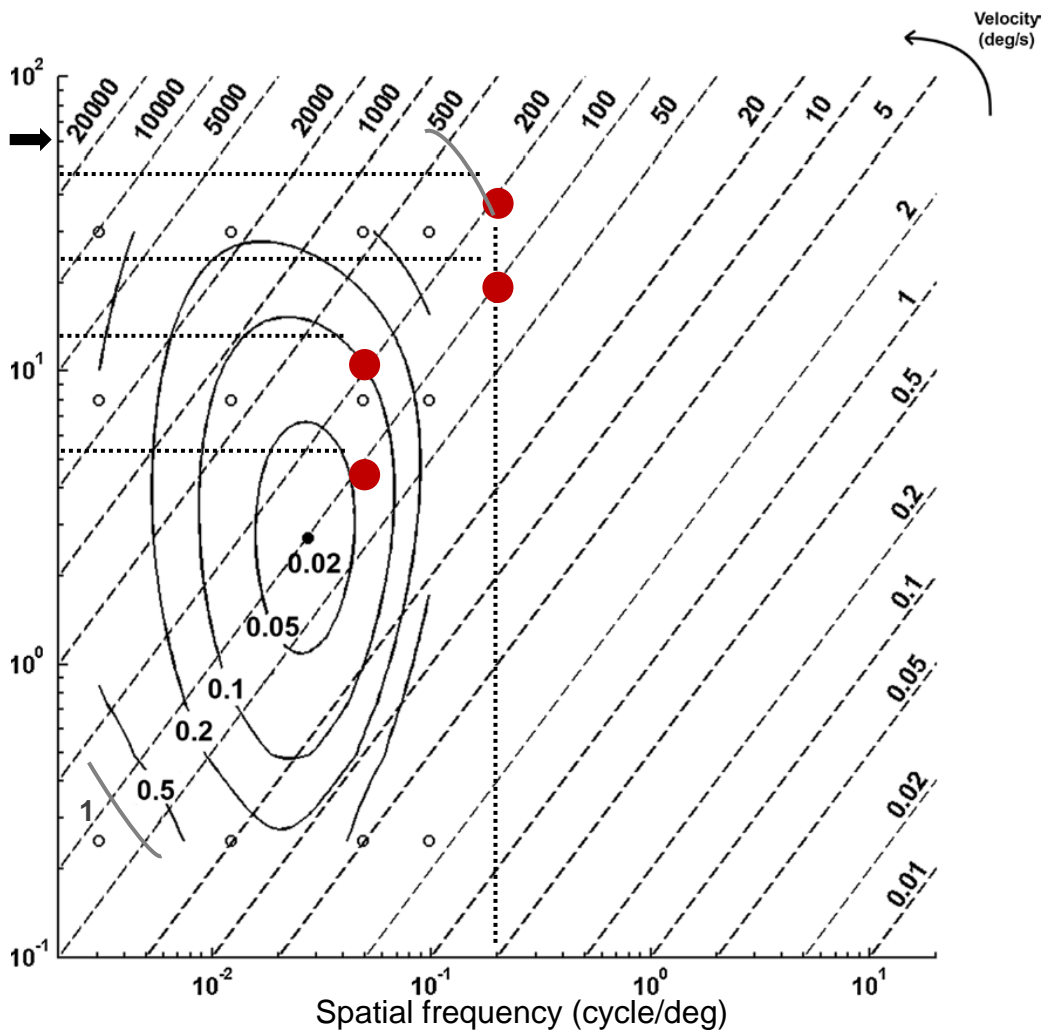


Figure 12 Points where the wide-striped and thin-striped prey lie in mantids spatio-temporal sensitivity domain. The red dots indicate, for each stripe width, the resulting temporal frequency whilst moving at slow (bottom dot of each vertical line) and fast (top dot of each vertical line) speed. The contour lines represent the isolines of mantids contrast threshold across SF-TF domain. The black arrow indicate the maximum temporal frequency mantids can perceive. Figure adapted from Nityananda et al. (2015)

5.3.4 Experimental procedure

The experimental protocol was similar to that already described in Chapter 4. Each individual praying mantis was placed upside-down on the viewing platform and allowed to acclimatise for 10 minutes. The mantis was free to move on the platform but the viewing distance (from eyes to screen) was set at 2.5 cm from the CRT monitor at the start of the session. After the acclimation period, an alignment stimulus (see Chapter 4 for detailed description) was displayed on the screen in order to ensure that the animal was responsive and looking towards the centre of the screen. The alignment stimulus was presented as many times as it was necessary to attract and align the animal's gaze. Alternatively a black-and-white checkboard full screen image was moved to the left or to the right until the animal was centrally aligned through an induced optomotor response (i.e. an innate response which turns the entire body in the direction of the movement; Poggio & Reichardt 1976). Once the animal was aligned to the centre of the screen, a prey presentation was initiated.

A prey presentation started with the test background being shown for 15 seconds before a prey appeared and crossed the screen. Each prey moved horizontally across the screen either from right to left or from left to right (direction of travel was balanced across prey presentations) in a straight line at a height that was directly in front of the mantid's head. Animals received prey presentations in two blocks of 80 presentations to ensure that they remained motivated to track prey. In each block, animals received 10 presentations of each prey type and background combination, randomised across the block. The speed was the same for all prey occurring within a single block: six animals received the slow and then the fast moving prey, and for the other six the order was reversed. Presentations were

separated by variable inter-stimuli intervals (from 15 to 90 seconds) and presented in randomized order.

If, for any reason, the animal left the viewing platform or stopped responding to the alignment stimulus, it was returned to its housing box for a minimum of 30 minutes after which it was replaced on the platform.

5.3.5 Data analysis

For each prey presentation, I recorded if the mantid's head moved to track the prey or not. My observations were made blind to what was being shown on the screen. At the end of each block, I ensured that the response rate to the black prey was equal to or exceeded 50%. This was because I expected low response rates towards camouflaged prey, and only wanted to include datasets from blocks if there was good evidence of tracking behaviour to a stimulus that is known to elicit high rates of tracking behaviour.

The binary dependent variable was whether tracking occurred or not, which was analysed with generalized estimating equations (GEE) using a binary logistic model in SPSS v23. In all analyses, mantis was included as a subject factor; details of each model used to test my predictions are given in the Results section.

5.4 Results

To test my first prediction that thin-striped prey will be better concealed at lower travel speed compared to wide-striped prey, I ran a full factorial GEE to compare the tracking responses between the wide-striped and thin-striped prey, including stripe width (i.e. spatial frequency), prey speed and background type as

factors in the model. As expected, prey were tracked less often if they had thin stripes (GEE, $\chi^2_1=62,9$, $P<0.001$, Figure 13), moved faster (GEE, $\chi^2_1=4,2$, $P=0.040$, Figure 13), and were moving against the uniform grey background (GEE, $\chi^2_1=7,9$, $P=0.005$, Figure 13). However, an interaction between stripe width and background (GEE, $\chi^2_1=3,9$, $P=0.048$) and a near significant interaction between stripe width and speed (GEE, $\chi^2_1=3,7$, $P=0.055$) suggested that the effects of speed and background were different for the two striped prey types (all other interactions were not significant: all $\chi^2_1<2.6$, $P>0.101$). Therefore, I analysed the data for each prey type separately using prey speed and background type as factors in the model. For the wide-striped prey, neither travel speed (GEE, $\chi^2_1=0.4$, $P=0.507$) nor the background type (GEE, $\chi^2_1=1,6$, $P=0.206$) affected tracking responses; there was no significant interaction between these two factors (GEE, $\chi^2_1=1,5$, $P=0.225$). However, as expected, increasing speed reduced tracking responses towards the thin-striped prey (GEE, $\chi^2_1=5.0$, $P=0.025$), and the prey were harder to detect against the grey background (GEE, $\chi^2_1=6.2$, $P=0.013$). There was no significant interaction between these two factors ($\chi^2_1=1.9$, $P=0.169$). These results support the prediction that striped patterns with higher spatial frequencies are harder to resolve, and this becomes even more difficult with increasing speed, where their pattern elements alternate at a frequency that exceeds the mantids' maximum resolvable temporal frequency (see Figure 12).

If the flicker fusion effect is occurring, repeated pattern elements should blur and the striped prey should become uniform. Therefore, at the high speed, but not at slow speed, responses towards the thin-striped and the uniform grey prey should be

the same, and neither should be visible and elicit tracking responses on the uniform grey background. As predicted, whilst moving at high speed, the thin-striped prey were equally tracked as the grey prey. On the grey background, the tracking was equal because there was no tracking behaviour shown to either of these prey types, indicating that the thin-striped and grey prey were not just equally visible, but were in fact *invisible* to the mantids. On the textured background, the tracking rates were also the same, and there was no significant difference between the two (GEE $\chi^2_3=6,743$, pairwise *post hoc*, $P=0.401$; Figure 14).

However, when the two prey types were moving at the slow speed, I found that the results did not quite fit my prediction. Surprisingly, thin-striped and grey prey were also tracked at the same rate whilst moving slowly against the textured background (GEE $\chi^2_3=6,743$, pairwise *post hoc*, $P=0.246$, Figure 14). However, when moving against the uniform grey background, the thin-striped prey were tracked more often than the grey prey (GEE $\chi^2_2=4,5$, pairwise *post hoc*, $P=0.034$, Figure 14) This last crucial comparison confirmed that the pattern of the thin-striped prey was visible to the mantids when the prey was slow moving. Therefore, it was the increase in prey speed that caused its pattern to become blurred to uniform grey.

Finally, the benefits in terms of reduced tracking with increasing in speed were only advantageous to those prey that matched the mean luminance of their background (Figure 15). When I analysed the tracking rate toward the black prey, with speed and background type as factors, I found that the black prey were tracked more often whilst fast moving (GEE, $\chi^2_1=7.6$, $P=0.006$), and neither the main effect of background (GEE, $\chi^2_1=3.2$, $P=0.07$) or the interaction (GEE, $\chi^2_1=0.7$, $P=0.4$) was

significant. This shows that the observed decrease in tracking rate toward the striped and grey prey was not simply because faster-moving prey are simply harder to track.

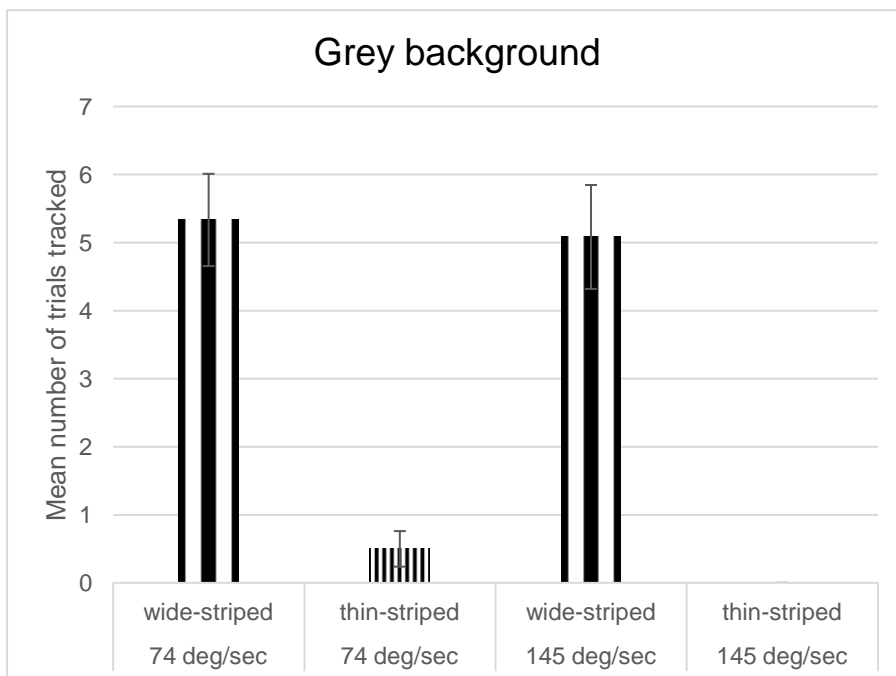
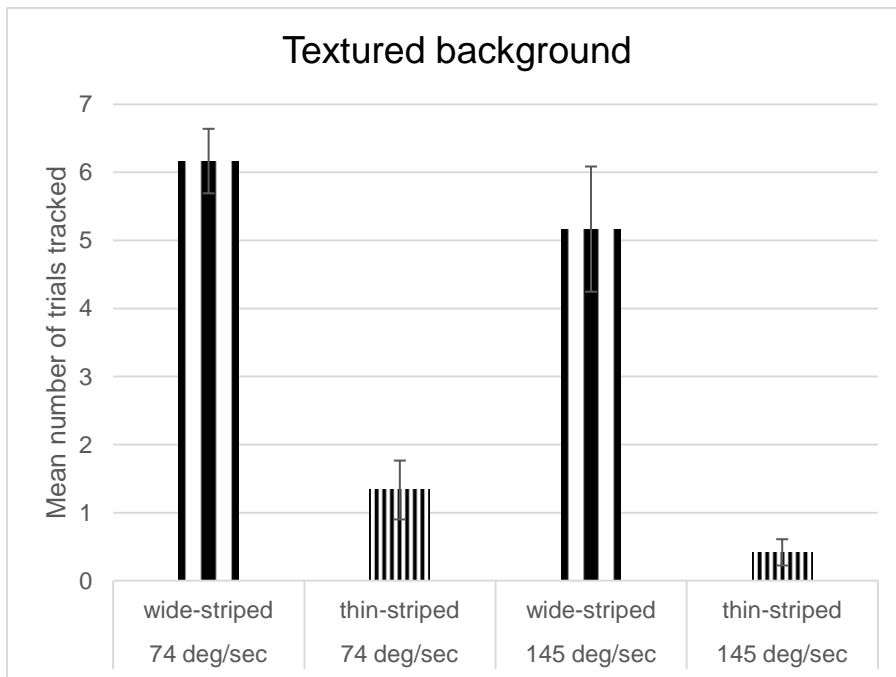


Figure 13 Mean number (\pm S.E.) of trials the mantises tracked the wide-striped and thin-striped prey out of 10 repetitions per condition showed to each 12 individuals of *S.lineola*.

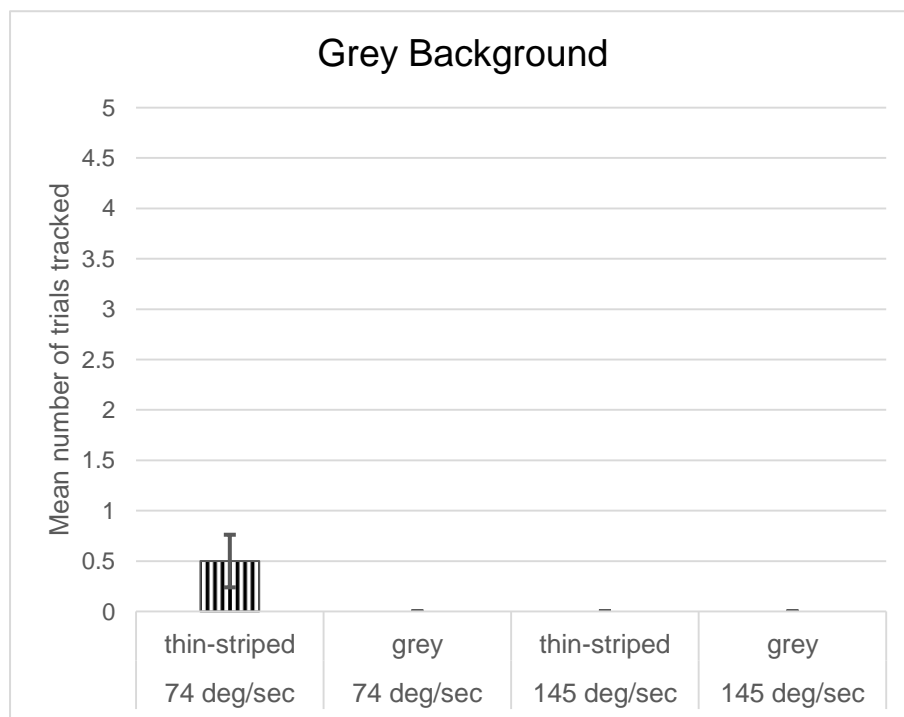
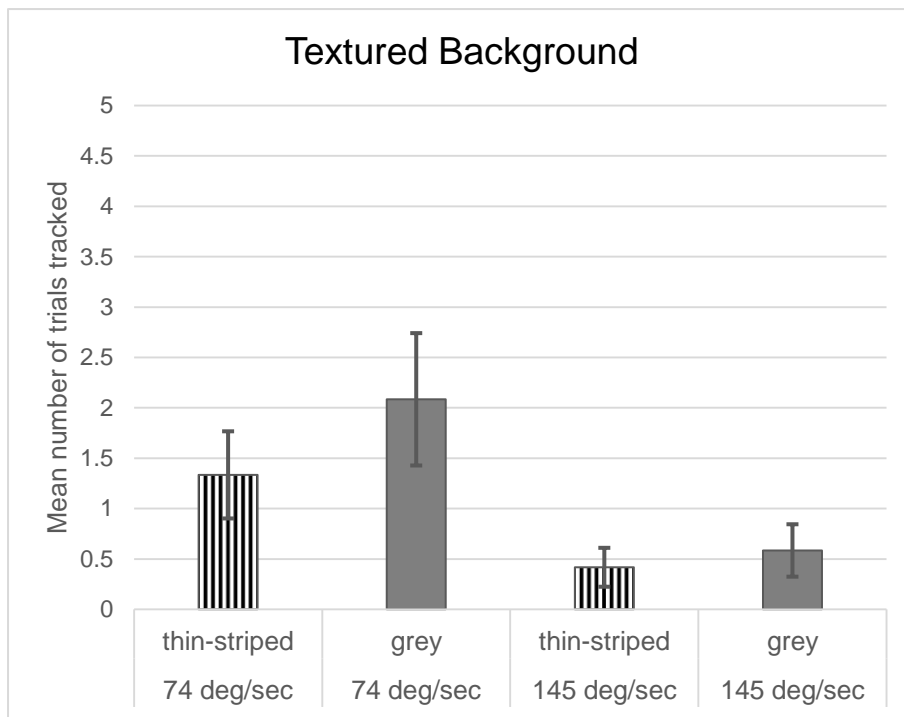


Figure 14 Mean number (\pm S.E.) of trials the mantises tracked the thin-striped and grey prey out of 10 repetitions per condition showed to each 12 individuals of *S.lineola*.

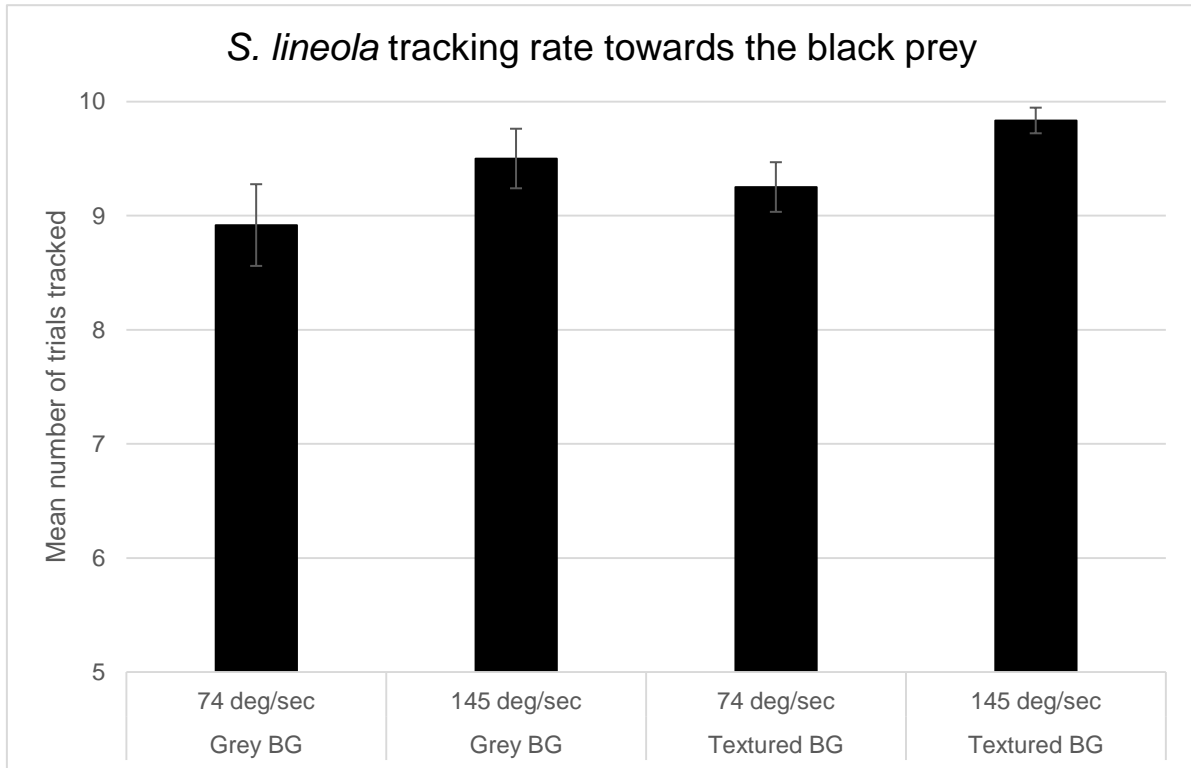


Figure 15 Mean number (\pm S.E.) of trials the mantises tracked the black prey whilst moving against the grey or the textured backgrounds (BG), out of 10 repetitions per condition showed to each 12 individuals of *S.lineola*.

5.5 Discussion

In this experiment, I tested if high contrast striped prey can conceal themselves whilst moving at sufficient speed for their pattern to appear blurred. By manipulating the stripes width of computer-generated prey and the speed at which they moved, I found that prey with thinner stripes will be concealed at a lower speed compared to prey with wider stripes, and that this appears to be because their patterns blur to a uniform grey. Taken together, my results provide the first empirical evidence that the flicker fusion effect could work against natural predators to conceal patterned prey if moving with sufficient speed.

My first prediction was that thin-striped prey would be camouflage at lower body speed comparing to wide-striped prey, because their stripes would alternate faster meaning that would achieve a higher temporal frequency. Indeed, I found that the thin-striped prey result camouflaged whilst moving at fast speed; it is also true that the thin-striped prey were less detectable than the wide-striped prey even at low speed, this result is again a consequence of how fast the stripes were alternating into praying mantids eyes: the thin-striped prey moving at slow speed were producing a temporal frequency higher than the one produced by the wide-striped prey at any speed tested (Figure 12). Although my model found that the interaction between prey speed and width of the stripes, i.e. pattern spatial frequency, was only tending towards significance, I did find that praying mantids' response towards the striped prey was affected by prey speed differently accordingly to whether the prey had thin or wide stripes. Meaning that prey having wider stripes, i.e. low spatial frequency pattern, will need to move at higher speed to be tracked significantly less than when slow moving. This results are consistent with the principle underlying the

flicker fusion effect that whether the change in prey' appearance will occur or not, depends on prey pattern spatial features and speed of motion.

Therefore, how effective is a certain prey pattern to reduce predation depends not only on whether the prey is moving or stay still, but also on the speed at which it moves. However, to date, only few study that investigate how movement affect prey defences explored this critical interaction between prey pattern and prey speed, and all used human "predators" (e.g. Scott-Samuel et al. 2011; Von Helversen et al. 2013), which spatial and temporal resolution differs from other vertebrate or from invertebrate species. However, because the occurrence of flicker fusion effect is really much dependent on the observer' visual acuity it is important to test the defensive efficacy of a certain prey pattern against its natural would-be predators. For instance, praying mantids are characterized by a notable high temporal acuity but, because of their compound eyes anatomy limits, low spatial resolution (Land & Nilsson 2012); thus indeed a certain prey that might not physically reach high travel speed, would still induce the flicker fusion effect in praying mantids if exhibit a pattern with finer details (i.e. higher spatial frequency). On the other hand, avian species like birds of prey are characterized by a high spatial and temporal acuity (Zeigler & Bischof 1993); however, under certain viewing condition, like increased distance or in dim light environment, prey might still be able to induce flicker fusion effect in their avian predators (see Chapter 2 for full details).

Second aim of this study was to test if the camouflage advantage a prey can benefit by inducing flicker fusion effect is due to the blurring of its pattern element into a uniform appearance. My experimental design here allowed me to do so, by testing the striped prey against a uniform grey background with which shared same mean luminance. Therefore, I expected that if the blurring was occurring, whilst fast

moving the thin-striped prey would completely blend against that background, as the uniform grey prey. Indeed, I found that once thin-striped prey were fast moving, praying mantids did not track them at all whilst moving against the grey background meaning that they were not able to resolve the stripes of their pattern and distinguish them from the background. This result crucially show that through flicker fusion effect prey can appear differently whilst fast moving comparing to how they appear at lower speed or whilst stationary. The observed decrease in detection rate towards the thin-striped prey, until it become undetectable against the uniform grey background, it can only be related to the flicker fusion effect and should not be confused with a motion dazzle. Indeed, motion dazzle is thought to occurs whilst the pattern of the prey is still fully visible to the observe and is supposed to impair capture (e.g. Stevens, 2011). On the other hand my results suggest that the pattern of the thin-striped prey is blurred and no longer visible, moreover, the antipredator advantages are due to a decrease in detection not in capture rate: therefore, the obtained results are due to flicker fusion effect and not to motion dazzle. Conversely to my prediction, however, the tracking rate toward the thin-striped prey moving at slow speed against the textured background was not higher than the tracking rate toward the grey prey, suggesting that perhaps the pattern of thin-striped prey started to blur even whilst the prey were moving at slow speed. This result might be partially due to the blurring effect occurring before than what predicted based on the optomotor response data, and partially a consequence of how background affected the visibility of the prey.

Clearly, the defence conferred by flicker fusion effect was more effective against the uniform grey background than against the textured one, and indeed I found that the type of background had an effect on praying mantids tracking rate different accordingly to whether the prey had wide-stripes, that were always

resolvable, or thin-striped, that blurred into uniform grey at fast speed, or was uniform grey which of course was not distinguishable from a grey background. Whilst moving against the textured background the thin-striped prey was not completely concealed even if inducing flicker fusion effect, but neither was the uniform grey prey. The reason behind this response is that, whilst moving across the screen, the prey were occluding patches of the background that were either lighter or darker than their own luminance, which made the prey more visible.

Moreover, I found that prey were tracked less at high speed only if matching the mean luminance of the background, suggesting that prey, even if patterned, might still reduce predation as long as they reduce their contrast against the background. Indeed, I found that prey that match the mean luminance of the background might become more difficult to track (the thin-striped and the grey prey) if increase their speed of motion or at least the increase in speed did not imply an increased predatory risk (the wide-striped prey). On the other hand an increase in speed for prey that do not match the mean luminance of the background, i.e. the black prey, could implicate an increase in detectability. Previous studies did report that *S.lineola* tracking rate towards moving stimuli increased as the contrast against the background increase, however those studies investigated how the two factors, i.e. prey luminance contrast against the background and speed, affected the predator' response separately but not combined together (Prete 1993; Prete et al. 2002; Prete et al. 2013). Similarly, my results suggest that luminance is a salient cue used by praying mantids to detect their prey.

It is important to highlight that the flicker fusion effect exploits the limits of predator' visual acuity, i.e. the predator is physically not able to resolve the pattern, to confer concealment to the prey. Therefore, we can speculate that the effect will

not be susceptible to predator habituation or improvement in detection as, instead, could happen with other strategies prey may use to avoid being recognized or to make predator pursuit harder, e.g. masquerade and motion dazzle (e.g. Stevens et al. 2008; Hughes et al. 2014).

Understanding the interaction between prey pattern features (e.g. spatial frequency and luminance) and prey speed interaction is crucial for understanding how prey pattern and behaviour might co-evolve to help defend prey against predation. My results suggest that striped pattern, for instance, might have a dual function: conspicuous whilst prey stay still and camouflage whilst in motion. Stripes and other patterns with repeating elements, are often found as part of other defensive strategy, such as aposematism or motion dazzle (Cott 1940; Endler 1978; Ruxton et al. 2004). Moreover, comparing to cryptic pattern, stripes and conspicuous pattern can be used by animals to communicate to conspecific, for instance for mating purposes, which will therefore positive select signals easily detectable and recognizable (e.g. Endler 1978). At the same time, as suggested by my results, high contrast pattern can also help to conceal prey when in motion by inducing the flicker fusion effect in their predator' eyes thus decrease probability of being detected. Therefore, the flicker fusion effect might well be one of the reasons why these patterns evolved and we find them today across so many different taxa which remind us, again, the importance of include movement when investigating the efficacy of defensive colorations.

Chapter 6: How speed affects the way in which different prey patterns reduce predation risk

6.1 Abstract

Movement makes prey easily distinguishable from their background. This means that camouflage strategies that hinder detection by predators whilst prey are stationary become ineffective once prey are moving. Recent studies have shown that once prey move, a background matching pattern is readily detectable, and gives no greater antipredator advantage compared to a range of other pattern types. However, moving prey could camouflage themselves through the flicker fusion effect: where the interaction of prey pattern and prey speed enhances prey concealment. Here, I test if prey with a background matching pattern would be more or less detectable whilst moving compared to prey with a high contrast striped pattern which induces a flicker fusion effect in their predator' eyes when travelling at sufficient high speed. By presenting computer-generated prey to praying mantids, I found that whilst all patterned prey were equally visible to the predator when moving slowly, having a background matching pattern was costly for prey at increasing prey speed compared to having a pattern that induced the flicker fusion effect. Taken together, my results demonstrate that speed affects the ways in which different patterns can reduce the chances of predation, and that at certain speeds, the flicker fusion effect might confer greater advantages than a background matching strategy.

6.2 Introduction

Animals have evolved a variety of strategies that allow them to reduce the chances of being detected, identified or captured by their predators. Camouflage strategies, such as masquerade, disruptive coloration or dazzle coloration might help prey deceive visual hunting predators by interfering at any, or all, of this three predation process stage (e.g. (Cott 1940; Niskanen & Mappes 2005; M Stevens & Merilaita 2009; Stevens et al. 2011; Skelhorn 2015)). For instance, prey can increase the chances that they are hidden from predators by having a pattern that resembles the appearance of the microhabitat where they spend the majority of their time, i.e. background matching (Endler 1978; Ruxton et al. 2004). On the other hand, for prey that live in multiple habitats, it could be more advantageous to adopt a background matching pattern that minimizes the predation risk across different backgrounds, i.e. optimal compromise for camouflage (e.g. Merilaita & Dimitrova 2014).

One problem in the study of camouflage is that most studies focus on how prey remain concealed when stationary. However, animals often need to move, to search for mates or a shelter, or to forage. This often involved the need to move across a visually heterogeneous habitat. Prey patterns that confer camouflage whilst they are stationary prove to be not so effective at reducing detection and capture when prey are in motion. For example, prey that match their background need to keep still to avoid being detected (Ioannou and Krause 2009). Once an animal moves, it becomes suddenly visible and reveals its body outline, regardless of whether or not it resembles the background or exhibits a disruptive coloration: these strategies do not confer an anti-predator advantage to moving prey (e.g. Stevens et al. 2011; Hall et al. 2013).

One interesting phenomenon that appears to emerge from studies of camouflaged moving prey, is that uniform grey prey that have the same mean luminance of the background, appear to survive at least as well as any other 'camouflaged' prey type. In computer games with humans 'hunting' computer-generated prey, for example, uniform targets that match the mean luminance of their background prove to be more difficult to capture and more likely to escape human "predators", despite being easily detected and captured whilst stationary (Stevens et al. 2011; Hall et al. 2013). This suggests that being unpatterned but luminance-matching the background may be the most effective defensive strategy for prey that move. This idea is supported by observations of cuttlefish (*Sepia officinalis*), which actively alter their mantle reflectance whilst moving. Although their patterns can be high contrast to help them be concealed on different backgrounds, once moving, they reduce the contrast in their pattern, perhaps to maximize crypsis whilst in motion (Josef et al. 2015).

To date, very few studies that have incorporated motion into the study of defensive coloration, have also explored the role of speed, and if or how prey pattern could elicit different predatory responses if prey are moving faster or slower (e.g. (Blakemore & Snowden 2000; Scott-Samuel et al. 2011; Von Helversen et al. 2013). Some studies appear to show that the appearance of the prey can alter the perception of speed of a moving target. For example, some high contrast patterns are effective in distorting speed perception of a target (as seen by human participants) whilst fast-moving, but not when the targets are moving more slowly (Scott-Samuel et al. 2011). Other studies have shown how the pattern and speed of motion of a target, or the complexity of the background, affects perceived speed, but not detectability (Blakemore & Snowden 2000; Von Helversen et al. 2013).

Whilst these studies suggest that prey with certain patterns may evade capture through the distortion of speed perception, it is not known if speed affects the chances that prey are detected in the first place, either for prey that are conspicuous or cryptic when stationary. However, the visual mechanism of the flicker fusion effect is based on this very interaction between prey pattern and speed of movement, which enables prey to appear differently whilst in motion compared to when they are stationary (Chapter 2). This mechanism provides a way in which moving prey can reduce their chances of being detected by inducing flicker fusion effect in their predator' eyes (see results in Chapter 5).

Whilst I have established that flicker fusion can occur in insect predators (Chapter 5), it is important to establish how increasing speed affects conspicuous patterned prey compared to prey that background match. Therefore, in this study, I investigated how different prey patterns interact with speed to reduce the chances of detection. I specifically asked whether or not, a striped pattern that induced flicker fusion could help hide prey better than a background matching pattern. I presented African lined mantids (*Sphodromantis lineola*) with computer-generated prey that had either a striped or background matching pattern, or had no-pattern at all, i.e. were uniform grey. The striped prey could have either thin or wide stripes (i.e. high or low spatial frequency pattern), whilst the pattern of the background matching prey was a random sample of the textured background against which the prey were moving. All prey moved at one of three different speeds and had the same mean luminance of the textured background.

I first tested if with increasing speed the conspicuously patterned thin-striped prey could induce the flicker fusion effect in mantids' eyes, and become as detectable to the uniform grey prey. I also tested if increasing prey speed caused

different behavioural changes in predators towards background matching prey and prey with the repeating high contrast stripes. I predicted that when slow moving, the two striped prey would be more conspicuous than the background matching prey, since the high contrast stripes of their patterns would excite the predators' motion detectors (Nordstrom et al 2006). However, at higher prey speed, I predicted that the thin-striped prey would be at least as concealed as the background matching prey, since flicker fusion causes these prey to appear uniform grey, which previous studies have shown is the most difficult type of target to track and catch (e.g. Stevens et al. 2008; Hughes et al. 2014)

6.3 Methods

The general methodology followed that of a previous experiment presented in Chapter 5 (see Chapters 5 four details of housing and experimental set-up). In this experiment I used six adult female African praying mantids (*Sphodromantis lineola*).

6.3.1 Computer-generated prey

Computer-generated prey were programmed and rendered using Psychophysics Toolbox 3 for Matlab (Mathworks). A prey presentation consisted of a rectangle (dimension: 1.6 × 1.0 cm, corresponding to 64 × 30 pixels) moving horizontally across the screen, either from left to right or vice versa (equal numbers of each occurred in both directions in a randomised sequence). To test my predictions, I presented praying mantids with five different prey types (Figure 16): wide-striped, thin-striped (striped prey mean luminance was 0.5), background matching (mean luminance was 0.5), uniform grey (luminance was 0.5) and uniform black (luminance was 0). The patterns of the striped prey were square black-and-

white wave gratings that were perpendicular to the prey movement vector. The patterns either contained two or four wave cycles for the wide-striped and the thin-striped prey, respectively. To ensure that the edges of the striped prey had the same mean luminance and that the entire length of the target stimuli was distinguishable by the mantises, the pattern in each striped prey was shifted such that both vertical edges were black (Figure 16). The pattern of the background matching prey consisted of a sample of the background pattern, randomly generated for every prey presentation.

Prey moved against a textured background, uniquely generated for each presentation using Matlab, which had luminance in the range 0 to 1, mean luminance was 0.5, and a $1/f$ spatial frequency spectrum resembling that of natural backgrounds.

All five prey types were tested at three speeds: 37, 74 and 145 deg/sec, corresponding respectively to 129, 259 and 501 px/sec. During one experiment all the conditions tested were rendered 10 times, with the repetition of each condition occurring randomly during the experiment.

The tested prey, except for the black prey, had the same mean luminance as the background (0.5; contrast levels defined as Michelson contrast) in order to exclude that mantids could rely on luminance cues to detect them. Because I expected low response rates for patterned and grey prey if camouflaged, I also presented uniform black prey to ensure that mantids were responsive during the test experiment: if mantids responded to the black prey on at least 50% of the presentations, I used the experimental data for my further analysis.

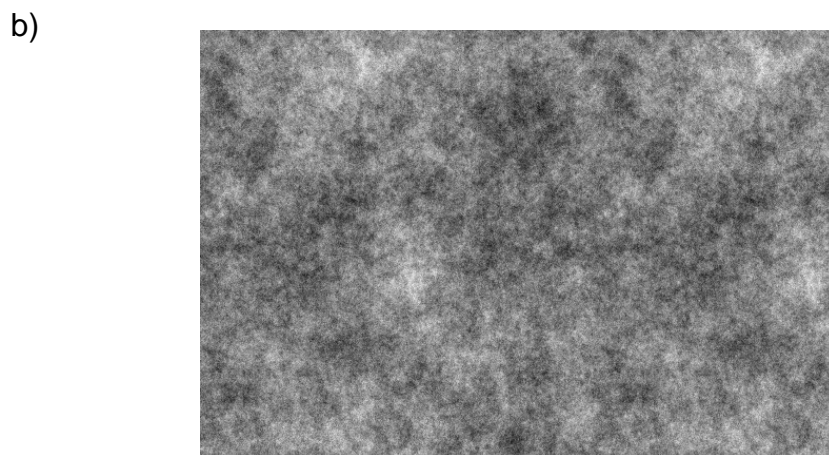
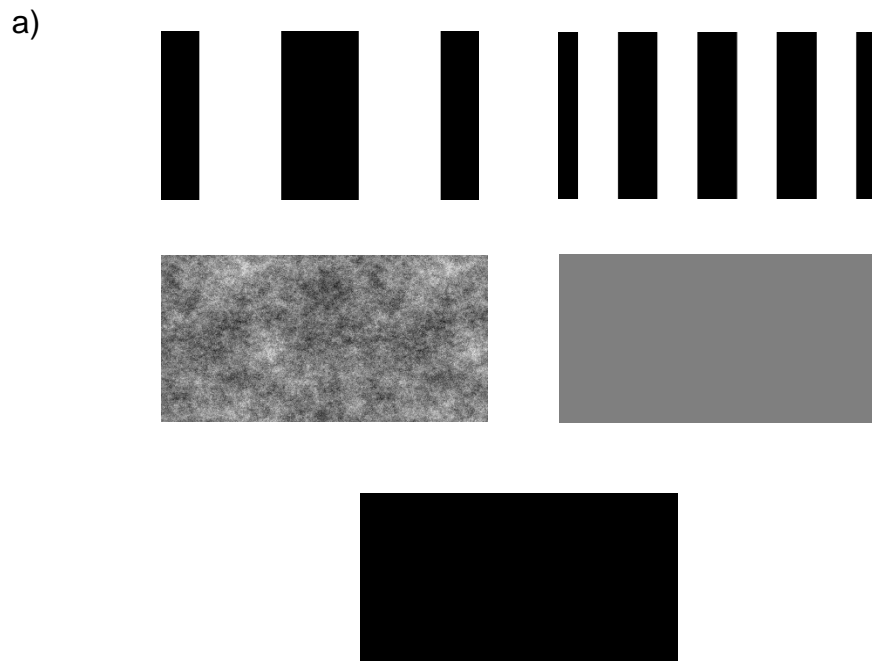


Figure 16 Examples of stimuli used in the experiment. A) the five prey types: wide-striped (top left), thin-striped prey (top right), background matching (middle left), grey (middle right), and black (bottom). B) An example textured background.

The tracking behaviour towards thin-striped prey in a previous experiment was lower than that predicted from their contrast sensitivity function based on behavioural data (see Chapter 5; Nityananda et al. 2015). This suggests that perhaps mantises found it difficult to resolve the spatio-temporal temporal combination of that pattern, even at lower speeds. This is supported by data from a recent experiment which found that the small target motion detection pathway of African praying mantids might have a lower sensitivity compared to the wide-field motion detection (Jones 2016). Therefore, I further developed the model of mantis vision for making predictions for small targets for this experiment.

As previously defined (Chapter 2), the threshold of flicker fusion is the highest temporal frequency (TF) at which a pattern having a given spatial frequency (SF) is visible. This value vary with pattern internal contrast levels, thus as pattern contrast increases the spatio-temporal frequencies the predator can resolve increase as well. Given a striped prey moving at a certain speed, a predator will be able to resolve its pattern if it has an internal contrast equal or above the contrast threshold specific for that pattern spatio-temporal features. The contrast threshold (C_{thresh}) is defined in psychophysics as the minimum contrast needed to obtain a fixed level of response from the observer and is described by:

$$\log_{10} C_{\text{thresh}} = c_{\text{TF}} \text{TF} + c_{\text{SF}} \text{SF} - c_0 - c_1 \log_{10} I$$

where I is the retinal illuminance (measured in Trolands) and the four parameters c_{TF} , c_{SF} , c_0 , c_1 describe the vision of the observer (Watson & Ahumada 2016). In our predator-prey contest, c_{TF} describe how predator sensitivity declines as a function of prey pattern temporal frequency, therefore, predators having higher CFF (critical flicker fusion frequency) will have lower c_{TF} . The parameter c_{SF} describe again how predator sensitivity declines for increasing spatial frequency of prey pattern, thus

predator with low c_{SF} will have better spatial acuity and be able to resolve finer details. Finally c_0 reflects the peak of sensitivity, predators with higher c_0 have more sensitive vision and c_1 describes their sensitivity benefits from the light conditions, thus predators with higher c_1 will benefit more from high illumination, i.e. their acuity increase more than what expected by a predator with low c_1 .

By defining the contrast threshold as the contrast needed to get mantids detect the black-and-white stimulus on half of trials, we obtain $C_{thresh}=1$, $\log_{10}C_{thresh}=0$. Being CFF the maximum temporal frequency ever visible to mantids and A_c the maximum spatial frequency that mantids compound eyes can resolve, we can rewrite the previous equation to obtain the maximum resolvable temporal frequency (TFF) given a pattern having a defined spatial frequency (SF):

$$TFF = CFF (1 - SF / A_c).$$

Based on Nityananda et al. (2015) data for *S. lineola* optomotor response, the estimated CFF is equal to 50 Hz and A_c equal to 0.25 cycle/degree for this species. The threshold for flicker fusion, thereby, will be:

$$TFF = 50 - 200 * (SF)$$

(Umeton, Rowe and Read, unpublished data). I will use this estimation to predict if a prey pattern having a certain spatial frequency, will produce a temporal frequency that exceed or not the TFF once the prey moves at certain speed.

Therefore, I design the spatio-temporal features of the striped prey in a way that would help me test the flicker fusion hypothesis on the basis of this estimation. The spatial frequency of the striped prey were 0.05 cycle/deg for the wide-striped prey and 0.1 cycle/deg for the thin-striped prey. The temporal frequencies whilst moving at the three speed are indicated in Table 5, and calculated as:

$$TF [Hz] = Speed[px/sec] \times SF[cycle/px]$$

Table 5 Temporal frequencies of the striped prey tested

Prey	Speed (deg/sec)	Speed (px/sec)	SF (cycle/deg)	SF (cycle/px)	TF (Hz)
wide-striped	37	129	0.05	1/32	4
wide-striped	75	259	0.05	1/32	8.1
wide-striped	145	501	0.05	1/32	15.7
thin-striped	37	129	0.1	1/16	8
thin-striped	75	259	0.1	1/16	16.2
thin-striped	145	501	0.1	1/16	31.3

Now, I expected that mantids would resolve the pattern of wide-striped prey, i.e. 0.05 cycle/deg, would be visible by mantids whilst prey move at any given speed because producing temporal frequencies far below mantids TFF (TFF for 0.05 spatial frequency is equal to 40 Hz). On the other hand, the pattern of the thin-striped prey should be resolvable by mantids whilst the prey move at 37 deg/sec, but it should fully blur once the prey move at the highest speed, i.e. 145 deg/sec, because producing a temporal frequency, 31.3 Hz, that exceed mantids threshold frequency for that spatial frequency pattern (TFF for 0.1 spatial frequency is equal to 30 Hz). Because the blurring effect is not abrupt but is a continuum process that starts even before a pattern reaches the thresholds, I expect that the thin-striped prey pattern would possibly appear less defined even whilst the prey move at 74 deg/sec.

6.3.2 Experimental procedure

The experimental procedure followed that described in Chapter 5. Once an individual mantids was positioned on the viewing platform, it was left to acclimatize

for 10 minutes. After that, the alignment stimulus was rendered and the first prey presentation was initiated. Each animal received 150 prey presentations in a single block, where each prey type was presented 10 times at each speed. Presentations were separated by variable inter-stimulus intervals (from 15 to 90 seconds) and were presented in randomized order. Animals that stopped responding or left the viewing platform, for any reason, were returned to their housing box for a minimum of 30 minutes before being replaced on the platform.

6.3.3 Data analysis

During the experiment, I observed mantis behaviour blind to the stimuli being shown on the screen, and recorded whether or not the animal performed tracking behaviour. I tested my predictions by analysing the number of presentations in which tracking occurred with generalized estimating equations (GEE) using a binary logistic model. Statistical analyses were carried out using SPSS v23.

6.4 Results

My first prediction was that both wide- and thin-striped prey would be equally visible to mantids whilst moving at 37 deg/sec. However, I expected the thin-striped prey to induce the flicker fusion effect in mantids' eyes whilst moving at the highest speed, i.e. 145 deg/sec, and, therefore, to be tracked less than the wide-striped prey: the thin-striped prey pattern would appear blurred and be harder to see comparing to the distinguishable black-and-white pattern of the wide-striped prey. To test this, I conducted a GEE on the tracking responses towards the striped prey across all speeds, with stripes width and prey speed as factors in the full factorial model. There

were a nearly significant interaction between prey stripes width and prey speed (GEE, $\chi^2_2 = 5,8$, $P=0.052$; stripes width $\chi^2_1 = 21,5$, $P<0.001$; prey speed $\chi^2_2 = 120$, $P<0.001$, Figure 17a). Indeed, when I compared the tracking rate towards the two striped prey at different speed I found that both prey were equally tracked when moving at the lowest speed, i.e. 37 deg/sec (GEE, $\chi^2_5 = 114,1$ *post hoc* $P=192$); whilst the thin-striped prey was tracked less than the wide-one both at medium, i.e. 74 deg/sec (GEE, $\chi^2_5 = 114,1$ *post hoc* $P<0.001$), and at fast speed, i.e. 145 deg/sec (GEE, $\chi^2_5 = 114,1$ *post hoc* $P=0.005$).

The observed decrease in tracking rate towards the thin-striped prey that were moving at increasing speed, i.e. 74 and 145 deg/sec, suggested that perhaps the prey were inducing flicker fusion effect in mantids' eyes. If this was the case the thin-striped prey would be tracked as they were uniformly grey patterned. To test this hypothesis, I conducted a GEE on mantids' responses towards the thin-striped and the grey prey indicating pattern type and prey speed as factors in the factorial model. I found a significant interaction of the two factors (GEE, $\chi^2_2 = 23,7$, $P<0.001$; main effect of prey speed $\chi^2_2 = 47,43$, $P<0.001$; no effect of prey pattern $\chi^2_1 = 2,7$, $P=0.099$); Figure 17b). Indeed, when comparing the response towards this prey at different speed I found that the thin-striped prey were tracked more often than the grey prey when moving at 37 deg/sec (GEE, $\chi^2_5 = 179,8$ *post hoc* $P=0.004$), whilst the two prey were equally tracked whilst moving at higher speed (GEE; 74 deg/sec: $\chi^2_5 = 179,8$ *post hoc* $P=0.295$; 145 deg/sec: $\chi^2_5 = 179,8$ *post hoc* $P=0.460$). This comparison suggest that, whilst the thin-striped prey were moving at fast speed, mantids were

not able to resolve their pattern which became as hard to track as if the prey were uniform grey.

This study aimed to test if through the flicker fusion effect, striped prey can achieve similar or greater anti-predator advantages compared to background matching camouflaged prey. Therefore, I compared mantids' responses towards the thin-striped and the background matching prey across all prey speed, using a GEE and indicating pattern type and prey speed as factor in the model. Again, there was a significant interaction of speed and pattern type in tracking behavior (GEE, $\chi^2_2=8,6$, $P=0.013$), a significant effect of prey speed (GEE, $\chi^2_2=149,4$, $P<0.001$), and a near-significant effect of prey pattern (GEE, $\chi^2_1=3,7$, $P=0.053$; Figure 17c). When I compare the tracking rates toward this two patterned prey at different speed values, I found that the thin-striped prey and the background matching prey (BM) were equally visible whilst moving at slow speed, i.e. 37 deg/sec (GEE, $\chi^2_5=271$, *post hoc* $P=0.445$). Interestingly, I found that at increasing speed the thin-striped prey were tracked significantly less than the background matching prey both at 74 deg/sec (GEE, $\chi^2_5=271$, *post hoc* $P=0.006$) and 145 deg/sec (GEE, $\chi^2_5=271$, *post hoc* $P=0.033$).

When I analysed the tracking responses towards the uniform black prey, indicating prey speed as main factor I found that an increase in speed did not affect the delectability for this prey (GEE, $\chi^2_1=0,1$, $P=0.751$) conversely to what I found in my previous study (Chapter 5). However, this might be due to the small number of animals tested during this study, which means that each prey-speed condition has been tested 60 times across the six individual, i.e. half comparing to the previous study. On the other hand, from the GEE analysis of the tracking rate towards the

other prey, analysing all prey type together and using speed as main factor in the model, I found that mantids' tracking response towards prey that were isoluminant with the background decreased at increasing speed (GEE $\chi^2_2 = 153,4$, $P < 0.001$). This result is consistent with previous findings, although here for each isoluminant-prey and speed combination I could rely on 240 repetitions across the six animals tested.

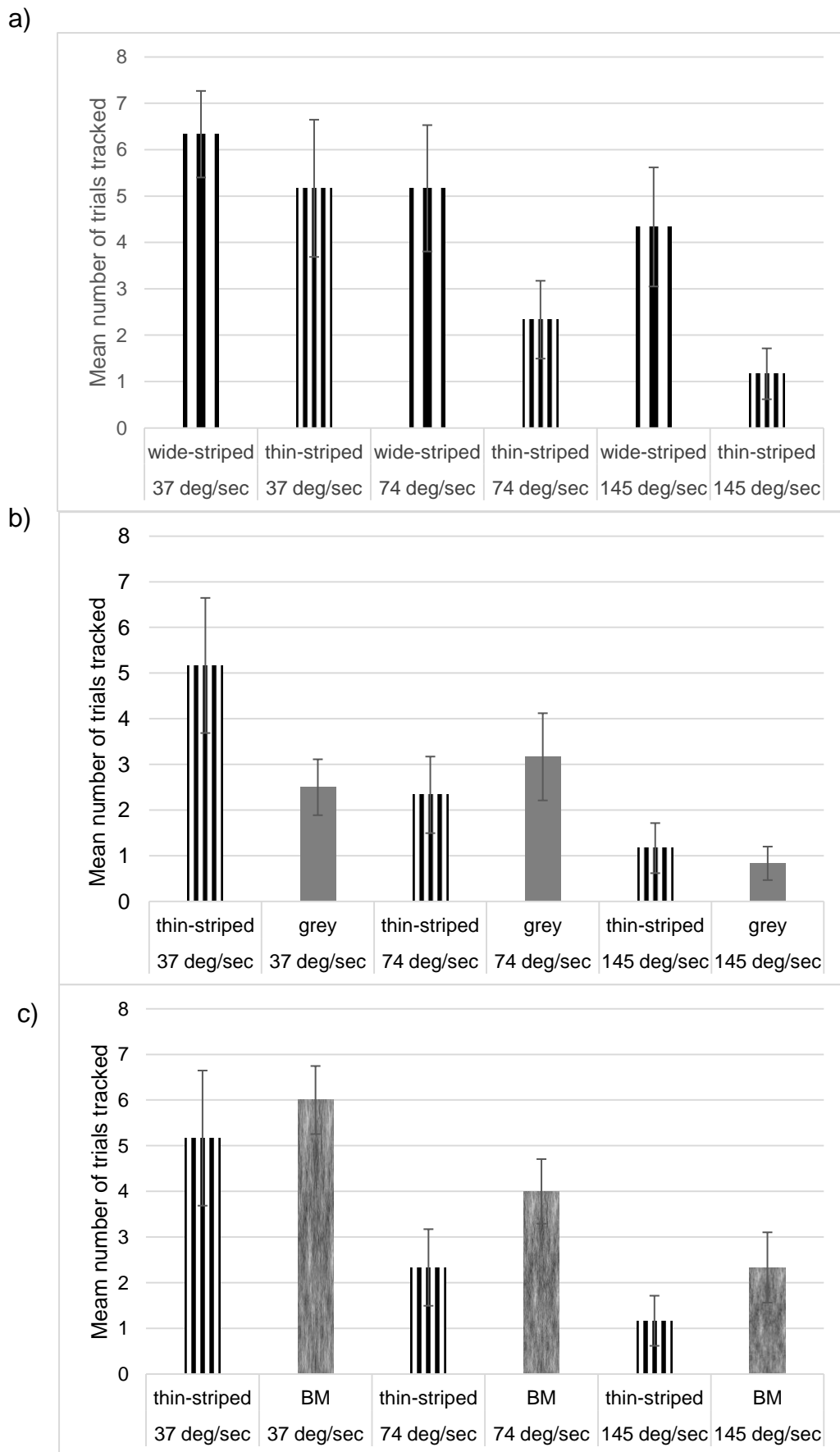


Figure 17 Mean number (\pm s.e.) of trials the mantises tracked each prey type at each speed out of 10 repetitions per condition (N=6)

6.5 Discussion

Taken together, my results show that speed differentially affects the ways in which different prey patterns reduce detection rates. Crucially, I found that background matching and high-contrast striped prey were equally tracked by mantises at the slowest speed (37 deg/sec), but at the two higher speeds (74 and 145 deg/sec) the thin-striped prey were tracked less often than background matching prey and the wide-striped prey. The reason behind this result, is that the striped prey with thin stripes, i.e. high spatial frequency pattern, by inducing flicker fusion effect in mantids' eyes were probably appearing as if they were uniformly grey coloured. Indeed, I found that whilst moving at 74 and 145 deg/sec the thin-striped prey and the grey prey were equally detected by mantids. My results support the idea that stripes can be advantageous for moving prey if the prey move at sufficient speed that they evoke a flicker fusion effect in their predators' eyes.

Indeed, not all the striped prey were effective in induce flicker fusion effect and result camouflaged. The wide-striped prey were detected by mantids more than the thin-striped and the background matching prey, even whilst moving at the highest speed, i.e. 145 deg/sec, as their pattern was resolvable by mantids and result conspicuous against the background, although also the tracking rate towards this prey decreased with increasing speed. This result confirms that the occurrence of flicker fusion effect depends on the interaction of the pattern spatial features and the speed at which the prey moves (see Chapters 2 and 5).

Accordingly to my calculations to estimate the threshold for flicker fusion (TFF) in this species of mantid, I expected that the pattern of the thin-striped prey would only appear completely blurred and grey to the predator once the prey were moving at the highest speed, 145 deg/sec. However, I found that the thin-striped

prey and the grey prey were tracked at the same rate even whilst moving at 74 deg/sec, suggesting that perhaps the pattern of the thin-striped prey may have appeared blurred already. If this was the case, it could be due to the size of the prey. My calculations were based upon wide-field stimuli rather than small targets, but perhaps the flicker fusion effect occurs at lower temporal frequencies for smaller than larger objects. For example, perhaps a smaller stimulus will excite fewer photoreceptors compared to bigger stimuli, and an observer will have less information to rely on when computing the visual task with accuracy.

Previous research using human participants catching targets in computer-game set-up, showed that whilst when stationary background matching target were the hardest to catch and most missed comparing to patterned or no-patterned ones (i.e. striped and uniform grey), once targets were in motion this camouflage strategy results ineffective but not necessarily costly (Stevens et al. 2011; Hall et al. 2013). Here, instead, I found that as prey speed increases it become increasingly costly for a prey to match the texture of the background relative to prey that had no pattern or that appeared uniform by inducing the flicker fusion effect. A possible explanation of why we observe so is because by reducing internal contrast the latter prey, i.e. grey and thin-striped, excite less the predator' small target motion detectors neurons, which are extremely sensitive to contrast (Nordström et al. 2006).

Is important to highlight that my study differs from previous studies of movement and camouflage since I have measured detection rate as opposed to capture rates (Stevens et al. 2011; Hall et al. 2013) or the latencies to attack (Hughes et al. 2014). Whilst these measures are certainly valuable, they do not allow detection to be measured independently of capture success. Therefore, for example, when grey prey are captured less often than other types of patterned prey, it is

impossible to know if this is because it is more difficult to detect that target, or if it is harder to follow grey prey along a path or assess its speed (or perhaps both). It is important to be able to disassociate these two things in order to know the mechanism, i.e. is a moving patterned prey better concealed or is the motion that is camouflaged? In my study, by recording mantids' tracking behaviour, I can demonstrate that pattern and speed can help prey reduce the chances of predation in the very first step of the predation process, i.e. in the detection stage. Therefore, the antipredator advantages I observed here for certain prey pattern-speed combinations are not due to prey being harder to follow and/or capture, or prey speed being misjudged (as suggested for motion dazzle), but result from prey being better concealed.

This study is, to my knowledge, the first empirical test that investigates how motion affects camouflage and detection across different prey speeds using a natural predator: all previous studies have used humans capturing targets presented on touchscreens (e.g. Stevens et al. 2011; Hall et al. 2013; Hughes et al. 2014). Certainly, for prey which pattern match the mean feature of the background, i.e. luminance, there is an advantage in moving faster, whilst this might not be true for prey that have higher contrast against their background, i.e. the black prey, which instead could be equally detectable regardless their speed, or perhaps more visible (see Chapter 5). However, my findings show that even for prey that match the mean luminance of the background, speed of motion plays an important role in camouflage, and interacts differently with different patterns to enhance prey survival.

This crucial interaction has implications for the evolution of prey defences, indeed, prey that need to move will gain survival advantages exhibiting one or another pattern depending on the speed at which they move. In fact, whilst

movement breaks the camouflage conferred by certain pattern, e.g. background matching, on the other hand it can enhance concealment or confer it to prey that exhibit other patterns, i.e. grey and striped respectively, if combined with the appropriate the speed of motion.

My findings are timely with an increasing interest in understanding what patterns prey should have to better defend themselves whilst moving. In particular, one of the big questions is whether or not any pattern can confer a survival advantage, and if so, how it could do so, i.e. which perceptual mechanism could it exploit (e.g. Kelley & Kelley 2014). My study highlights that to test if a prey can be camouflaged whilst moving, it is necessary to test prediction about how the speed of motion affect its defences.

Chapter 7: General discussion and conclusions

7.1 Review of thesis' aim

“When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, and the black-grouse that of peaty earth, we must believe that these tints are of service to these birds and insects in preserving them from danger.”

Darwin wrote this passage over 150 years ago, recognising the importance of camouflage for prey survival (Darwin 1859). Since then, researchers have been fascinated by the incredible variety of animal colour patterns, and wondered if and how some patterns might be able to help reduce predation. Whilst the antipredator function of animal patterns have been largely investigated using stationary prey (e.g. Ruxton et al. 2004), researchers now face the challenge of understanding how those patterns interact with movement. Many animals need to move around their environment in their search for resources, and it is important to understand how that impacts on the defensive coloration strategies.

In this thesis, I attempted to fill some of the gaps in our knowledge relating to the interaction of movement speed and colour pattern. Specifically, I aimed to review an old, but poorly investigated, hypothesis that prey can be camouflaged whilst in motion by inducing a flicker fusion effect in their predators' eyes. Therefore, I empirically tested the putative concealing function of the flicker fusion effect using praying mantids tracking computer-generated prey. I also investigated more generally, how speed of motion affects the camouflage efficacy of different prey patterns. Using mantids as model predators to test the defensive function of the

flicker fusion opens up novel perspectives and avenues for future research. In particular, since insects' visual systems are extremely sensitive to motion (O'Carroll et al. 1996), it will be fascinating to explore how patterns could camouflage prey from an insect predator's perspective.

7.2 Speed affects prey detection differently according to prey pattern

Movement itself is conspicuous, and reveals animals' body outlines. Therefore, even patterns that help prey hide when they remain still are ineffective when it comes to moving (e.g. Hall et al. 2013). Moreover, a commonly accepted principle is that a pattern that is conspicuous when the animal is stationary, will be even more conspicuous when it moves (Cott 1940). My results (Chapters 5 and 6) demonstrate that this is not the case: contrary to expectation, high contrast patterns, which are conspicuous whilst the animal is stationary (e.g. Stevens et al. 2011), can confer concealment to a prey when it moves by inducing flicker fusion effect in their predators' eyes.

Moreover because several factors can affect whether or not flicker fusion effect might occur, the illusion is likely to be more widespread across taxa and prevalent than what previously expected (as reviewed in Chapter 2). For instance, I tested the extreme case of prey having black-and-white stripes, the highest internal contrast that exists. However, prey might have stripes having chromatic but not necessarily brightness contrast. A reduced contrast between pattern elements will promote the occurrence of the illusion. Additionally, all other things being equal, i.e. pattern contrast and spatial features, smaller prey might induce the flicker fusion effect in their predators at lower body speed compared to larger prey. Indeed, my

results suggest (Chapters 5 and 6) that the maximum temporal frequency a predator can resolve vary accordingly with pattern spatial features and the size of the prey. Moreover, certain viewing condition might particularly facilitate the occurrence of the illusion, as pattern details of a prey will become gradually less resolvable with increasing distance from it. Sunset and sunrise, the habitats under forest canopy or in the depth see, are all contexts characterized by low light level, which again is a condition that increases the chances that an animal will appear differently whilst moving through flicker fusion effect. Therefore, the efficacy of the camouflage depends as much on the visual appearance of the prey and of its surrounding, e.g. luminance contrast against the background or environment light conditions, as on the visual acuity of the predator.

Overall, my study highlights the crucial role of luminance for prey detection. In visual science is well known that motion detectors are extremely sensitive to luminance contrast (Watson & Ahumada 2016). However, behavioural ecologist are have only recently start to empirically investigate what are the implications for the evolution of pattern that might defend a prey whilst in motion (e.g. Stevens et al. 2011; Hughes et al. 2014). Appearing differently whilst in motion in order to enhance crypsis was thought to be exclusive to those species capable of dynamic camouflage, i.e. those which can actively produce a camouflage pattern (Hanlon 2007). Despite conferring camouflage advantages against a wide range of backgrounds, the strategy of rapidly changing appearance might, however, be physiologically and phylogenetically constrained; indeed dynamic camouflage does appear to be restricted to just two taxa, Cephalopoda and Chamaeleonidae (e.g. Zylinski et al. 2009). On the other hand, by simply combining pattern spatial features

and speed of motion, an animal can alter how it is perceived by a predator, allowing it to be concealed in motion if it better matches its background.

Measuring the efficacy of the flicker fusion effect can help us understand how it might have evolved and how conspicuous animal patterns might have been selected by predators. Moreover, animal coloration results from a number of selection pressures and it can enable an animal to signal across different contexts, e.g. in courtship or other social interactions, and to different receivers, predators or conspecifics; therefore repeating pattern might serve other functions. A conspicuous and repeating pattern often increases the chances that a signal will be received, for example, in the context of attracting mates or intimidating rivals (e.g. Swaddle & Cuthill 1994; Roulin et al. 2010; Gluckman & Cardoso 2010). Additionally, as Endler reported, courtship or mating behaviour often include unusual movement different from locomotion or fleeing movements (Endler 1978). Taken together this evidences suggest that an additional advantage for animals that exhibit pattern with repeating elements could thus be that it would enable them camouflage whilst fleeing by flicker fusion effect, and at the same time communicate in other context or to other predators. Indeed, aposematic colorations, which are known to be visual signals directed to would-be predators, are often combined with regular patterns that might enhance predator learning. For instance, blue tits (*Cyanistes caeruleus*) learn about unprofitable prey faster if their pattern has regular stripes comparing to prey having other type of patterns (Aronsson & Gamberale-Stille 2013); although colour seems to be still the primary cue birds attend to when learning a warning signal (Aronsson & Gamberale-Stille 2008). Therefore, we can indulge in some conjecture about the double antipredator function of striped, or regular, patterns: signalling defences to

susceptible predators, and camouflage whilst fleeing from less-susceptible predators.

Throughout my thesis, I have highlighted the fact that camouflage whilst in motion results from combining a certain pattern with an appropriate movement, in this case, speed of motion. However, is it not clear whether the pattern or the movement evolved first, or whether the two components of the effect have been selected together. During the mating season of some snake species of the genus *Vipera* has been observed a male dichromatism, which suggest that perhaps the striped pattern could have evolved as sexual dimorphism, enabling individual to convey information about quality, and later maintained and even spread to both sexes in other species (Lindell & Forsman 1996). However the evolutionary dynamic of some morphology trait saw them to be genetically associated with behavioural one, as it was found for the anti-predator behaviour and coloration of the garter snake (*Thamnophis ordinoides*) which two traits are genetically inter-dependent (Brodie 1992). Similarly, in their recent comparative study, Allen et al. found that the dorsal patterns of snakes is strongly related to their behaviour, particularly antipredator behaviour, rather than to their habitat type(Allen et al. 2013). These findings suggest that even if appearance and behaviour did not evolved together, the two traits might have now become coupled.

7.3 Variability of species visual acuity and the consequences for prey defences

Eye morphology is closely related to eye function (Land & Nilsson 2012; Dial et al. 2008). In my first study (Chapter 4), I aimed to understand if mantids with different eye morphology differed in their visual acuity, and as a consequence, could

exert different selection pressures on their preys' coloration patterns. Mantids were an ideal model, with being voracious predators with variable eye morphology, and where their attack behaviour is strongly visually guided (e.g. Prakash 2010; Prete et al. 1990; Nityananda et al. 2016). These predatory group are widespread and commonly found, and consequently, are likely to exert strong selection on their prey's visual appearance.

In addition, a comparative study has found that the morphological differences found across different species of praying mantis appear to be strongly related to their habitat type, rather than phylogeny (Svenson & Whiting 2009). This suggests that that their morphology might have been shaped to accomplish a specific function relating to their environmental conditions. Therefore, I wanted to ask if praying mantids with different eye morphology differed in the ways in which they see their environment and prey?

To answer this question, I choose four species of praying mantids that differed in their eye shape and investigated their acuity. My statistical model fail to find any significant differences in visual acuity across species, however, this could be due to a number of reasons (see next paragraph). However, the sensitivity to moving grating stimuli having low internal contrast (i.e. 0.25 contrast in Figure 8, Chapter 4) it seems to vary across species, at least at first sight. This result, might subtend finer differences in contrast sensitivity across species. We can indeed hypothesize that species adapted to open and bright light habitats, as it could be the case of *Sibylla pretiosa* and *Creobroter gemmatus*, might not need to have a high sensitivity to low contrast visual stimuli. On the other hand species like *Phyllocrania paradoxa* and *Sphodromantis lineola*, living under the forest canopy or in the bushes might need better sensitivity to detect and catch their prey under lower light conditions

comparing to the one in which the other species are active. As previously mentioned, prey pattern internal contrast and contrast against their background can be a crucial cue predators use for detect their prey. This means that predators with low contrast sensitivity will have different probability to resolve their prey pattern or spot them against the background, and their prey will have greater chances to induce flicker fusion in their eyes, for instance. Therefore, if there were differences in predator' contrast sensitivity this could affect how they would select the design of prey denfeces. Moreover, investigating species' visual acuity can certainly give us valuable information about the visual patterns that an animal can or can not resolve, however, it does not tell us if the animal will classify that visual stimulus as a potential prey or not. Indeed, previous studies have found that species of praying mantids exhibit different predatory responses to different target stimuli, which might reflect some sorts of prey preferences but not necessarily visual acuity differences (e.g.Prete et al. 2011). Therefore, investigating the visual acuities of morphologically different species in relation to their predatory behaviour, will still be a fruitful research path to follow.

Lastly, if differences in eye morphology are not related to visual acuity, then what are the selective factors that shaped praying mantids' eyes? This is certainly a challenging question to answer having only fragmented information about species' ecology. However, as predators, praying mantids need to detect prey that are trying to hide from them, as well as they ensuring that they are camouflaged against their prey and their own predators too. Indeed, some model species seem to resemble a leaf or flower, and surely be able to avoid their own predators might also have being an important selective pressure. This offers the possibility to investigate if their

camouflage might have a potential dual function, aggressive and defensive, of not being detected by would-be prey nor by would-be predators.

7.4 Limitations of the empirical work

As in any study, there are limitations to the empirical studies presented in this thesis. The first is that the sample sizes did not always allow robust conclusions to be made. However, there were time constraints and difficulties in sourcing the animals, which meant that the numbers of animals were low, both for studies within and across species. In particular, small sample sizes might contribute to why there was no significant interaction between stripes and speed in my first test of flicker fusion (Chapter 5). Small sample sizes might account for some lack of replication between the studies presented in Chapters 5 and 6, and is something that could be improved upon in future work. Finally, the time constraint was enhanced by the need of carry out multiple pilot studies before address the kind of set-up, stimuli and experimental procedure that could give the best responsiveness in the animals. Contrary to other studies (e.g. Nityananda et al. 2016), for my study the animals were not immobilized or mutilated (e.g. with cut wings), but free to move: this was my specific choice and not a requirement, however, it did increase the time needed to complete the experiments.

When it came to comparing visual acuities across species, having small sample sizes was not my only challenge. In order to properly understand the variability in eyes across mantids, I would have ideally liked to have been able to measure the interommatidial angles and the rhabdomen structure in each species. This would have given me a better understanding of the visual acuity of each

species, and allowed me to make clearer predictions about how these predators see the world. Similarly, measure the visual field of each species would have add information about how different eye morphologies affect the binocular overlap and the amplitude of each animal field of view. However, historical methods to obtain such measurements not wholly accurate (e.g. Seidl & Kaiser 1981),), and only recently have researchers begun to develop and implement new techniques (e.g. Gonzalez-Bellido et al. 2011; Bergman & Rutowski 2016). However, given this limitation, I was able to explore the range of temporal and spatial frequencies each species could resolve through behavioural experiments. This is an important step in understanding how the visual systems of different predators could select differently on prey patterns.

Despite my prediction about when flicker fusion would occur for striped prey, I found that both in my second and third study (i.e. Chapters 5 and 6), the tracking rate towards the striped prey was equal to the tracking rate towards the grey prey at prey speed lower than what expected. This results suggest that perhaps the stripes were already perceived as blurred and mantids were unable to resolve the striped pattern even whilst producing a temporal frequency far from be above the TFF. This outcome could be attributable to the size of the prey stimuli: recent study suggest praying mantids spatio-temporal sensitivity decrease for small targets (Jones, 2016), however the reasons of why this occur are still unclear. Therefore, whilst the observed results are not completely in line with my prediction, to my point of view this outcome could be a starting point for fruitful further investigations rather than a limitation.

Despite those limitations, I think that my thesis makes an important contribution to what we know about how praying mantids see the world, and the

ways in which predators detect moving prey. In particular, my work reviews current perspectives on flicker fusion, and provides the first empirical evidence that the flicker fusion effect can confer concealment to moving prey using natural predators. I think that this is an important step in developing research into how the speed of motion affects the detection of prey with different patterns.

7.5 Future work

The aim of my thesis was to explore how movement affects prey camouflage, and whether or not certain prey patterns might confer concealment or enhance camouflage if prey were travelling at an appropriate speed. Whilst my empirical work was the first to test if the flicker fusion effect could help to conceal prey whilst moving, I only tested one of the several putative antipredator functions that the effect might have. A future challenge would certainly be to test whether flicker fusion effect might exploit predators' visual limits and confer protection to prey in different ways, for example, hiding the final resting position of the prey or deterring the predator.

For my study I investigated the efficacy of flicker fusion effect only against one predator species. However, previous researcher have highlight that the efficacy of aposematic coloration, for instance (e.g. Fabricant & Smith 2014), vary accordingly to the predator against which the prey is presented. Therefore, a certainly intrigues future researches field would be investigate whether prey could modulate their fleeing speed to induce flicker fusion effect in a broader range of relevant predators. A comparative study similarly designed might also help researchers to understand whether or not flicker fusion effect can have different function and if those are or not mutually exclusive.

In future, a more comprehensive study of praying mantids' visual acuity combined with behavioural experiments and information about their ecology would certainly help us unveil whether or not predation is the factor driving such diverse eye morphology. In future, it might be possible to combine this study with the investigation if praying mantids use other perceptual cue to select their prey and if different species are likely to exert different selective pressure on their prey based on other sensory modalities. Researchers found, for instance, that aversion towards bitter taste vary with gender in the praying mantids *Tenodera aridifolia* (Carle et al. 2015), which suggest that males and females might show different aversions towards toxic and unprofitable prey. Moreover, we can't exclude that there could be a trade-off between praying mantids visual and other sensory systems.

Lastly, the idea of animal camouflage through movement is relatively new and unexplored. Motion can interact with prey appearance in three, not mutually exclusive, ways: (1) by concealing the animal itself, and (2) by concealing its motion or (3) by camouflage both. In the first case where the prey is better camouflaged, movement will reduce the detection or recognition of a patterned prey. One example of this could be stick insects swaying in response to wind, where their movements could help them better blend into their moving background (e.g. Bian et al. 2016). In the second case, the movement of the animal itself can be camouflaged. For example, dragonflies are known to deceive their prey by moving in a way that will make them appear stationary although they are approaching to intercept their prey (e.g. Mizutani et al. 2003). Although this is a predator hiding its attack path to a potential prey, prey can also hide the direction or the speed at which they move. Researchers have suggested that motion dazzle patterns can alter speed perception in humans (e.g. Scott-Samuel et al. 2011), and that these patterns make an observer

misjudge the speed and the direction of moving targets (e.g. Cott 1940). Finally, as mentioned, the third way in which animal motion and appearance can be combined to confer it survival advantages is by camouflaging both the movement and the animal itself. As suggested by my results, a prey can conceal itself whilst by inducing flicker fusion effect in its predator eyes. However, the three functions that motion and appearance can achieve when combine together are, to date, often confuse and even the terminology used in rather disorientating. For instance, the term “motion camouflage” has been broadly use and for different purposes, i.e. camouflage the movement (e.g. Mizutani et al. 2003) and camouflage the animal (e.g. How & Zanker 2014). What it seems urgent is therefore investigate further how animal camouflage works whilst in motion and coin an umbrella term under which the study of camouflage induced by motion and pattern can be grouped.

My research highlights how the field of motion induced camouflage suffer of a lack of clear definitions and profound understanding, but it certainly represent a promising research niche that is still relatively unexplored.

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