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The role of colour and pattern in background matching camouflage

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A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy in the *Faculty of Biological Sciences, School of Biological Sciences*

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Abstract

Camouflage is a phenotypic trait that significantly impacts the likelihood of survival in predators and prey alike. The objective of this thesis is to identify the specific attributes of background-matching camouflage when faced by multiple, differing, backgrounds. Chapter 2 examines the phenomenon of egg camouflage in plovers (Aves: Charadriiformes), utilising colour and texture analysis of calibrated photographs to assess camouflage against beach and saltmarsh habitats. I show that eggs are an excellent colour-match to the subset of backgrounds that are found in both habitats, but the patterning of the maculation makes eggs and backgrounds reliably discriminable at close viewing distances. Chapter 3 focuses on chick camouflage, specifically exploring possible sex differences that might explain higher mortality in female than male chicks. I show that there is no sex difference in plumage colouration but males are found on backgrounds to which they are a better match. Chapter 4 examines camouflage from a different perspective, assessing the discriminability of chicks from different backgrounds using humans as model predators. The results are consistent with the visual modelling of chapter 3, and show that chicks are a better match to mud than vegetated backgrounds, suggesting stronger selection for camouflage against backgrounds where physical hiding is not possible. Chapter 5, moving away from the plovers to ultilise an experimental paradigm of artificial moth-like prey on woodland tree bark, investigates the phenomenon of whether to specialize on a particular background or adopt a camouflage pattern that is a compromise between multiple substrates. I show that matching the average colour of a background is more important than matching the visual texture, but also that a background which has a complex texture is more ‘forgiving’ of mismatches than a texturally simple background.

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Carrying out a PhD is not easy, if other aspects are added to it, such as kilometers from your country, in a place that you do not know with a different culture and far from family, it becomes an even more complicated task. That is why I want to dedicate this small but probably the most significant space, humanly speaking, to all the people who have contributed (be it a grain of sand or a sack) so that everything has come to a satisfactory end.

Obviously starting with my family, from the closest person physically Felipe Sánchez Espinoza, my husband and beloved companion who has been patient with me, has cared for me and loved me as only he could have done, giving me support that I don't know if I will be able to repay him in the same way ever, thanks for everything. To all my family in Chile: my mother Samanda Ojeda Soto, my brothers Felipe and Gustavo, my grandparents María and Gustavo, uncle Gustavo and aunt O, cousin Nicolás and paternal family (Marcos, Jimena, Ayline and Sara), to all of them many thank you for all the love, affection and support that you have given me throughout all my years of life, clearly without all that, my present and future would not be the same, a piece of this thesis is not only dedicated to you, but it is also thanks to you, especially my mother who has always been an example (without wanting to be) of a strong woman.

I also want to thank my tutor professors, Innes Cuthill probably the most capable professor and academic I have ever met, literally always willing to help me with everything, which has been the key to not giving up or feeling unable to complete this PhD. Tamas Székely, thank you for believing in me from the beginning, when I still did not have a clear idea other than knowing that I wanted to continue my path in the academy, thank you for showing me that it is possible to live from the study of birds. Thank you Robert Kelsh for having a patience that perhaps I did not deserve at the beginning and always contributing with ideas and proposals to improve throughout this process.

Lastly, I would like to thank everyone who has been part of my life in recent years, whether outside or inside the academy, and who have been a contribution to my training as a person or professional, whether when I was at school or taking part, for example. of some field work for this thesis, to make an acknowledgment in which I will only mention some names in order not to name them all so as not to make the mistake of leaving someone out of the list, if reading this small space you feel that your name could be here, surely it is because it is so. Some of the people recognized as representing everyone are: Thania Beltrán, Daniel González-Acuña, Lucila Moreno, María Carolina Silva, Karin Bahamonde. I want to express my sincere gratitude to you all. This work was funded by the National Agency for Research and Development (ANID) / Scholarship Program / DOCTORADO BECAS CHILE/2018 – 72190138.

Covid-19 statement

The initial program and concept of the thesis aimed to examine the camouflage and survival strategies of two species of chicks, namely *Charadrius modestus* and *Ch. falklandicus*, during a minimum period of 3-4 years in the Falkland Islands. My plans were disrupted by the travel restrictions imposed by the COVID-19 pandemic. Although I had carried out a pilot field study on Bleaker Island in the Falklands in 2019, travel to the islands was banned just before my first planned full field season, and was still impossible the following year. All borders were either closed or required a mandatory quarantine, making it impossible for me to carry out the remaining field work during the reproductive season in the southern hemisphere. In 2021, it became possible to travel to the Falklands, but you were required to undergo quarantine at designated facilities. The costs associated with these facilities were exorbitant for a student to afford, especially when considering other expenses such as flights, accommodation, and food.

Consequently, I regrettably had to abandon the initial plan. Amidst the uncertainty surrounding global events, my supervisors and I decided to embark on a supplementary project that was not constrained by restrictions on overseas travel and instead involved field experiments using artificial prey in woodlands near to Bristol. While seemingly distinct from our original focus on plover camouflage, it addressed similar questions on how to be camouflaged against multiple backgrounds, and would equip me with valuable skills in image analysis and computation as well as serving as a chapter in my thesis (chapter 5). Once the decision to abandon the plan of conducting research in the Falkland Islands was made, I also then relied on photographs provided by my collaborators to carry out analyses of background matching and also computer experiments with humans as model predators (chapters 3 and 4). In order to ensure that I didn't miss out on the opportunity to gain field work experience, I also arranged for field work in Spain (chapter 2, on camouflage in plover eggs).

While it is true that we managed to resolve successfully most of the issues encountered, all of the aforementioned situations were highly stressful since they required not just minor adjustments to the thesis work, but a substantial overhaul of the techniques and objectives.

Author’s Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author. [redacted]

SIGNED: DATE: 12/12/223

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Chapter One: General Introduction

1.1 The importance of colouration

Apart from physically hiding, camouflage is the main way that animals avoid being detected, either as prey or as predators. Beyond the military context (its first definition), the Oxford English Dictionary states that camouflage is "The natural disguise or concealment of an animal (or its nest or eggs) from predators or prey brought about by colouration, markings, features of shape or behaviour, etc., that make it difficult to distinguish from its surroundings (www.oed.com, accessed 05-10-2023). In this chapter, I place camouflage in the context of other functions of colouration, outline the historical development of influential ideas in the field, then summarise the evidence, both correlational and experimental, for the mechanisms behind camouflage.

The study of camouflage has been historically significant, attracting research interest from various fields, including biologists, psychologists, and computer scientists, among others (Cuthill & Troscianko, 2009). Some of the most active areas of camouflage research integrate the colouration and vision of animals, because 'colour' cannot be understood without reference to the viewer (Endler, 1978; Endler, 1990; Bennett et al., 1994; Merilaita & Stevens, 2011). Colouration has been, and continues to be, a tractable phenotype to investigate because a simple marker such as the presence or absence of melanin (revealed as dark or light colouration) can shed light on topics from genetics and development right through to the ecology and evolution of species (Majerus, 1998; Cuthill et al., 2017). However, when considering patterning, colouration can often be a complex attribute with far-reaching implications for many aspects of an organism's biology. The study of colouration yields important insights into developmental control and pattern formation, evolutionary processes such as sexual selection and speciation, as well as predator-prey interactions, and ecological dynamics (Turing, 1952; Monteiro et al., 1994; Tullberg et al., 2005; Hill, 2006; Jablonski & Chaplin, 2010; Barnett & Cuthill, 2014; Marshall & Stevens, 2014; Cuthill et al., 2017; Brown et al., 2017). Listed below are some of the functions of colour.

a) Camouflage: entails the ability of organisms to merge in with their surroundings or disguise their form, so as to remain undetected, or promoting misidentification through mimicry of irrelevant objects; in both cases thereby protecting themselves from predators (Cuthill, 2019; Stevens & Merilaita, 2009b).

b) Signalling: colouration is essential for intra- and inter-species communication, including mate attraction, courtship displays, and signalling dominance or aggression. It includes sexually selected signals, warning signals, Batesian and Mullerian mimicry, deimatic displays (refer to the behaviour exhibited by prey when they are under attack, when they abruptly deploy surprising defensive mechanisms to intimidate their predators and halt the attack (Umbers et al., 2015), as well as non-sexual social signals as examples. For instance, colouration is frequently subject to sexual selection, in which characteristics that increase reproductive success are favoured. As an example, Endler (1983) showed that female guppies, a small topical fish, tend to favour males with particular colour patterns, indicating that colouration plays a role in mate attraction. Males with brighter, more elaborate colouring had a competitive advantage when attempting to attract partners (Endler, 1983). In terms of warning signals, an organism's bright and conspicuous colouring can serve as a warning signal to potential predators, indicating that it possesses a particular defence mechanism, such as toxins or venom. This concept is known as aposematism, and it is common in many venomous or poisonous species (Ruxton et al., 2018).

c) Non-visual functions: Colour appearance can also be a by-product of functions of the colour-producing pigments or structures that have nothing to do with the appearance itself. For example, thermoregulation, in this non-visual function colour patterns can assist animals in regulating their body temperature (Stuart-Fox & Moussalli, 2009). Usually, it works because black surfaces absorb more solar energy than light surfaces, all other factors being equal (Stuart-Fox et al., 2017). For instance, bearded dragon lizards (*Pogona vitticeps*) change their dorsal colouration to darker at lower temperatures to absorb more heat (Smith et al., 2016). Melanin, the pigment most common in dark browns and blacks, also increases resistance to abrasion (e.g. Bonser, 1995) and bacterial degradation.

As previously mentioned, one of the reasons why colouration is important is because it can influence visual predation. To avoid becoming prey, creatures must first detect the presence of a possible predator, then recognize it as a threat. Animals might detect and recognise predator cues aurally, olfactorily or through other senses (Ruxton, 2009; Grieves et al., 2022), but it is vision that is relevant to this thesis. Visual indicators, such as shape, size, colouration and movement, can provide essential information regarding the identity and even intent of a potential predator (Rosier & Langkilde, 2011). Colour can also act as protection post-detection and recognition, either through facilitating recognition by the predator as potentially dangerous (aposematism or Batesian mimicry) or more generally unprofitable (pursuit-deterrence signals), delay attack through an unexpected display (deimatism), or interfering with targeting during attack (so-called dazzle colouration). These can be viewed as part of a set of defence strategies, 'the survivability onion', that can be employed at successive stages of the predation sequence (Lima & Dill, 1990; Cuthill, 2019).

While the majority of research on defensive colouration concerns species-specific adaptations to particular ecologies or life-histories, colouration can also influence differences in predation rates between sexes. There is a strong tradition of research on sex-differences in colouration in the context of conflicts between sexual and viability selection (e.g. Endler, 1983, 1988). This is because it is often observed (or assumed) that males are more vulnerable to predation due to their more conspicuous colouration (Andersson, 1994; Zuk & Kolluru, 1998), as they are often more brightly coloured than females (Godin & McDonough, 2003). This is added to the fact that males can frequently be more active than females and, as a result, predators are more likely to detect them more easily (Endler, 1983). As an example of the trade-offs between mate attraction and avoiding detection by predators, Kodric-Brown (1984) investigated how female mate preferences for male colouration in guppies have an indirect impact on the survival rates of vividly coloured males. The study revealed that females favour males with more intense colouring, putting these males at a greater risk of predation. As a result, there is a balance between the benefits of attracting partners and the costs of increased visibility to predators. Endler (1992) investigated the function of visual predation in the formation of colouration patterns in guppies (*Poecilia reticulata*). The study revealed that male guppies, with their bright and conspicuous colours, are subjected to a greater predation pressure than females. This difference in predation rates between sexes has led to the evolution of sexually dimorphic colouration, in which males exhibit bright colours to attract mates but also become more visible to predators, however, there has been inconsistent empirical support for this hypothesis (Kemp et al., 2023). In contrast, Pocklington & Dill (1995) discovered that vividly coloured male *P. reticulata* were subject to equal or less predation than dull females. In lizards, population-level differences in colouration have been attributed to variations in predation pressure, which opposes sexual selection (Baird et al., 1997; Macedonia, 2002; Kwiatkowski, 2003; Stuart-Fox & Ord, 2004), despite the fact that these studies used a variety of techniques to estimate predation intensity. Regardless of the significant geographical separation of study sites, a consistent pattern emerged: increased colour contrast between a lizard model and the rocks it was placed on corresponded to a higher incidence of predator attacks. This observation supports the trade-off principle that, while increased conspicuity may have benefits, it also increases the risk of predation.

1.2 The importance of camouflage as a defence against predation

Since it enables creatures to blend in with their surroundings and so reduce detectability, or disguise their true form and so remain unidentified, camouflage is essential to many animal's survival (Merilaita & Stevens, 2011; Diamond & Bond, 2013; Caro, 2014; Cuthill, 2019). Animals that are camouflaged decrease their chance of being discovered or identified as prey, thus improving their odds of surviving and procreating. However, camouflage can also be an effective way for predators to get within striking range of prey, either passively (sit and wait predators) or through stealthy approach (Merilaita & Stevens, 2011; Diamond & Bond, 2013; Caro, 2014; Cuthill, 2019). However, camouflage is not a single strategy or form of colouration; it is a suite of adaptations. Several are commonly grouped together as ‘crypsis’ – strategies to reduce detection or ‘hide in plain sight’ (Sherratt et al., 2005) – while masquerade relies on misidentification as an irrelevant object (Skelhorn et al., 2010b). Currently described camouflage techniques include the following:

a) One of the most prevalent varieties of animal camouflage is background matching, a form of crypsis. It entails an organism's capacity to blend in with its surroundings through the use of colour schemes and textures that resemble the elements found in its ecosystem. Cryptic camouflage, according to Merilaita et al. (2017) framework, enables animals to evade detection through minimizing the signal to noise ratio, where the ‘signal’ is the pattern of the animal and the ’noise’ is the pattern of the background. The camouflage of cuttlefish (e.g. Shohet et al., 2007; Barbosa et al., 2008; Zylinski et al., 2011) and the fur of arctic animals (Mills et al., 2013; Zimova et al., 2016) are two noteworthy examples. Background matching is discussed in greater detail later, as this is the type of camouflage most relevant to this thesis.

b) Transparency, like background matching, minimizes the visual difference between the organism and its background and allows organisms to virtually disappear, but by allowing light to pass through the body rather than concealment through colour and pattern. As such, unlike other types of camouflage, transparency affects the entire body, not just the exterior (Johnsen, 2001; Stevens & Merilaita, 2008). Jellyfish and various other marine organisms are among the most known examples of transparency in animals, probably because the refractive indices of tissue and water are more similar than tissue and air (Johnsen, 2001; Stevens & Merilaita, 2008).

c) Disruptive colouration employs high contrast patterns near to body’s edge to break up the organism's contour and shape (Thayer, 1909; Cott, 1940) or other distinctive features such as eyes (Cott, 1940; Cuthill & Szekely, 2009). Viewed in the framework of reducing the signal-to-noise ratio (Merilaita et al., 2017), by making the shape and silhouette of the organism harder to see, the signal is reduced, while the strong contrast between internal colour patches increases the noise through ‘false edges’ (Stevens & Cuthill, 2006). The effectiveness of disruptive colouration above and beyond background matching has been experimentally verified with artificial prey (Cuthill et al., 2005; Stevens et al., 2006), and the panda’s black-and-white patterns are a striking example of how camouflage can only be understood with knowledge of the background against which it is seen (Caro et al., 2017; Nokelainen et al., 2021).

c) Countershading – darker pigmentation on the side of the body facing the light (Poulton, 1890; Thayer, 1896) allows camouflage by more than one potential mechanism (Kiltie, 1988; Ruxton et al., 2004; Rowland, 2009; Ruxton et al., 2018) but, for simplicity, is discussed under one heading. The original hypothesis of Poulton (1890) and, independently, Thayer (1896) was that the gradient of its skin tones counteract the shadows created by directional ambient lighting. Thus, the sun above creates a dorso-ventral gradient from light to dark on an animal's body and the dorso-ventral gradient in pigmentation from dark to light counteracts this (Penacchio et al., 2015a). Consistent with this is the more intense countershading of ungulates in open habitats near the equator (Allen et al., 2012) and the illumination-dependency of the effectiveness of countershading as camouflage has been experimentally verified (Cuthill et al., 2016). Self-shadow concealment through countershading is thus an example of disguising 3D shape-from-shading cues (Penacchio et al., 2015a) and thus shares with disruptive colouration the function of disguising shape. However, countershading can also act as camouflage through simple background matching, if the darker side of the animal is consistently seen against a darker background and the lighter side against a light background (Kiltie, 1988; Ruxton et al., 2018). Countershading in pelagic fish and seabirds are the most frequently discussed example here, the ocean depths being dark and the sky light, although supporting evidence is lacking (Kelley & Merilaita, 2015).

e) Masquerade occurs when an organism takes on the appearance of an irrelevant object, potentially causing its predators or, in the case of predators, their prey to mistake it for something of no interest (Skelhorn & Ruxton, 2010; 2014; Skelhorn et al., 2010a; 2010b; 2011). The aggressive masquerade hypothesis states that predators can also use disguise to draw in prey or to hide themselves from them. Crab spiders are one example, which use their appearance as bird droppings to trick their victims (Yu et al., 2022).

1.3 Background matching

The term "background matching" refers to how well the animal's body pattern and colour match the hue and texture[*] of the environment in which it is situated. Numerous studies have emphasised the value of background matching as an adaptive feature (reviewed in Merilaita & Stevens, 2011). Our understanding of this phenomenon has been enhanced by a combination of comparative studies that show a correlation between animal colours and their backgrounds (e.g. Endler, 1984; Allen et al., 2009; Nokelainen et al., 2020), investigations of the underlying genetics of coat colouration (e.g. Harris et al., 2020), field studies that relate colour matching to fitness (e.g. Troscianko et al., 2016a; Wilson-Aggarwal et al., 2016) and laboratory studies with artificial prey (e.g. Sherratt et al., 2007). Of major significance has been the incorporation of models of colour vision in the evolutionarily relevant species, rather than relying on human judgements of colour match (Endler, 1984; Sherratt et al., 2007; Allen et al., 2011; Troscianko et al., 2016a; Wilson-Aggarwal et al., 2016).

In particular, Endler (1978, 1980, 1983, 1987a, b, 1991) has studied the mechanisms underpinning background-matching camouflage, and trade-offs with other functions of colour, in great detail. His work underlines the importance of vision in other species, the light environment, and how to quantify the relevant colour and pattern information (Endler, 1984, 1993; Endler & Thery, 1996; Endler & Mielke, 2005; Kemp et al., 2015).

Studies on camouflage included observations of actual animals in their natural environments in addition to studies with artificial prey. In one study, Stevens et al. (2017) showed an improvement of individual nest camouflage through background choice by parent ground-nesting birds. The colour of the bird's eggs and their own plumage matched the background colour of an individual’s own nesting place better than the nest-sites of other individuals, suggesting active background choice with respect to personal appearance. Further research on some of the species (coursers and plovers; Glareolidae) showed that the eggs' pattern, such as speckling, increased the camouflage's efficiency, with higher survival in clutches that better matched the background

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[*] In the vision sciences, ‘texture’ is used to describe the 2D pattern that is seen, rather than the 3D texture itself.

(Troscianko et al., 2016b). Further work suggested that individuals had some awareness of their own degree of camouflage, as incubating plover and courser parents fled the nest sooner, in the face of an approaching threat, when their eggs were a poorer match to the background (Wilson-Aggarwal et al., 2016).

Studies with artificial prey, paper ‘moths’ or pastry ‘caterpillars’, have been particularly useful in understanding the different mechanisms of camouflage, particularly when combined with visual modelling of the colours as seen by avian predators. Experiments such as this have provided evidence for the importance of background matching (Michalis et al., 2017), disruptive colouration (e.g. Cuthill et al., 2005; Stevens & Cuthill, 2006; Stevens et al., 2006) coincident disruptive colouration (Cuthill & Szekely, 2009), disguise of 3D shape through countershading, the costs of body symmetry (Cuthill et al., 2006a,b) and evidence against other mechanisms such as distraction marks (Stevens et al., 2008; Stevens et al., 2013a). Understanding these systems can help us better understand how colouring has evolved in various contexts and the selection pressures that have influenced this development.

1.4 History of camouflage research: Darwin, Wallace, Thayer, Poulton, Cott

The theories and achievements of various significant individuals in the realms of biology, evolution, and art are closely related to the history of camouflage. Charles Darwin, Alfred Russel Wallace, Abbott Handerson Thayer, Edward B. Poulton, and Hugh Cott are notable names among them. These people had a huge impact on how people understood both the mechanisms and evolution of camouflage and its importance as a defence against predators. In Cott’s case, the influence extended to the military as well as biology, as he served as a camouflage adviser to the British Army in the Second World War (Forsyth, 2014).

Natural selection was discussed in depth by renowned naturalist Charles Darwin in his influential book “On the Origin of Species” (1859). Although he did not address the mechanisms by which camouflage works specifically, his concepts created the groundwork for its comprehension. Darwin argued that individuals would pass on features that helped them reproduce and live to their offspring, causing populations to gradually adapt to their environments. Darwin provided evidence for natural selection and adaptation, and some of these examples included animal camouflage. While travelling on the HMS Beagle, Darwin gathered a vast amount of empirical data and noted in "On the Origin of Species" different types of animal mimicry and protective colouration.

Alfred Russel Wallace, a much younger contemporary of Charles Darwin, developed the theory of evolution through natural selection on his own. He understood how crucial camouflage is to a species' ability to survive and reproduce. In his book "Darwinism" (1889), Wallace emphasised the significance of protective colouration and the capacity of animals to mimic their surroundings in order to evade notice. He also emphasised how animal behaviour and interactions between predators and prey are affected by camouflage. Wallace, like Darwin, used his excursions abroad to collect empirical data. His study of camouflage was influenced by his observations of diverse animals in Southeast Asia and the Malay Archipelago, examining various instances of disruptive colouring, mimicry, and protective resemblance. To demonstrate the value of camouflage tactics in deterring predators or boosting hunting success, he provided in-depth descriptions and images of many species, including butterflies and beetles.

The concept of camouflage was further refined by British entomologist and evolutionary biologist Edward B. Poulton. Poulton examined the many shades of animal colour and their significance in terms of adaptation in his book "The Colours of Animals" (1890). As well as coining terms like “crypsis” and “aposematism”, Poulton divided camouflage into various categories of what he called “protective resemblance”, distinguishing between “general resemblance” (background matching) and “special resemblance” (what we would now call masquerade). To demonstrate how well camouflage works in boosting survival, Poulton's research depended on comprehensive observations of animals and their surroundings.

After the biologists of Darwin’s era, significant contributions were made by artists, perhaps not surprising because of their familiarity with the use of colour to influence a viewer’s perception

(Cuthill & Troscianko, 2009). American artist and naturalist Abbott Handerson Thayer made substantial early contributions to the field of camouflage research. In his work "Concealing Coloration in the Animal Kingdom" (1909), Thayer put out several influential ideas: camouflage as “sampling the background”, the principles of disruptive colouration (although he called it “ruptive”) and the obliteration of shape-from-shading cues through countershading. In his view, an animal's colouring and patterning help to conceal it from predators and prey by sampling the colours and patterns in its surroundings and by breaking up its silhouette. With the help of several examples and drawings, Thayer supported his arguments and incorporated his artistic expertise into his work.

Furthermore, aside from a successful career as a biologist (lectureships at Bristol, Glasgow and, finally, Cambridge), Hugh Cott became a military advisor who worked on camouflage research both during and after World War II, making significant contributions to the field. His book "Adaptive Coloration in Animals" (1940) is regarded as a classic on the subject. Cott broadened the definition of camouflage to include other adaptive strategies outside animal colouring, such as mimicry, behaviour, and postures. He offered samples from a variety of species and thoroughly documented numerous camouflage techniques. Cott's research into the application of camouflage in military settings had an impact on the creation of military camouflage tactics (Forsyth, 2014).

Cott's proof of camouflage covered a variety of species and consisted of both field observations and real-life demonstrations. Cott provided a thorough review of camouflage tactics, including colour, markings, and behaviours in "Adaptive Coloration in Animals". He discussed how animals' adaptive colouring relates to their settings using images and illustrations of creatures from various habitats. Cott supported his beliefs with evidence based on comparative research and, although we do not today describe them as true experiments, demonstrations of how colour and shading could produce misleading effects on the human viewer have been used to this day.

1.5 The Endler 'random sample' definition

Following Hugh Cott, arguably the most significant contributions to our understanding of animal camouflage and the function of colouration more generally, has been the work of John Endler, from the late 1970’s onwards. I have already discussed his influential work on the conflicts between sexual and viability selection, and on the measurement of colouration. Here I focus on his definitions, as they have both guided the field and, in relation to the term crypsis, provoked some disagreements. Endler (1981) defines different relationships between mimicry and crypsis. In this paper, and others before and since (Endler, 1978, 1983, 1988), he tells us that an individual is cryptic if it resembles a random sample from the background. In the context of the discussions in Endler (1981), he was concerned with species that are cryptic to hide from their predators, but the same principles apply to predators hiding from their prey. After his 1978 paper, many investigators adopted Endler's crypsis definition; however, today the most widely adopted definition is broader, so it is important to understand why.

First, and probably uncontroversially, crypsis involves many more features than just physical appearance (e.g. colouration), as it may also involve behavioural traits, or both together, to avoid detection (Merilaita & Stevens, 2011; Cuthill et al., 2019; Stevens & Ruxton, 2019). A stick insect not only looks like part of its background, it moves like it (Bian et al., 2016). Endler might argue that ‘random sample’ should include the temporal characteristics of the background as well as its colouration, which is why I consider this extension of the term crypsis to be uncontroversial.

Note also that it could be easy to confuse crypsis and concealment; however, Merilaita and Stevens (2011) mention that the second corresponds to the fact of simply being hidden (including behind an object in the environment), whereas crypsis is ‘hiding in plain sight’. Hiding does not constitute crypsis (see also Edmunds, 1974) since there is no possibility that the receiver detects the animal. Crypsis must be considered to be the animal's characteristics that reduce the risk of detection when the animal is in sight (Stevens & Merilaita, 2008).

The main reason to have concerns with Endler's definition is that it implicitly assumes that all random samples in the background will be equally cryptic. This is not only unlikely on logical grounds (random samples include rare samples that are necessarily going to be different from many backgrounds an animal might be viewed against; Cuthill & Troscianko, 2009), it has been shown empirically not to be the case (Merilaita & Lind, 2005). There may even be spatial mismatches in simple random backgrounds where an animal can be seen as a result of its characteristic features, such as its edges (Kelman et al., 2007). In addition, matching a random sample from one type of background (for Endler (1978) “the time and place at which the prey are most vulnerable to predation”) will not necessarily minimise the risk of detection when an animal can be seen against multiple backgrounds (Merilaita et al., 2001; Houston et al., 2007; Sherratt et al., 2007). In other words, although Endler (1978) helped to promote research on the subject, the definition should be updated (Merilaita & Stevens, 2011). Once the specification that the sample be random has been removed, Merilaita & Stevens (2011) and Ruxton et al., (2018) argue that there are good reasons to see ‘crypsis’ as all strategies for avoiding detection ‘in plain sight’. However, strategies for avoiding recognition (masquerade or Poulton’s ‘special resemblance’) should not be included under crypsis because, as Ruxton et al., (2018) argue, otherwise ‘crypsis’ and ‘camouflage’ would mean the same thing and the term crypsis would be redundant. Because the risk of detection can be reduced in ways other than matching the background, for example by hiding one's shadow (Rowland, 2009) or through disruptive markings that break the animal’s contour (Thayer, 1909; Cott, 1940; Stevens & Merilaita, 2009b), strategies such as countershading and disruptive colouration can be included under crypsis.

1.6 Evidence from natural systems

1.6.1 How colouration varies with habitat/background, suggestive of background-matching camouflage

One would think that background matching would be a phenotypic characteristic that is distinct and simple to recognise and, when it is, such as in those arctic animals that change colour to white in time for winter snows, background matching has considerable, quantifiable effects on fitness (Zimova et al., 2016). With climate change leading to delayed and/or less predictable snowfall, Zimova, Mills and colleagues have documented how snowshoe hares (*Lepus americanus*) are under strong selection for changes in the timing of moult to the white winter coat, and even in some populations remaining brown year-round (Mills et al., 2013, 2018; Zimova et al., 2014, 2016). Thus, when the animal's and the background's colours are simple to quantify, camouflage is a perfect subject for researching the evolutionary processes that underlie adaptation (and maladaptation). Indeed, probably the most well-known example of evolution by natural selection concerns background matching: industrial melanism in peppered moths of the genus *Biston* (Kettlewell, 1955; Cook & Saccher, 2013). The classic story is that the pale-coloured wild type was camouflaged against lichen but, due to the darkening of previously light-coloured, lichen-covered, trees brought on by coal soot of the Industrial Revolution in Britain, peppered moths were given a fresh environmental niche. The darker moths in this new environment had lower detectability, which resulted in lower predation and greater survival rates than the pale wild-type; with reduced pollution through the Clean Air Acts of the mid-20th century, the wild type moth again became more frequent (Majerus, 1998; Cook & Saccher, 2013). The true pattern of selection on *Biston* is more complicated but, despite accusations of fraud on the part of the original scientist, Kettlewell (Hooper, 2002), selection on colouration in relation to camouflage against bird predators has been proven to be a core part of the explanation for the rise and fall of melanic forms (Cook & Saccher, 2013). The missing part of the jigsaw has always been that the degree of background matching has been judged based on subjective human criteria (or simply assumed). Background matching in the eyes of avian predators, and how this affects predation in the field, was only quantified recently (Walton & Stevens, 2018). This is the reason for the cautious wording at the start of the paragraph: one would think that background matching would be simple to quantify but, because it is appearance in the eyes of other species that matters, it may not be.

For background matching to be effective, there must of course be a correlation between the animal's colouration and its background's. This can be generated by active choice or colour change, as discussed later, or natural selection in combination with a stable environment. For example, in the snowshoe hare example discussed above, the hares show no evidence of selecting backgrounds on the basis of their own colour (e.g. white hares selecting snow, brown hares selecting earth; Zimova et al., 2014) so, to be adaptive, their colour change has relied on snowfall being temporally predictable; which is why they are at risk now. For most animals, successful evasion of predator detection by a match between their body colours and those of the background relies on past selection having created the phenotype-environment correlation (Endler, 1986). This has led to multiple studies using the comparative method to link variation in species appearance to variation in the appearance of the background. For example, a study by Ortolani & Caro (1996), later verified by Ortolani (1999), showed that camouflage, not communication or physiological reasons such as thermoregulation, is the primary driver of species differences in cat coat patterns. Allen et al. (2011) took this further; rather than relying on simple subjective categorisation of coat appearance ('spotted', 'striped', etc.), they matched coat patterns to realistic models of pattern development. Cats with plain coat patterns are found in evenly coloured, textured, and lit surroundings, whereas species of cat with pattern coat patterns are found in areas with plenty of trees, shrubs, and intricate shadows (Allen et al., 2011).

Important early examples of coat colouration in the wild and its connection to natural selection were provided by studies on colour matching in *Peromyscus* mice. Early studies, like as those by Dice (1940) and Haldane (1948), showed that there were significant relationships between the dorsal coat colour of *Peromyscus* populations and the colour of the nearby soil (albeit judged by human eye), indicating the importance of spatially variable selection in the emergence of locally adapted phenotypes. These results provided early evidence that colour matching can be influenced by selection in several species. In Florida's coastal sand dunes and abandoned agricultural lands, for example, certain subspecies of *Peromyscus polionotus* have distinctive colour adaptations (Sumner, 1929) although, again, colour was judged by their appearance to a human observer. Sahara-Sahelian rodent species offer a more robust example of how camouflage adaptation has emerged in response to strong and varied selection pressures brought on by dryness and temperature. Using visual models of their predators' colour vision, Nokelainen et al. (2020) showed that the fur of most species matched their background colours at a large geographical scale, suggesting a generalist matching strategy. Some species matched backgrounds at even a relatively local scale, although Nokelainen et al. could not determine whether this was through active choice by the animals or local adaptation.

In order to link evolution to the mechanisms underlying development (‘evo-devo’), investigations into the genetic causes of crypsis in vertebrate systems have drawn more and more attention (Harris et al., 2020). In order to avoid predators that hunt by sight, melanin-based colouration has evolved in animals as a result of the geographic patterns that create diverse selective settings (Protas & Patel, 2008). As a result, numerous studies have been conducted to examine genetic variation within the same melanin pathway, comparable ecological stresses, and adaptation that takes place in close physical and temporal proximity. All of this offers a rare chance to evaluate and contrast the results of evolution in multiple vertebrate species (Harris et al., 2020) and provides further evidence of the utility of studying colouration for integrating different biological questions (Cuthill et al., 2017).

1.6.2 Crypsis through background choice

Animal concealment is greatly aided by the choice of appropriate backgrounds, particularly when the habitat is heterogeneous, so it is natural to assume that many species have evolved the capacity to do so in order to increase their crypticity. However, as we have already seen with snowshoe hares failing to choose backgrounds that match their white or brown fur (Zimova et al., 2016), not all animals show camouflage-optimising choices even when it might seem obviously adaptive to do so. There are also cases where a visual match to the background is achieved using other sensory cues. For example, in an elegant experiment where the clear acetate sheet was used to block tactile but not visual cues, Sargent (1969) showed that two striped species of moth orient to their striped background using touch. The development of prey or predators' concealment tactics therefore depends critically on our understanding of predators' sensory abilities particularly, if vision is the sense used, their retinal sensitivities, visual acuities, and cognitive processing (Stoddard, 2012; Skelhorn & Rowe, 2016).

Trying to better understand this phenomenon, Kang, Stevens, Moon, Lee, and Jablonski have focused on moths and their camouflage behaviour (Kang et al., 2012, 2013a, 2014). Their research reveals the complex interaction between moths and the substrates on which they rest. Moths actively choose places that enhance their concealment and lower their danger of predation. These results suggest that the degree of crypticity in a moth's pattern also influences how it behaves. Moths that land in locations with high crypticity tend to stay put, whereas moths that first land in locations with poor crypticity move around to improve their camouflage (Kang et al., 2013a). However, in some cases a generalist technique may perform better than specialisation, minimising conflicts in matching various backgrounds, if many habitat types show enough similarity (Merilaita et al., 2001; Houston et al., 2007; Hughes et al., 2019)**.**

1.6.3 Crypsis through colour change

Some animals also use colour change to reduce their conspicuousness. Duarte et al. (2017) and Umbers et al. (2014) reviewed colour change in a wide variety of species, shedding light on the tempo and relevance of this facultative response where animals can adapt to environmental changes by changing their colour, which enables them to adjust their appearance to match their habitat. In cuttlefish and other cephalopods, colour change is under neural control and can happen in fractions of a second (Hanlon, 2007); in others, such as crabs, it may take hours or days (Stevens et al., 2013b); and in some the change is an irreversible part on an ontogenetic process where the adult and larval strategies differ. While the chameleon is probably the best-known colour changer to the general public, in fact the colour change is less associated with the capacity to blend in with different backgrounds for concealment purposes, than social selection favouring the development of noticeable conspecific signals (Stuart-Fox & Moussalli, 2008). In cephalopods, however, although colour change is certainly used in intra- and interspecific signalling (Adamo et al., 2006; Langridge et al., 2007), camouflage is certainly a vital function (e.g. Hanlon et al., 2007; Shohet et al., 2007). Furthermore, camouflage is achieved not just by a change in colouration, but by altering the 3D texture of their skin (Allen et al., 2014) and both postural (Barbosa et al., 2012) and overall shape changes (Hanlon et al., 1999; Hanlon et al., 2010). Cuttlefish are probably the best understood of any group with respect to how the visual appearance of the background is mapped to their own colouration, particularly how they interpret contrast and object edges (e.g. Chiao & Hanlon, 2001; Barbosa et al., 2008; Zylinski et al., 2012, 2016). However, the most surprising fact is that they are colour-blind (Mathger et al., 2006). Presumably luminance variation is sufficiently well correlated with colour (the sea-floor is shades of brown) that "colour-blind camouflage" is possible (Marshall & Messenger, 1996).

1.7 Experimental studies in the lab

Experiments in the laboratory, for their part, help to understand the mechanisms and functions of camouflage, all this because researchers can manipulate variables and viewing conditions in a tightly controlled way, and observe the effects on the effectiveness of camouflage and predator-prey interactions. Dimitrova and Merilaita (2014) by using artificial patterns on both prey and background, in aviary experiments with blue tits (*Cyanistes caeruleus*), were able to systematically investigate the importance of both pattern shape and element density on the effectiveness of background pattern matching. They concluded that, because both factors affected detection success, "there are no shortcuts to effective background matching". Experiments using humans as surrogate predators are more common than captive animal studies, not just because they are logistically easier and cheaper, but because a human can be instructed on a specific task. For example, Loeffler-Henry et al. (2018), in an experiment to determine the effect of 'flash colouration' on subsequent prey detection (a cryptic animal displaying a bright colour, moving, and then returning to crypsis), asked human participants to track a moving square that changed colour (or not) and then moved and reappeared on another screen. It would have been hard to train a blue tit, for example, to do this sort of task.

The separation of the effect of the different components of background matching, or camouflage more generally, is difficult with natural prey on natural backgrounds. However, the greater experimental control possible with artificial prey and backgrounds comes at a cost of reduced "ecological validity". This is a term, commonly used by psychologists, to describe the degree to which an effect demonstrated in the lab also applies in real-life situations (e.g. Aronson & Carlsmith, 1968). Because of this issue, the most convincing studies have often combined field experiments (usually with natural predators) with experiments in the lab under controlled conditions (often using humans); if both converge on the same answer, the conclusions are more robust. For example, Michalis et al. (2017) paired the field experiment on optimal background matching, mentioned in the previous section, with an experiment on humans searching for pictures of the same targets and backgrounds, and it is the similarity of the results that made the conclusions more convincing. Likewise, Fraser et al. (2007) used similar artificial prey to those used in field experiments with birds (Cuthill et al., 2005; Stevens et al., 2006) and reached the same conclusion that disruptive colouration can be more effective camouflage than simple background matching, but only if the component colours are ones common in the background. Webster et al. (2013) extended this approach by using eye-trackers on human participants (something not yet easily done with other animals), showing that disruptive colouration interfered with object recognition, not only detection. Sharman et al. (2018) reached the same conclusion using a different experimental approach, but again an experiment that would have been hard to do with non-human animals, because instruction on the specific task was essential.

A more ambitious approach is to combine computer-based search tasks with artificial evolution of the 'prey'. For example, Sherratt et al. (2007) investigated the relationship between the colouration and pattern of targets and their susceptibility to predation by human "predators" on uniform and heterogeneous backgrounds. They utilised pixelated squares with varying colour patterns and placed them on backgrounds with varying colour and pattern patterns. The researchers were able to evaluate the effect of camouflage on capture rates and allow the survivors to 'reproduce', with some mutation, to populate the next generation that the participants had to search for. On uniform backgrounds, prey evolved colouration that closely matched the background colour and pattern. However, in treatments where the background was highly heterogeneous, prey evolved to specialize on matching one background type, a theme continued below.

1.8 Multiple backgrounds – compromise crypsis

While background matching is a prevalent occurrence in camouflage, there are instances in which animals encounter multiple backgrounds of varying colour and pattern. In such situations, compromise crypsis, in which individuals attempt to match the average appearance of the backgrounds, can in theory be an effective tactic. Merilaita et al. (1999), using an optimization model, were the first to investigate the situations in which compromise camouflage might be favoured over matching one of the possible background. The conclusion was that it depends on the shape of the trade-off curve between detecting a prey rapidly on one background compared to another. When this is convex (the difficulty of detecting a prey on one background is not fully compensated for by an improvement in detection on the other background) compromise camouflage can be favoured. If the curve is concave, specialization on just one or other background is favoured. In an aviary experiment with Great tits (*Parus major*) and artificial prey, the first prediction was fulfilled, but they did not investigate a situation where specialism might be favoured. Several other studies on this phenomenon using artificial prey have cast light on the mechanisms and effects of camouflage in relation to multiple backgrounds, and these issues are explored further in Chapter 5.

The study of compromise crypsis in camouflage sheds light on the adaptive strategies employed by animals to deal with multiple backgrounds. This phenomenon has significant implications for predator-prey interactions as well as our comprehension of evolutionary processes and ecological dynamics. Understanding the underlying mechanisms of compromise crypsis can cast light on how animals integrate information from multiple backgrounds to optimise their camouflage. It also emphasises the adaptability of animals, in which evolution modifies their colouration and body shape to attain intermediate camouflage effectiveness in a variety of environments.

1.9 The study systems

Currently there are approximately 250 species of shorebirds, also known as waders, that belong to the order Charadriiformes (Gill and Donsker, 2018). The diversity within the group gives us an excellent opportunity to understand how evolution works, particularly in relation to mating and parental behaviour (Pitelka et al., 1974; Oring, 1986; Owens, 2002; Székely et al., 2014). Some waders are polyandrous, some polygynous and others monogamous; the parental care systems vary from uniparental (either male or female caring for the young alone) to biparental (Szekely et al., 2006; Székely et al., 2014). This group of birds also has very diverse ecology: they live and reproduce on all continents, congregating on wetlands, marshes and coasts; however, they also inhabit places less commonly associated with waders, such as forests, grasslands or deserts (Székely et al., 2014). The following two species feature in the next four chapters in this thesis, in various ways.

Kentish plover (*Charadrius alexandrinus*)

The Kentish plover (Fig.1.1) is a small bird, usually reaching a length of about 15 centimeters. It is named after the county of Kent in southeastern England, where it was first described but no longer breeds. This species is widespread in Europe, Asia, and Africa and inhabits a variety of habitats, including coastal areas, sandy beaches, salt marshes, mudflats, and estuaries (Norte & Ramos, 2004). The Kentish plover is known for its distinctive appearance, with a compact body, short bill, and a black band extending from the forehead to the eyes. Plumage varies between breeding and non-breeding seasons, with breeding birds having a sandy brown back, white underside and black markings on the face. They are very social birds, often found in small flocks or pairs. Kentish plovers have a distinctive feeding behaviour: they probe and peck in the sand or mudflats to prey on small invertebrates such as insects, crustaceans, and molluscs. Kentish plovers often form small flocks or pairs and exhibit highly social behaviour (Székely & Williams, 1995). It exhibits sexual dimorphism, with males having bolder plumage colours and patterns compared to females. During the breeding season, males have a sandy brown back, white underside, and distinct black markings on the face. Females, on the other hand, display more subdued plumage. The Kentish Plover breeds monogamously, with both parents sharing nest building and incubation of the eggs (del Hoyo et al., 2021).

Figure 1.1. *Ch. alexandrinus* in Spain reproduced with permission by Nuria Martin ©.

Kittlitz's Plover (*Charadrius pecuarius*)

The Kittlitz's plover (Fig. 1.4) is a small to medium-sized bird with a length of 18-21 centimetres. It exhibits sexual dimorphism, with males and females having slight differences in plumage. They have dark brown to black backs that contrast with white underparts, including belly and breast. The legs are strikingly yellow (Wiersma et al., 2020). This species of plover is widespread in sub-Saharan Africa, especially in the wetlands of freshwater lakes, swamps, and rivers. It is adaptable and can also be found in coastal areas, estuaries, and even agricultural fields near water sources (Morris & Hawkins, 1998). Kittlitz's plovers are known for their distinctive behaviour and song. They can often be seen walking along the shoreline, using their long legs to run quickly along the shoreline in search of small aquatic invertebrates and insects. They build their nests on the ground, often in sparsely vegetated areas near water bodies, using pebbles and plant material (Brown et al., 1982).

Figure 1.2. *Ch. pecuarius* in Queen Elizabeth II NP--Kasenyi Track by Shailesh Pinto.

1.10 Thesis outline

This thesis encompasses fieldwork on free-living animals, technical photography, image analysis, computational models of vision, experiments with artificial prey and avian predators, and computer-based visual search experiments using humans as model predators. The uniting theme is camouflage against heterogeneous environments, and the major study system concerns various species of plover, focusing on the colour patterns of their eggs (in nests) and chicks, in two countries: Spain and Madagascar. The original plan was a study based exclusively in the Falkland Islands, in the South Atlantic but, soon after a pilot trip to establish field protocols and exact study sites, the COVID pandemic started. With travel restrictions to the islands in place for nearly 2 years, the initial project was abandoned and this also explains the distinct chapter involving field experiments with artificial 'moths' in a woodland in North Somerset. In 2020, this was the only experimental work possible. The chapters from two to five have been designed to be published as separate articles in peer-reviewed journals upon the completion of this thesis, with this chapter reviewing the literature and placing the research in context, and chapter six synthesising the results. Chapter two uses calibrated photography and visual modelling to examine the camouflage qualities of plover eggs in relation to their background. Chronologically, this was the last research carried out, the fieldwork having been done exclusively by me in two study sites near Cadiz, Spain. Chapter three involves the examination of the colour patterns of plover chicks, again using calibrated photography and image analysis in order to determine the characteristics of their camouflage in relation to their surroundings, as well as to investigate any differences between males and females. The latter is of interest, as explained in the chapter, because of known differences in the population sex ratio, with male chicks surviving better than females. The possibility tested here is that differences in camouflage between males and females might explain that difference in mortality. The photographs were not taken by me but utilised an archive of photographs built up over several years by my co-supervisor, Professor Tamas Székely, from his study populations in Madagascar. These analyses took place during COVID travel restrictions (and subsequently), which explains why I did not take the photographs myself. They were, however, taken using the same standardized protocol that I used in Chapter two. Chapter four examines the detectability of chicks – both the whole animal and, separately, just their plumage – in relation to their natural environment, using computer-based visual search experiments with humans, specifically focusing on the influence of different types of background. The objective is to assess whether there is a significant difference in the likelihood of chicks being noticed based on the difference types of background they are normally found on. In chapter five, situated at a distance from the plovers, both geographically and the type of experiment, but still within the realm of camouflage, the investigation explores the merits of individuals specializing in camouflage to a specific background vs those that adopt a camouflage pattern that is a compromise between the different backgrounds they might be viewed against. Finally, in chapter six, an overview of the main findings is presented, accompanied by a discussion of the principal conclusions and possible applications. Additionally, future projections pertaining to the subject matter are provided.

Chapter Two: Egg Camouflage

2.1 Abstract

The present study investigates egg camouflage in the Kentish plover, *Charadrius alexandrinus*, a small species of wader studied in two different coastal habitats in Cádiz province, Spain. The analysis focused on the correlation between the eggs' camouflage patterns and the specific backgrounds against which they are discovered, notably on the beach and on saltmarshes. Using calibrated photographs taken *in situ*, neurophysiologically plausible models of colour and pattern vision were used to assess the predicted discriminability of egg colour and visual texture from those of backgrounds, for likely predators (avian and mammalian carnivore) and, for comparison, humans. The findings suggest that at close range *Ch*. *alexandrinus* eggs are more susceptible to detection by visual predators based on their patterns rather than their colours, but at distances beyond which individual pattern elements can be resolved they are highly cryptic. Although the colours and patterns (visual texture) of the saltmarsh and beach nest sites differ, the colours and surface patterning of eggs do not, suggesting that there is no local adaptation. However, the colours of eggs are similar to the types of background colours that overlap between the beach and saltmarsh. This suggests that strategic placement of eggs in regard to this factor is predicted to be crucial for their survival.

2.2 Introduction

Charadriiformes, shorebirds including the waders Charadrii, are avian species that exhibit ground-nesting and foraging behaviours, often in relatively exposed habitats. For such birds, nest predation has been identified as the primary factor contributing to reproductive failure within the order (Sládeček et al., 2021), and so covering the nest with vegetation (Troscianko et al., 2016a; Gomez et al., 2018) and the distraction from, or physical defence of, nests are features of parental care in many plover species (Walter, 1982; Gómez-Serrano & López-López, 2016). However, egg camouflage is the primary adaptation to protect their eggs from predators (Troscianko et al., 2016b; Stevens et al., 2017). Among the Plovers (Charadriinae), in particular, in some species and populations eggs often exhibit colouring and patterning that mimics their surroundings, such as rocks, vegetation, or sand, while in other cases the match appears poor (Stoddard et al., 2011). However, most studies have assessed egg camouflage using human judgements, so the extent to which eggs are actually cryptic in the eyes of their predators remains under-researched (Stoddard et al., 2011).

Although the focus of this thesis is camouflage, we must remember that concealment is not the only function of egg colouration; pigments can also affect heat loss or gain, with species in colder climates tending to have darker shells that promote heat absorption (Wisocki et al., 2020). However, because pigmentation will also reduce transmitted light and transfer of heat to the embryo by this route, there can be a trade-off between the effects of pigments on transmittance versus absorption (Lahti & Ardia, 2016). One can also imagine trade-offs between thermal and camouflage benefits of various types and densities of pigment. Such trade-offs do not only have the potential to affect egg colour. Previous research has examined the nesting behaviour of certain species of Charadriiformes, revealing their ability to choose nest materials that possess reflective properties to mitigate overheating (Mayer et al., 2009). Conversely, other studies have shown that these species also select materials that minimize heat loss (Reid et al., 2002). Therefore it is worth noting that the selection of nest materials not only serves as an additional camouflage strategy but also influences the thermal characteristics and humidity levels of the nest (Hilton et al., 2004; Prokop & Trnka, 2011). Moreover, the enhancement of egg camouflage, in conjunction with its contribution to thermoregulation, has been documented as an illustrative instance in Kittlitz's plovers (*Ch. pecuarius*) which, upon departing from their nests, engage in a behaviour known as a 'leaving-scuffle', as documented by Hall (1958, 1960). During this process, the plovers position themselves with their legs on either side of the nest and proceed to cover their clutch with either plant or inorganic material. Notably, they employ a kicking motion to introduce the material from the sides, occasionally rotating in place to ensure comprehensive coverage of the eggs. The aforementioned actions would not only yield advantages for the nest itself, but also for the parents, as it grants them the liberty to temporarily depart from incubation duties and engage in foraging activities. The case of *Ch. alexandrinus* is also exemplified by a study conducted by Amat et al. (2012), which revealed that the nest cover of these birds serves a dual purpose. Firstly, it offers concealment for the nest when the adult is absent, and secondly, it aids in thermoregulation.

The pigments of the eggshell determine how well the eggs are disguised as well as their thermal properties. These pigments are added to the eggshell during egg laying and contribute to the overall colouring and pattern of the eggs (Kilner, 2006; Cherry & Gosler, 2010). From an evolutionary perspective, the specific camouflage patterns on bird eggs are likely to be determined by the nesting site and the ecological pressures faced by each species. For instance, a study by Stevens et al., (2017) found that plovers (as well as ground-nesting coursers, Glareolidae, and nightjars, Caprimulgidae) select nesting locations that provide their eggs the best chance of appearing concealed. In order to conceal their eggs from predators, birds also change the visual environment by covering their nests with materials that blend in with the surroundings (Troscianko et al., 2016b). The importance of the individual choice of microhabitat and the use of nest materials for the nest-site-specific camouflage of plovers' eggs was also shown in a study by Gomez et al. (2018). It is worth noting that neither of these studies showed how parents achieved the individual-specific match between their eggs and their nest site. In fact, in field studies like this, the match could be the result of natural selection (nests that were poorly camouflaged suffered predation), rather than individual choice.

That parents might be aware of their individual degree of camouflage is suggested by a study by Wilson-Aggarwal et al., (2016). When a simulated predatory threat approached the nest (a human), ground-nesting plovers fled, but those with poorer camouflage (as assessed by visual modelling) flew off when the ‘predator’ was further from the nest. This suggests that the birds were aware that the poorer their camouflage, the greater their risk of detection was. That said, this is only correlational evidence; the wariness of birds with poorer camouflage could have been because they experienced more disturbance by predators in the past and so it could be this, not self-awareness of camouflage, that has caused the difference between parents. Therefore, direct evidence of background choice with respect to egg colour is required. Therefore, one of the most extensively reported experiments is that of Lovell et al. (2013), who conducted a study in which female quails, *Coturnix japonica*, exhibited a preference for laying their eggs on substrates that reduced detectability specifically for their own eggs' patterning. The researchers gave female quail a choice between four differently coloured backgrounds on which to lay their eggs, then observed a statistically significant interaction between the type of substratum and whether their eggs were relatively uniform in colour or highly maculated (speckled). Quail with moderate-to-high levels of maculation on their eggs chose substrates that matched the dark maculation, while quail with eggs having the least maculation chose lighter backgrounds that matched the ground colour of their eggs. This suggests that quails have a preference for laying substrata that align with the visual characteristics of their eggs. According to the authors, Japanese quail employ a combination of disruptive camouflage (all quail chose substrates that reduced the prominence of the egg's outline) and, for those with unmaculated eggs, background matching strategies in order to optimize their camouflage effectiveness. By inference (they did not measure detection directly), this would minimize the probability of being detected by visual predators. How the birds know what colours and patterns their own eggs will be, prior to laying, remains unknown. Also, to my knowledge, there are no other published studies involving a direct experimental test similar to that of Lovell et al. (2013), so the generality of the finding is unknown.

Several studies have demonstrated the significance of nest camouflage to shorebirds in various natural settings. For instance, Skrade and Dinsmore (2013) found that the degree of colour contrast between mountain plover eggs and their nest surroundings directly influences the effectiveness of their camouflage. Specifically, a smaller contrast between egg colour and the surrounding habitat enhances camouflage, hence increasing the likelihood of successful nest brooding and subsequent survival. However, contrast was quantified using human-specific colour measures (RGB and L*a*b* colour spaces; see section 2.2.3) and there is no mention in their paper of use of colour standards or camera calibration. In addition, according to Summers and Hockey (1980), it was observed that the White-fronted plover (*Ch. marginatus*), frequently employed sand as a protective measure to conceal their nests when they saw potential threats from predators or human intruders, afterwards abandoning their nests. Hancock et al. (2023)

recently used 3D reconstruction of the terrain around lapwing (*Vanellus vanellus*) nests to show that, despite nesting in the open, the parents exploited slight variations in elevation such that the eggs would not be visible to a terrestrial predator from even 1.5 metres away. In addition to this, the eggs were an excellent colour match to backgrounds of fallow or bare fields, but less so vegetated areas, as assessed using visual modelling for fox or raptor vision. However, quantitative studies of background matching in the eggs of ground-nesting birds are relatively rare. Most studies invoking camouflage are descriptive. For example, in the study conducted by Kaur and Khera (2017), it was observed that Red-wattled Lapwings (*Vanellus indicus*) deposit eggs that possess a grey-green colouration, accompanied by black specks. These eggs plausibly exhibit a camouflage effect, according to the authors allowing them to blend seamlessly with their nesting places on the ground and so gain protection against potential predators. Similarly, Greeshma & Jayson (2018) found that Yellow-wattled Lapwings (*V. malabaricus*) also produce eggs with similar characteristics, although their assessment of what they describe as highly effective camouflage was solely with respect to subjective human judgement. In the present study, I use visual modelling to assess how easily Kentish plover (*Ch. alexandrinus*) eggs can be discriminated from their backgrounds in two, visually different, habitats in southern Spain: sandy beach and saltmarsh. Subjectively these two habitats differ in terms of the background against which eggs would be viewed by a predator so, first, I quantify the visual differences and then investigate whether there is evidence of local adaptation (camouflage-improving differences in colouration of the eggs found in the two habitats). I also determine whether, if there is no difference in egg colouration between habitats, the eggs are specialised to match one habitat better (the other being a 'second best' nesting site) or show 'compromise camouflage'. The latter is where a camouflage pattern is intermediate between two background types and yet, while suboptimal on either alone, has higher fitness on average across both (Merilaita et al., 1999; Hughes et al., 2001, 2019).

2.3 Methods

2.3.1 Study site

The research conducted on eggs was focused on *Ch*. *alexandrinus*, with fieldwork conducted on terrestrial habitats in Puerto Real, near Cadiz in south-west Spain (Figure 2.1). The fieldwork involved doing a visual survey to locate nests, which were afterwards documented through photography (Figure 2.2) using a NIKON D3500 digital SLR camera (Nikon Corp., Tokyo, Japan). The camera had previously been calibrated so that the non-linear relationship between pixel value and photons entering the camera was known (Pike, 2011; Stevens et al., 2007). A total of 28 nests were photographed on the beach (latitude N 36° 11' 12.266'', longitude W 5° 55' 2.391'' and latitude N 36° 31' 29.941'' longitude W 6° 13' 40.895''), while an additional 60 nests were found in the “Las Salinas” (saltmarsh) area (latitude N 36° 30' 47.029'', longitude W 6° 9' 4.755''), from April 15 to May 31, 2022. These two areas were chosen because of the difference in habitat and thus type of background against which eggs might be viewed. Nests on the beach were often laid on fine yellow sand, with the only other background components being shells, stones and occasional (mainly dead) vegetation or washed-up debris (Figure 2.3a-d). The saltmarsh was more variable, with nests found on both sand and dried mud that varied in colour from brown to grey, or on shingle (small stones), between larger patches of salt-tolerant plants such as *Salicornia* spp. and a greater size range of stones and debris (Figure 2.3 e-h). Nests were simple unlined scrapes (shallow depressions), and all contained three eggs at the time of surveying.

Figure 2.1. Map of the site of Study in Spain. The city of Cádiz, where the fieldwork was conducted in an area of beach and on saltmarsh ("Salina La Esperanza"), is marked with a red marker.

Figure 2.2. A photograph of a plover nest at a beach location, showing the type of image employed in the research. The four important elements are: the nest containing three eggs, the surrounding background, the ruler (for scale), and the colour chart (for colour calibration).

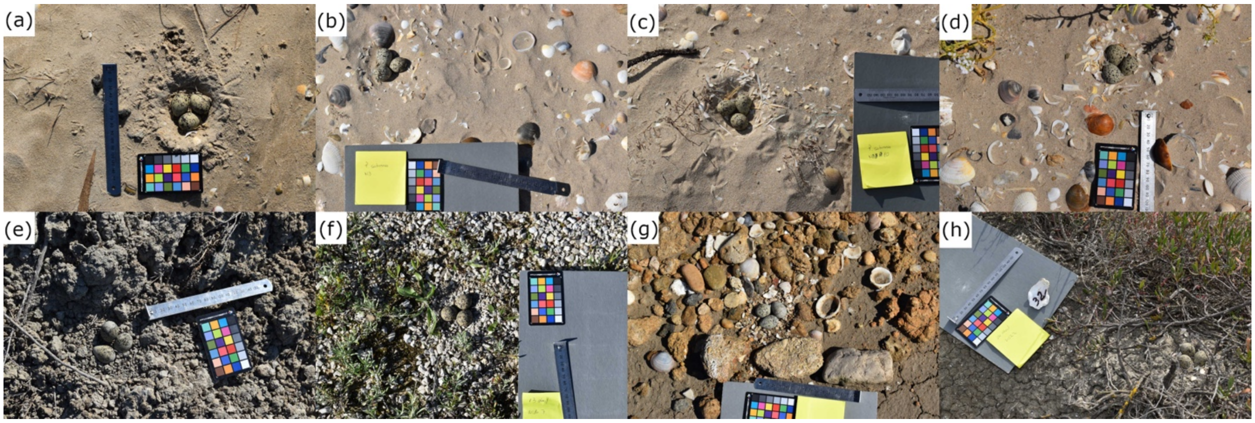

Figure 2.3. Examples of nests at the beach (a to d) and saltmarsh (e to h) sites.

2.3.2 Photography and image calibration

In order to perform the analysis, three steps were necessary: (i) calibrating the photographs such that they represented standardized measures of reflectance rather than camera- and illumination-dependent RGB pixel values; (ii) scaling the photographs to a standard size; (iii) extraction of measures of colour and pattern relevant to different predator visual systems (Stevens et al., 2007; Renoult et al., 2017). This was possible because all photographs contained a colour standard (Colour Card 24; greywhitebalancecolourcard.co.uk) and a ruler. The colour chart had been cross-calibrated with an X-Rite ColorChecker Passport (X-Rite, Grand Rapids, MI, USA) and was used in preference to the latter because, although probably manufactured at a lower precision, the Colour Card 24 was waterproof.

So that the analysis program could identify the relevant objects in the pictures, it was necessary to first create ‘masks’ manually, by selecting certain areas of the photos with digital drawing tools and a mouse. A ‘mask’ is a digital layer, equal in size to the photograph, that contains 1’s where the object is present and 0’s where it is not. This provides a way, in software, to extract different parts of the photograph as needed. For this process, an efficient approach was to create five masks (grey standard, ruler, three eggs) in the one image, each mask being of a different colour that could, subsequently, be used as a key to extract a different part of the matching photograph of a nest: three colours were used for the three different eggs (cyan, magenta and yellow), one green mask for a 40 mm length of the ruler and one red mask for the third darkest grey square of the colour chart (Figure 2.4a). The open-source GIMP-2.1O photo-editing program (www.gimp.org) was used for this, also for equivalent selection of background samples (red for the grey card, green for the ruler, and blue for the background; Figure 2.4b). Then, using the red and green masks, the photos were standardized for colour and size based on the RGB values of the grey card (of which the correct values in sRGB colour space are known), and ruler respectively. So that samples of equivalent size and shape were used to characterise the background as for the eggs, for each photograph, one egg mask was randomly selected and then used as a mask to select a series of egg-shaped samples of the background from within the rectangular area designated as ‘background’ (Figure 2.4b). The xy coordinates for each egg-shaped sample were selected at random, using the R function runif. Twenty-seven random, egg-shaped, background samples were taken from each photograph, such that each photograph gave 30 samples: three eggs and 27 from the background. The number 27 is somewhat arbitrary: large enough to get a better characterisation of each background’s colour and pattern variation but making the calculation of the probability of correctly classifying a sample as ‘egg’ at random straightforward (3 in 30, or 0.1). Lastly, the size-and-colour-calibrated photos were analysed to extract the colours and textures (pattern) of eggs and backgrounds for different visual systems, using mapping functions (matrix multiplication) previously determined when the camera was calibrated. Regarding to the chosen visual systems, were avian, as birds of prey (gulls and corvids are the most likely visual predators), and mammalian carnivore (e.g. canids such as red fox *Vulpes vulpes* or domestic dog *Canis domesticus*, and mustelids). Given the type of birds involved, a VS (violet-sensitive) rather than UVS (ultraviolet-sensitive) visual system was used, the cone sensitivities being that of the peacock *Pavo cristatus* (not because peacocks were likely predators but because it is a well characterised and widely used VS visual system for modelling; Hart, 2002; Maia et al., 2019). Mammalian carnivores are dichromats and the visual system used was that of the ferret *Mustela furo* (Calderone & Jacobs, 2003). Colours were also modelled for human vision, purely for comparison and to provide a form of ground-truth (did the model outputs match what we could see in the photographs?) All calibration and extraction of colour and pattern measures were done using a custom program, written by my supervisor, I. Cuthill, in R (R Core Team, 2023) and the package OpenImageR (Mouselimis, 2023).

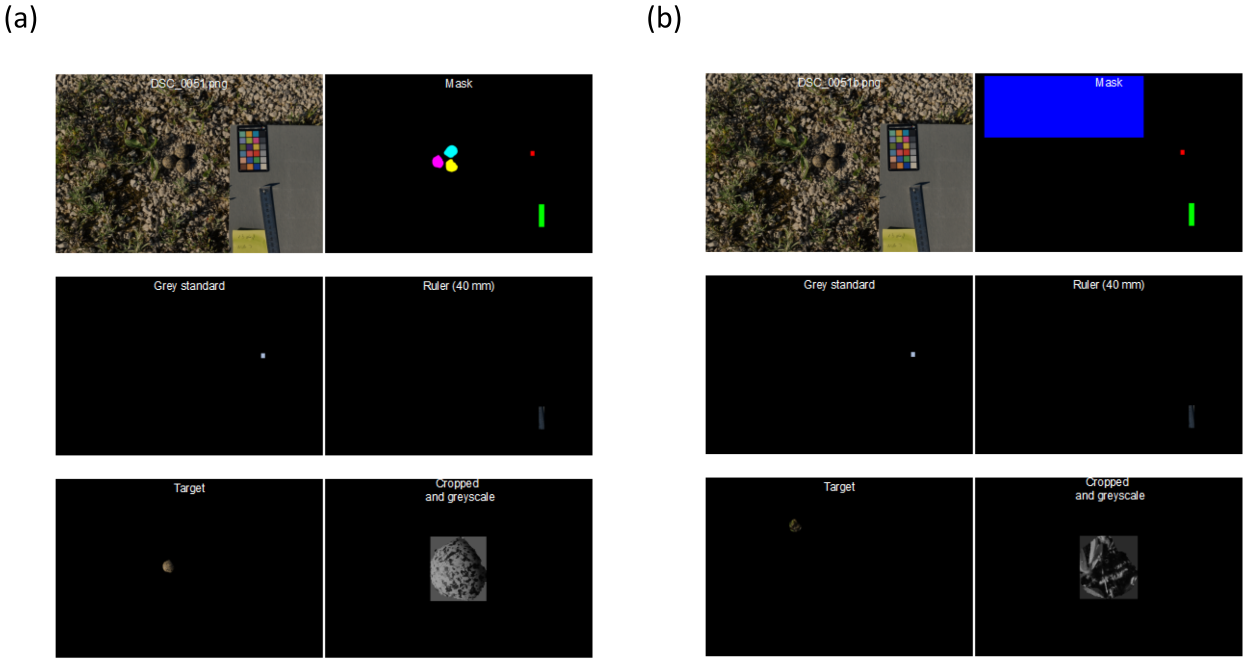

Figure 2.4. Images obtained from the R program to perform the analysis. (a) Selecting one of the three eggs; (b) randomly selecting an egg-shaped region of background. In each case, the six panels are: top left: image as it was taken; top right: masks created manually to select sites of interest (red: grey square; green: 40 mm of the ruler; cyan, magenta and yellow: eggs; blue: background); middle left: grey square used to obtain an equal colour balance across R, G and B colour channels ('white point balancing'); middle right: selected 40 mm piece of the ruler to standardize size; bottom left: selection of target (egg or background); bottom right: target, in greyscale for pattern analysis, after size standardization.

2.3.3 Colour analysis

The colour and texture[1] (pattern) analysis followed that in Michalis et al. (2017) and Barnett et al. (2018a,b). 'Colour' was defined by three variables: luminance (achromatic brightness), red-green chromatic contrast and yellow-blue chromatic contrast. For humans, the L*a*b* colour space is a well characterized representation of this type (L = luminance, a = red-green, b = yellow-

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[1] In vision science, the term 'texture' is used to describe a visual pattern rather than the physical texture of an object, although the two are naturally correlated (what you see predicts the material properties of the surface).

blue) in which distances in this 3-dimensional colour space match perceived colour differences (CIE, 1976). An avian equivalent was also calculated, where luminance was represented by the calculated photon catches of the double-cone receptors, red-green by the contrast in photon catches of the long- and medium-wave single cones, and yellow-blue by the contrast in photon catches of the long- and medium-wave single cones combined compared to the short-wave cones (see discussion and justification in (Xiao & Cuthill, 2016). The VS cone was not used in calculations because, without a camera with distinct blue and violet (or ultraviolet) sensors, the values for VS and SWS cones are very highly correlated. That UV information can be ignored is an untested assumption, but the melanin that creates the brown colour of plover eggs also absorbs strongly in the UV (Kollias, 1995).

2.3.4 Texture analysis

As in Michalis et al. (2017), Barnett et al. (2018a,b) and Talas et al., (2017) texture was characterized by the output of a log-Gabor filter bank of six spatial scales and eight orientations, applied to the luminance plane of each image (Figure 2.5). The luminance signal was used as this is the main contributor to pattern vision for the species modelled (Kelber et al., 2003; Jones & Osorio, 2004). In practice, the same texture analysis was used for all three visual systems (avian, carnivore, humans) because the calculated luminance values for the images (eggs and backgrounds) were so highly correlated: avian-carnivore r = 0.96, avian-human r = 0.99, human-carnivore r = 0.98 (n = 2640; 30 samples from each of 88 nests). Gabor filters are a standard tool in image processing, used to describe textures or detect visual structure. A single Gabor filter is a 2D sine or cosine wave of a given spatial frequency and orientation multiplied by a 2D Gaussian (normal) distribution of a given standard deviation. So, when multiplied by a patch of an image of the same size, the product will have the highest value when the pattern in the image-patch matches the structure of the Gabor filter. When you multiply a whole image by a given Gabor filter (by successively moving it, pixel-by-pixel, across all the rows and columns of the image), the largest values will show you the areas of the image where the orientation and spatial frequency (from coarse to fine grain) match that Gabor. If you repeat this process with a whole set of Gabor filters of different spatial frequencies and orientations, you get a comprehensive description of the patterns of light and dark, of given sizes and orientations, in that image. Rather than, for example, describing a 256x256 pixel image with 65536 numbers (the intensity values of the 65536 pixels), the pattern in the image is described with 48 numbers (6 spatial scales and 8 orientations) (Figure 2.5). Numerous vision specialists in the present era have concluded that the frequency and orientation representations exhibited by Gabor filters bear resemblance to the response properties of certain neurones in the human visual system (e.g. Field, 1987; Field & Olshausen, 1996; Olshausen & Field, 1996; Ruderman et al., 1998). The log of the Gabor output (hence ‘log-Gabor filter’) was used for statistical reasons: the output of a simple Gabor filter is always zero or positive, so correlated with mean luminance, while logged values can be negative.

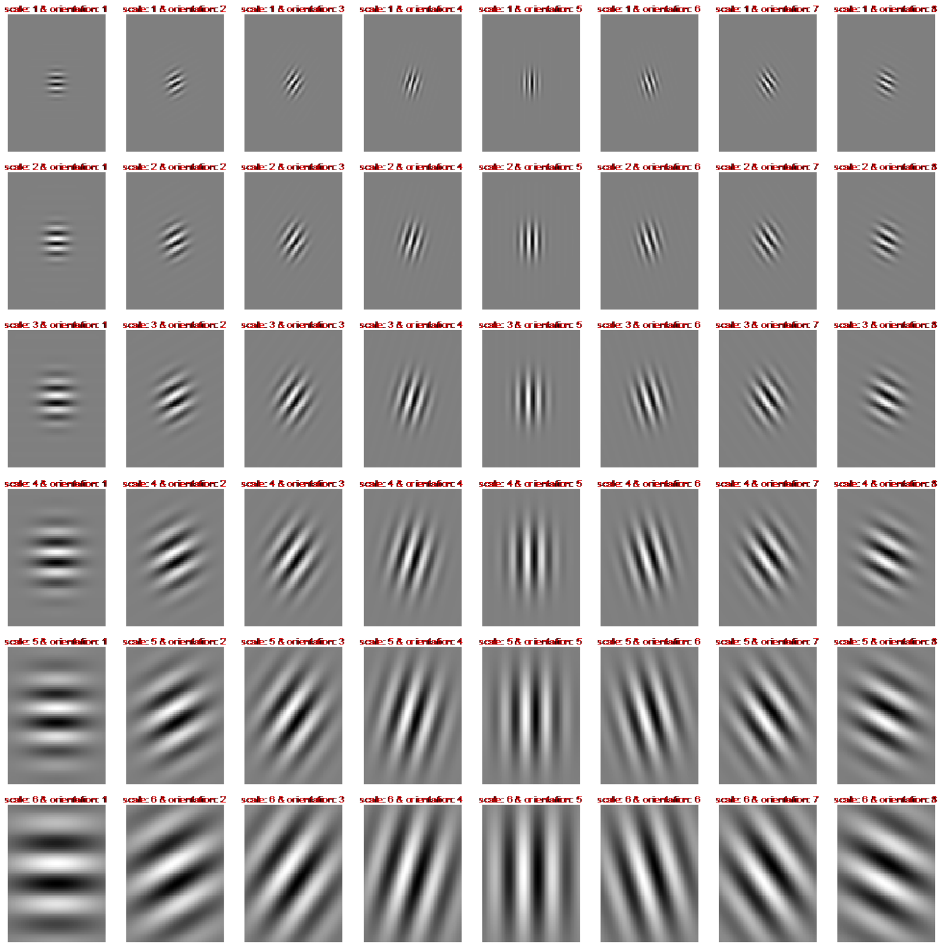

Figure 2.5. The Gabor filter is a linear filter employed in texture analysis. Its primary function is to quantify the presence of distinct frequency components inside a picture, specifically in predetermined directions within a localized area surrounding the point or region of investigation. Shown here are Gabor filter with 6 scales and 8 orientations, as used in this study.

The output of log-Gabor filters like this, when applied to natural images, are correlated because of the fractal nature (self-similarity) of natural scenes (Burton & Moorhead, 1987; Turiel et al., 2000; Párraga et al., 2002); for example, when there is high contrast at large spatial scales there tends to be high contrast at low spatial scales. Because of this, and to reduce the number of response variables to be analysed, Principal Component Analysis was carried out on the correlation matrix of the dataset using the *princomp* function in base R (the approach taken by Talas et al., 2017). Four components had eigenvalues greater than 1 (i.e. explained more variation than any of the original variables) and captured 83% of the total variation in the 48 Gabor outputs (Figure 2.6a; 54, 18, 6 and 5% for PC1 to 4 respectively). We can understand what the components represent by examining their loadings: the contribution of the original variables to each component (Figure 2.6b). The first component (PC1) loads positively on all 48 original Gabor measures: it captures ‘contrast’ regardless of spatial scale (an image with a high value of PC1 would have areas of very light and very dark at both fine and coarse grain). PC2 loads positively on the Gabor filters capturing fine detail and negatively loaded on those capturing coarse detail; an image with a high positive value of PC1 would have more fine detail and few large objects (e.g. sand), while a high negative value would indicate mainly large objects (e.g. pebbles). PC3 and 4 together capture the orientation of edges in an image. The fact that they appear as 180 out-of-phase sine waves in Figure 2.6b is really an artifact of the method: by definition, principal components must be orthogonal (uncorrelated) so, if PC3 captures the relative importance of one set of orientations, PC4 is always likely to show the opposite pattern of loadings. The specific angles involved are not of interest for this study (these eggs and backgrounds are not striped), unlike the orientation of striped moths on striped tree bark (e.g. Kang et al., 2012; 2013b; 2014). Note that the analysis is at the level of ‘egg-sized’ objects and so any spatial variation in light and dark greater than this is not captured by our Gabor features or the principal components derived from them.

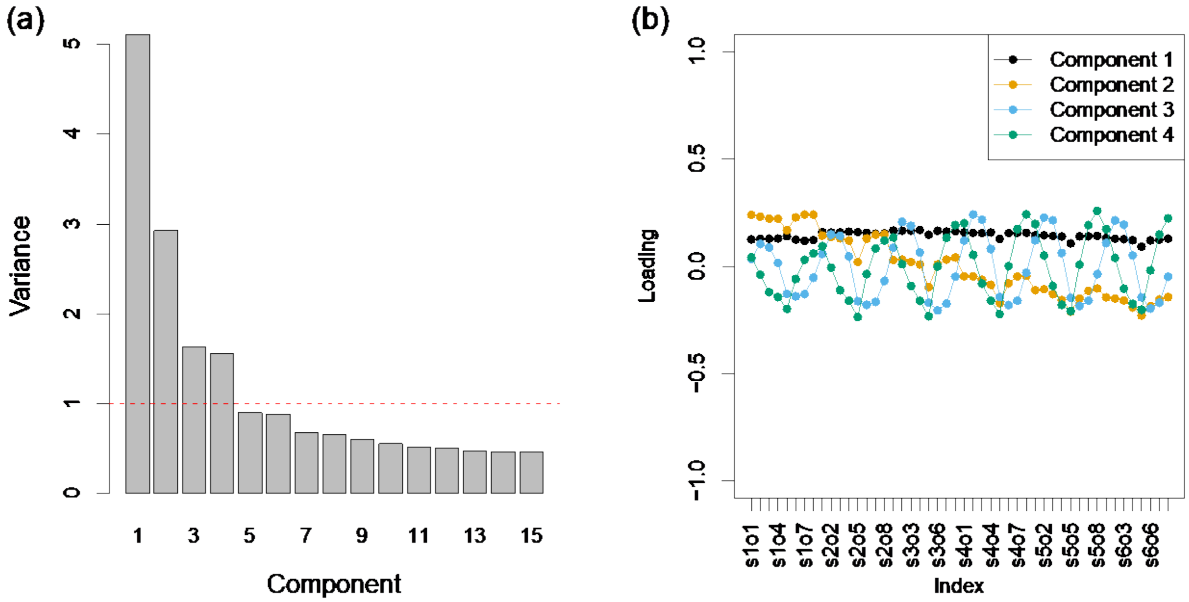

Figure 2.6. (a) The eigenvalues (variance) of the first 15 (of 48) principal components derived from Principal Component Analysis of the 48 log-Gabor filter outputs used to describe the texture (spatial pattern) of the eggs and backgrounds. (b) The loadings of the principal components on the original 48 variables: i.e. the contribution of the original variables to each component. The original Gabor variables (x-axis) are named such that the first two letters (s1, s2,…, s6) describe the spatial scale (1 is fine detail, 6 is the coarsest detail) and the second two letters (,o1, o2,… o8) describe the orientation of the filter, from horizontal (o1) turning anti-clockwise. For further help in interpretation, refer to Figure 2.5 for images of the filters themselves.

2.3.5 Statistical analysis

Analysis of the differences in the means of the response variables describing colour and texture was by linear mixed models, using the function lmer from the lme4 package (Bates et al., 2015). With multiple replicates (3 eggs, 27 background samples) taken from each photograph/nest, photograph was included as a random effect in all models. The predictors were either location (beach vs saltmarsh) or object type (egg vs background) according to the question involved. The lmerTest package was used to obtain p-values from t- tests using Satterthwaite's method to calculate the appropriate degrees of freedom (Kuznetsova et al., 2017). For the texture measures based on PCA of the log-Gabor filter outputs, I also carried out Multivariate Analysis of Variance

(MANOVA) on all four principal components as joint response variables, using Pillai's trace as both a test statistic and measure of effect size equivalent to R^2 (Pillai, 1955). This is a multivariate equivalent of R^2 in regression and is also equivalent to the partial eta^2 statistic provided by the widely used statistics package SPSS. To obtain a p-value I used the approximate F test provided by the MANOVA function in R, based on Pillai's trace and the ratio of the location variance to the between-nest (i.e. photograph) variance. The reason to use MANOVA to analyse the texture measures jointly was both as a protection against the elevated Type I (false positive) error rates of testing PC1 to PC4 separately but also, and more importantly, because these statistical measures of texture do not have the same perceptual interpretation as the colour measures. That is, the separate neural processing of luminance and colour (hue) is understood, but perceptual dimensions of texture ('pattern') are not (Stoddard & Osorio, 2019).

Of greater relevance to camouflage than differences between the mean colours or patterns of eggs and their backgrounds is their discriminability/confusability (Xiao & Cuthill, 2016; Michalis et al., 2017; Barnett et al., 2018b, 2021). If one imagines egg colours and background colours as two clouds of points in a colour space, how much do the distributions overlap (Endler & Mielke, 2005)? This is a signal detection problem, with the egg features being the signal and the background features the noise (Merilaita et al., 2017). Unless the two distributions do not overlap, there is no single criterion that can perfectly distinguish one from the other: a threshold that classifies more eggs correctly will incorrectly classify more background features as belonging to eggs (false positives), and a threshold that classifies more backgrounds correctly will incorrectly classify more egg features as being part of the background (failed detections). That trade-off can be visualized as an ROC (Receiver Operating Characteristic) curve, where 'sensitivity' (correct classifications of eggs as eggs) is plotted against 'specificity' (correct classification of backgrounds as backgrounds) (Wickens, 2002). This is standard practice in machine learning, as is the procedure of "cross validation" of the discrimination model (Lantz, 2013). The goodness of fit of a model to a set of data will always be better than the success of that model when applied to new data of the same type, known as 'over-fitting'. This is because some of the variation in any one sample of data is random noise, so a model fitted to those data will not fit a new sample (with different random sampling variation) as well as it did the original data. In machine learning, the solution to this is to fit a model to one set of data (‘training’) but test it with a different set of data (Lantz, 2013). There are different ways you can do this (e.g. randomly divide the dataset in two, an approach taken by Barnett et al., (2021), when analysing camouflage in leaf-mimicking toads) but I used the computationally more intensive leave-one-out cross validation, because it makes fuller use of the data (Lantz, 2013). As the name suggest, the discrimination model is fitted to the data of all-but-one nest, then the model’s success in correctly classifying the eggs and background samples from the remaining nest is assessed (the probability of the object being an egg, or background, is the output). The process is repeated for every nest, each time training the model on the other nests. The discrimination model used was a generalized linear mixed model with binomial error, fitted using the glmer function from the lme4 package. The response variable was object type (egg or background), the fixed effect predictors the colour or pattern metrics for different visual systems, and the random effect photograph (nest). Classification errors were calculated using the confusionMatrix function from the caret package (Kuhn, 2008) and ROC curves were fitted using the pROC function from the package of the same name (Robin et al., 2011).

2.4 Results

Viewing the colours of eggs and backgrounds from the beach and saltmarsh as they appear to us gives an immediate impression that the egg colours are similar from the two habitats but, as a background, the saltmarsh is more variable and, on average, darker than the beach (Figure 2.7). Statistical analysis, using linear mixed models, of the components of both avian and carnivore colour models mirrors this subjective view from human perception. Analysing all the data together with respect to both object type (egg/background) and location (beach/saltmarsh), there are significant type*location interactions for all measures of colour and pattern (Table 2.1). One can break this interaction down in two ways and both are of interest. First, analysing eggs and backgrounds separately, do egg colours and patterns differ between the beach and saltmarsh (indicating either local adaptation or background choice) and the matching question of do the backgrounds differ? But another split of the data is of direct relevance to quantifying camouflage in the two habitats: analysing beach and saltmarsh habitats separately, how do egg and background colours and textures differ, and how confusable are they?

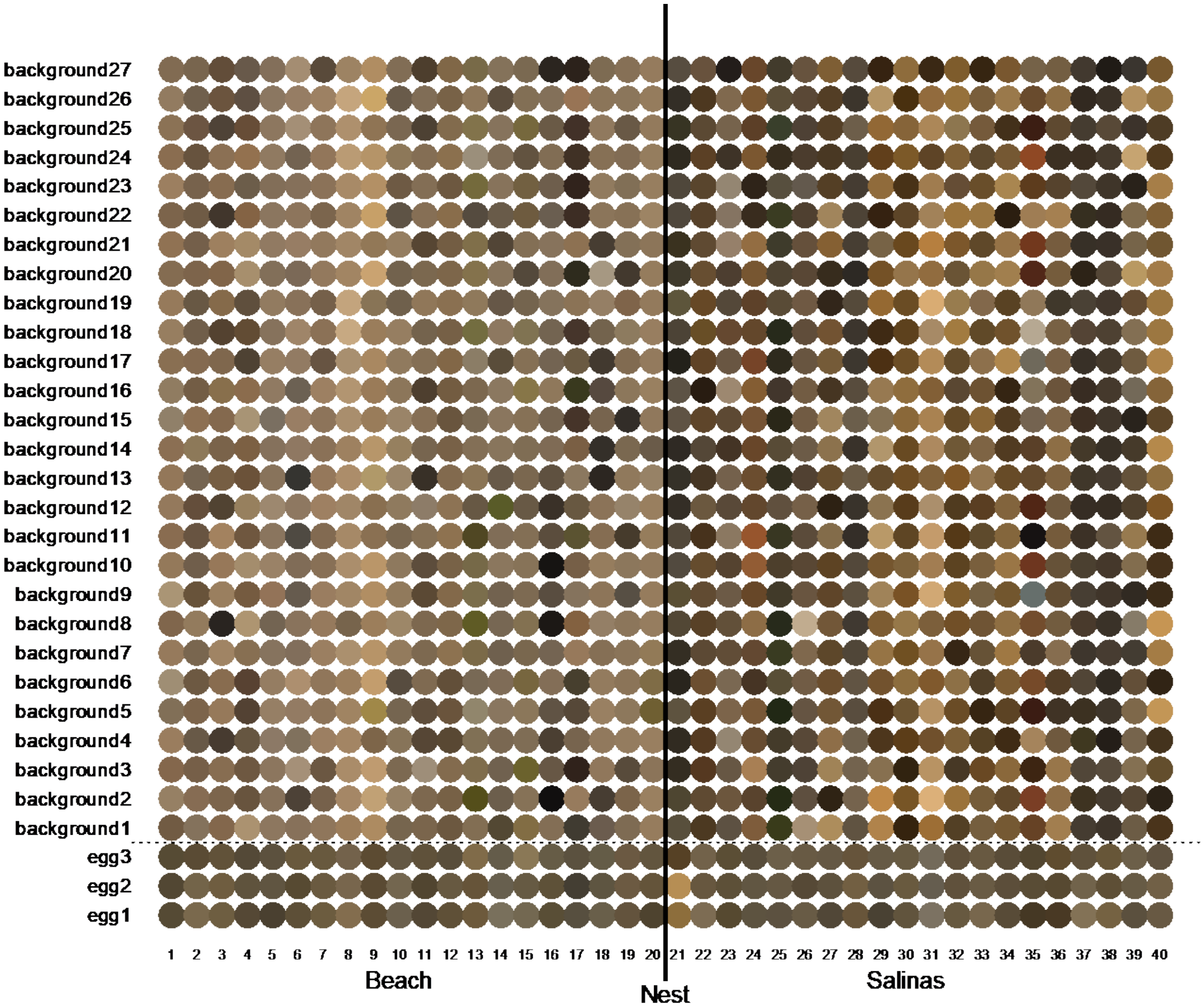

Figure 2.7. Examples of the colours of the three eggs in each nest, and their respective 27 background samples, based on a random sample of 20 nests from the beach and saltmarsh.

Table 2.1. Analysing egg and background colours and textures: tests of the interaction between object type (egg/background) and location (beach/saltmarsh) based on linear mixed models.

	t or F	df	p
Avian luminance	4.999	2550	<0.001
Avian RG	4.507	2550	<0.001
Avian YB	11.706	2550	<0.001
Carnivore luminance	7.841	2550	<0.001
Carnivore YB	11.504	2550	<0.001
PC1-4 jointly (F)	33.910	4, 2547	<0.001
PC1	2.234	2550	0.026
PC2	5.801	2550	<0.001
PC3	6.944	2550	<0.001
PC4	6.624	2550	<0.001

The test statistic for all measures is Satterthwaite's t from linear mixed models, except for the joint analysis of the texture measures PC1 to 4, which is an approximate F-test from MANOVA.

First, do the eggs in the two habitats differ in appearance? To an avian predator, the beach and saltmarsh eggs are not significantly different in mean luminance, red-green or yellow-blue colour measures (Table 2.2). Similarly, to a mammalian carnivore, there is no detectable difference in mean luminance or yellow-blue colour measures (Table 2.2). There is also no detectable difference in texture (Table 2.2), assumed to be similar for both visual systems. Conversely, to an avian predator, the saltmarsh backgrounds are on average darker and slightly, but significantly, more reddish-brown than the beach (higher red-green and yellow-blue values; Table 2.2). Likewise, a mammalian carnivore would perceive the saltmarsh backgrounds as, on average, darker and browner (Table 2.2). The textures of the backgrounds also differ, the saltmarsh having higher overall contrast (PC1), being coarser-grained and having a different distribution of edge orientations from the beach (PC3 and 4; Table 2.2). This tallies with the higher proportion of pebbles and patches of vegetation in the saltmarsh.

Table 2.2. Comparison of mean colour and texture measures between the beach and saltmarsh habitats, separately for eggs and backgrounds.

	Eggs			Backgrounds		
Measure	t or F	df	p	t or F	df	p
Avian luminance	1.821	86	0.072	5.497	86	<0.001
Avian RG	0.100	86	0.920	2.335	86	0.022
Avian YB	0.431	86	0.667	4.872	86	<0.001
Carnivore luminance	1.661	86	0.100	8.706	86	<0.001
Carnivore YB	0.572	86	0.569	4.837	86	<0.001
PC1-4 jointly (F)	1.295	4,83	0.279	30.234	4,83	<0.001
PC1	1.408	86	0.163	3.975	86	<0.001
PC2	2.167	86	0.033	9.155	86	<0.001
PC3	1.708	86	0.091	2.852	86	0.005
PC4	1.359	86	0.178	3.033	86	0.003

The test statistic for all measures is Satterthwaite's t from linear mixed models, except for the joint analysis of the texture measures PC1 to 4, which is an approximate F-test from MANOVA.

In terms of the mean values of colour and texture metrics, plover eggs do not match the background in either habitat, for either avian or carnivore visual system (Table 2.3). The significant object-type*location interaction reported earlier (Table 2.1) arises because the eggs mismatch the two habitats in different ways. In both habitats, eggs are on average darker than the background but, in the beach habitat, the difference is larger (Table 2.3; Figures 2.8, 2.9). On the beach, the eggs are slightly yellower than the background but, in the saltmarsh, less yellow; the eggs are less red than the backgrounds in both habitats but the difference is greater in the saltmarsh (Table 2.3; Figures 2.8, 2.9). Note that 'yellower' and 'less red' are purely with respect to these colour dimensions; these are all shades of brown. Considering texture (Table 2.3; Figure 2.10), the mismatch between eggs and backgrounds for PC1 (overall contrast) is greater in the beach than saltmarsh, the latter habitat having a greater range of dark and light objects than the beach and the eggs, being essentially two-tone (dark maculation on lighter background), also high in contrast. Conversely, the mismatch for PC2 (relative amount of fine- to coarse-grain patterning) is greater for the saltmarsh, the latter having more pebbles that are smaller than an egg but larger in size than the finer-grained maculation of the eggs. PC3 and PC4 are much more similar between the habitats, but the means are still significantly different (Table 2.2) and the eggs differ more from the beach means than the saltmarsh (Table 2.3; Figure 2.10).

Table 2.3. Comparison of mean colour and texture measures between eggs and backgrounds, separately analysed for the beach and saltmarsh habitats.

	Beach				Saltmarsh			
	Effect	t or F	df	p	Effect	t or F	df	p
Avian luminance	-0.105	10.910	811	<0.001	-0.030	3.208	1739	0.001
Avian RG	-0.011	9.847	811	<0.001	-0.020	16.650	1739	<0.001
Avian YB	0.004	2.380	811	0.018	-0.034	16.390	1739	<0.001
Carnivore luminance	-0.086	10.960	811	<0.001	0.004	0.533	1739	0.594
Carnivore YB	0.006	3.073	811	0.002	-0.038	15.510	1739	<0.001
PC1-4 jointly (F)	0.453	167.100	4, 808	<0.001	0.456	363.890	4, 1736	<0.001
PC1	1.807	4.405	811	<0.001	0.481	1.346	1739	0.1785
PC2	3.672	15.103	811	<0.001	5.228	36.310	1739	<0.001
PC3	1.878	11.776	811	<0.001	0.598	5.894	1739	<0.001
PC4	1.919	12.283	811	<0.001	0.718	7.179	1739	<0.001

With the exception of the joint analysis of the texture measures PC1 to PC4, where the effect measure is Pillai's trace from MANOVA, the effect size is the difference in standardised mean between egg and background (so a negative sign means a lower value for the egg than the background). The test statistic for all measures is Satterthwaite's t from linear mixed models, except for the joint analysis of the texture measures PC1 to 4, which is an approximate F-test from MANOVA.

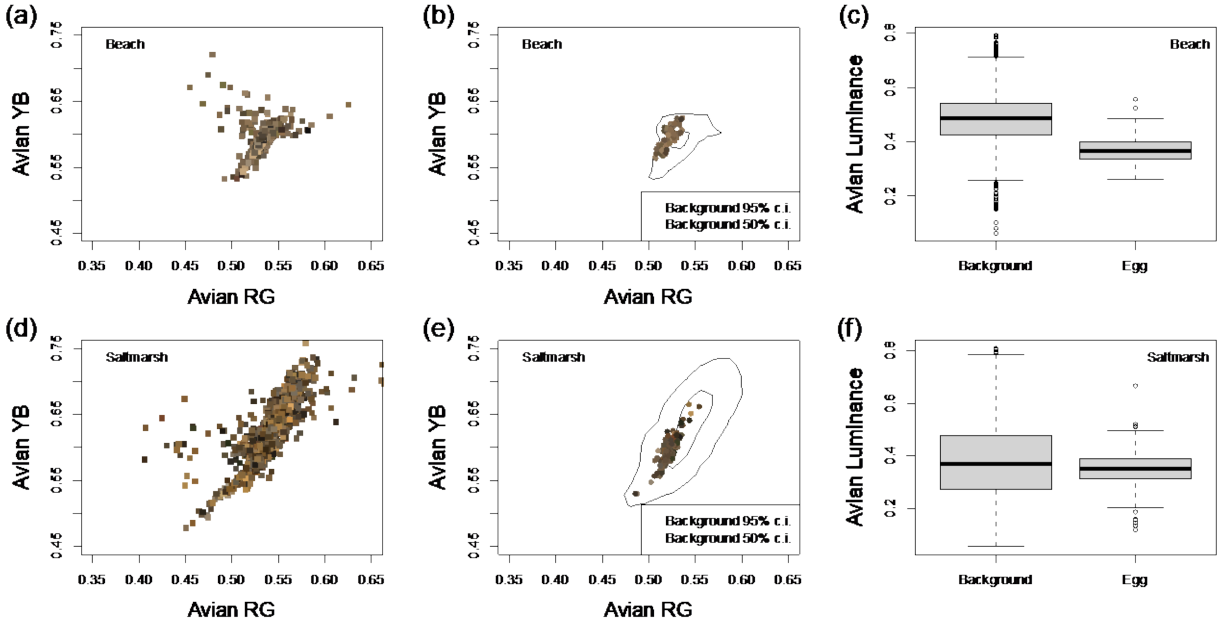

Figure 2.8. Avian-perceived colours of eggs and backgrounds in the beach (top row) and saltmarsh (bottom row) habitats. (a) The hues of background samples represented in avian red-green (RG) and yellow-blue (YB) opponent space. (b) The background distributions in panel (a) are summarised by their 95% and 50% kernels, with the hues of eggs in the beach habitat superimposed as individual points. The point colours in both panels represent the colours as seen by humans. (c) The avian luminance (double cone catch) distribution of background samples and eggs, represented as boxplots. The thick horizontal line is the median; the box spans the lower to upper quartile; the 'whiskers' extend to the last data point within 1.5 inter-quartile ranges of the nearest quartile; the open circles are points outside the whiskers. Panels (d) to (f) are the equivalent plots for the saltmarsh habitat.

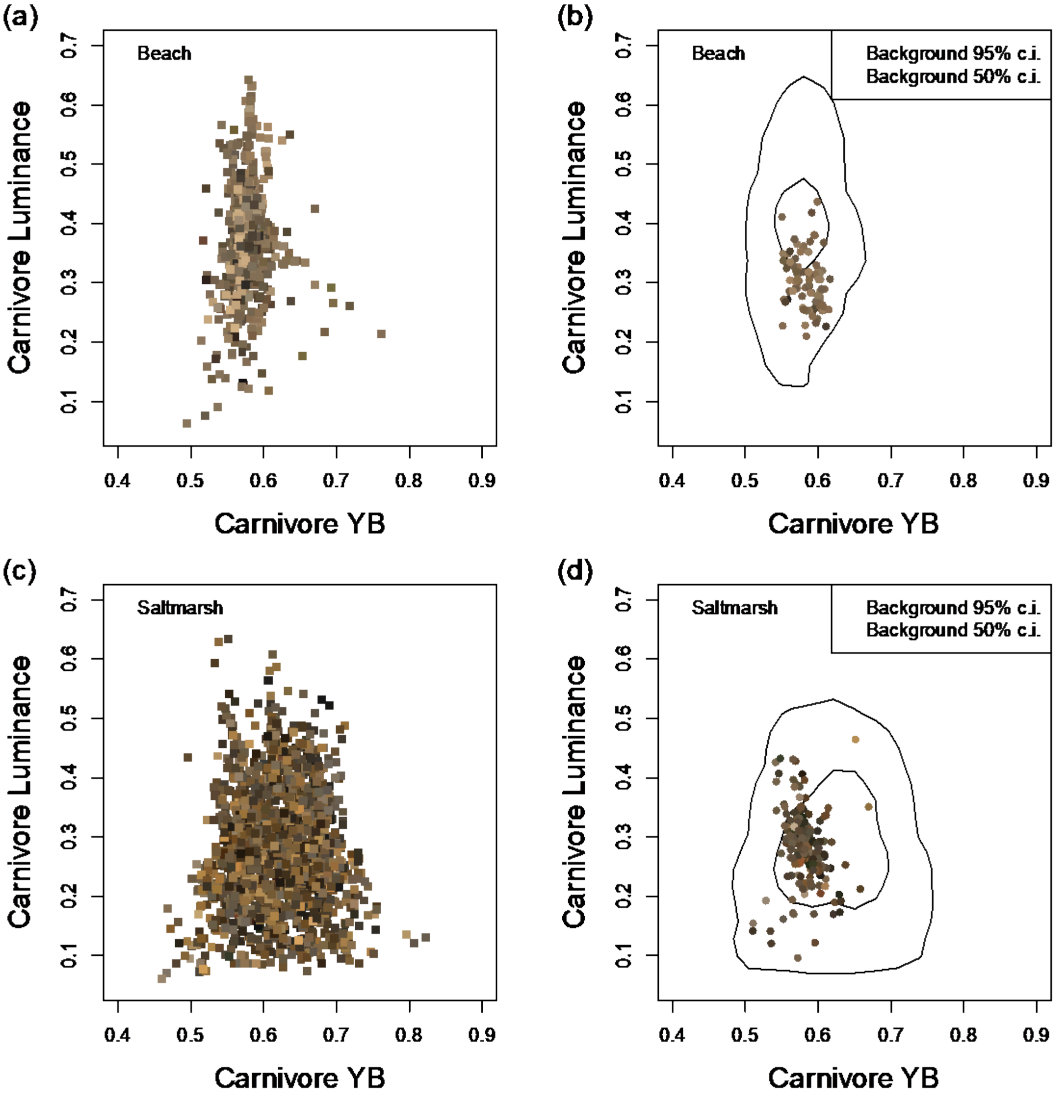

Figure 2.9. Colours of eggs and backgrounds in mammalian carnivore colour space, in the beach (top row) and saltmarsh (bottom row) habitats. (a) Carnivores are dichromats, so the colours of background samples can be fully represented in a luminance and yellow-blue (YB) opponent colour space. (b) The background distributions in panel (a) are summarised by their 95% and 50% kernels, with the colours of eggs in the beach habitat superimposed as individual points. The point colours in both panels represent the colours as seen by humans. Panels (c) and (d) are the equivalent plots for the saltmarsh habitat.

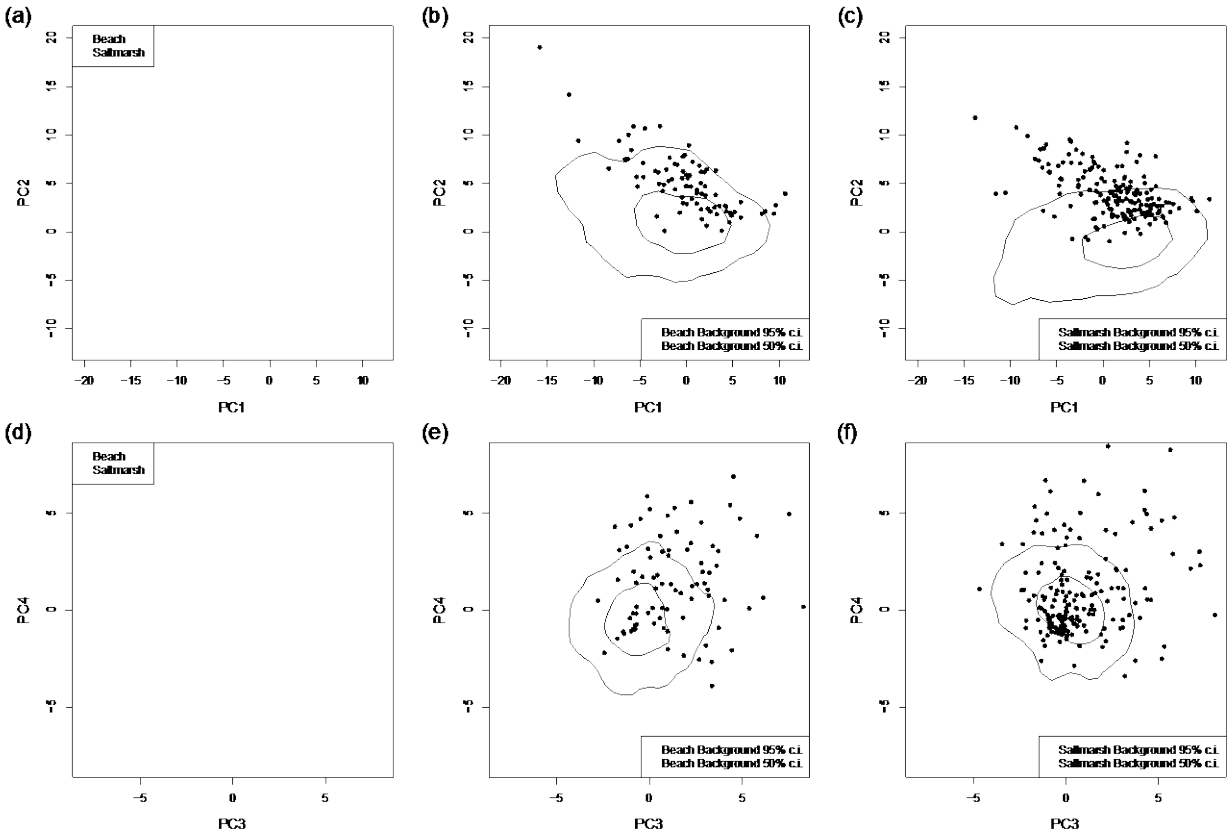

Figure 2.10. Differences between backgrounds and eggs for the principal components describing texture (top row: PC2 vs. PC1; bottom row: PC4 vs. PC3). (a) PC2 (relative amount of fine- to coarse-grain patterning) plotted against PC1 (overall contrast) for background samples from the beach (grey) and saltmarsh (red). (b) Background data summarised by their 95% and 50% kernels, with the PC1 and 2 values of eggs in the beach habitat superimposed as individual points. (c) 95% and 50% kernels for the saltmarsh backgrounds with the PC1 and 2 values of eggs in the beach habitat superimposed as individual points. (d) to (f) are the equivalent graphs for PC4 plotted against PC3; both PCs capture variation in line and edge orientations.

Figure 2.11 plots the same colour and texture data in a different way, a way that is relevant to understanding whether the eggs have ‘compromise camouflage’ intermediate to the beach and saltmarsh backgrounds. One can see that the hues of the beach and saltmarsh backgrounds, as seen by birds (Figure 2.11a) or mammalian carnivores (Figure 2.11c), while on average different (Table 2.2), overlap considerably. The eggs hues fall in the regions of overlap, although the egg luminance, for either visual system, is closer to the saltmarsh in distribution (Figure 2.11b,c). The patterning of the eggs, in terms of overall contrast (PC1) or relative amount of fine-grained detail (PC2) overlaps that of the beach somewhat more but is close to the centre of neither background distribution (Figure 2.11d; PC3 and 4 are not plotted as their distributions are more similar for the two habitats: Figure 2.10d).

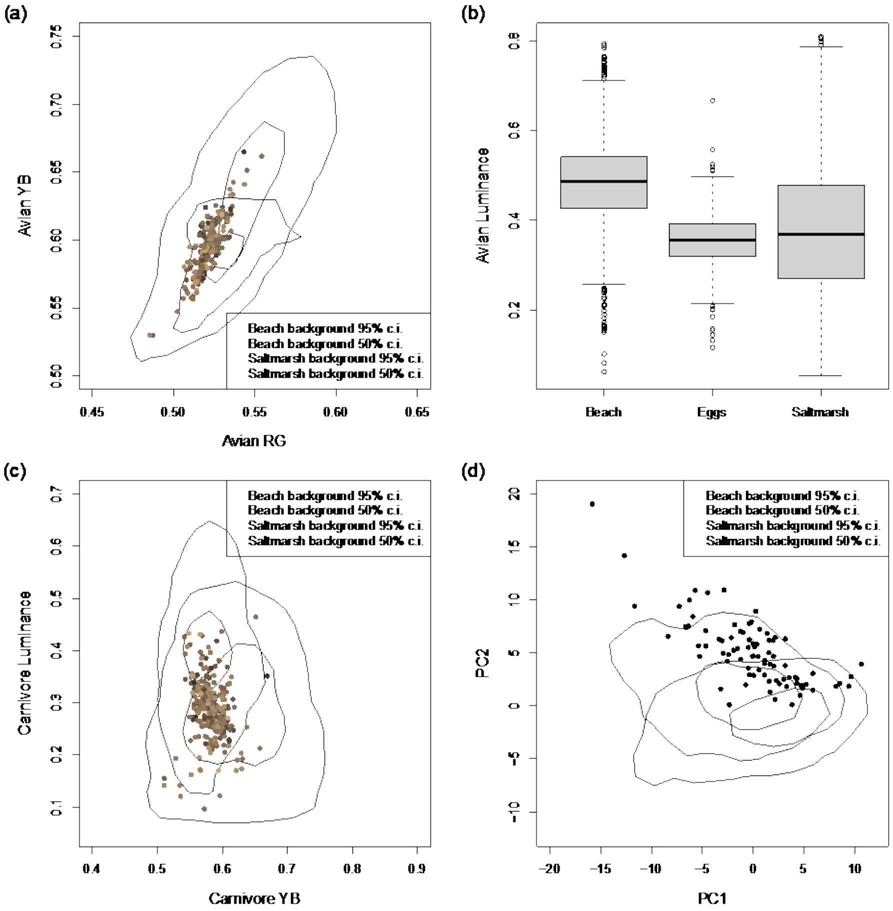

Figure 2.11. (a) Overlap in the 95% (darker) and 50% (lighter) kernels of the background samples from beach (grey) and saltmarsh (red) represented in avian red-green (RG) and yellow-blue (YB) opponent space, with the hues of eggs superimposed as individual points. The point colours represent the colours as seen by humans. (b) The avian luminance (double cone catch) distribution of background samples from, left to right, beach, eggs and saltmarsh, represented as boxplots. The thick horizontal line is the median; the box spans the lower to upper quartile; the

‘whiskers’ extend to the last data point within 1.5 inter-quartile ranges of the nearest quartile; the open circles are points outside the whiskers. (c) Overlap in the 95% (darker) and 50% (lighter) kernels of the background samples from beach (grey) and saltmarsh (red) represented in mammalian carnivore luminance and yellow-blue (YB) opponent colour space, with the hues of eggs superimposed as individual points. (d) Overlap in the 95% and 50% kernels of PC2 (relative amount of fine- to coarse-grain patterning) and PC1 (overall contrast) for background samples from the beach (grey) and saltmarsh (red). As with the colour space plots, the PC1 and 2 values of eggs are superimposed as individual points.

Although eggs and backgrounds in either habitat differ in their mean values for all aspects of colour and texture, it is clear that the distributions overlap considerably for both avian and carnivore vision (Figures 2.8 to 2.11). Confusion matrices and ROC curves based on classification models with leave-one-out cross-validation quantify that overlap: the discriminability (converse: confusability) of the colours and textures. Classification accuracy appears high, but it is important to remember that there were nine times as many background as egg samples (27 background samples and 3 eggs per nest), so the naïve rule of ‘classify all objects as background’ would have an accuracy of 0.9 (all backgrounds correct, all eggs incorrect). This is known as the ‘no information rate’ and the obtained accuracies using colour measures alone (for human, bird or carnivore vision) are lower than this. Few or no eggs are correctly classified based on colour alone. There is no clear difference between the habitats (correct identification of eggs is slightly higher in the saltmarsh, but correct identification of backgrounds is slightly higher in the beach; Table 2.4). Incorporating texture information yields greater classification success, with pattern alone being a better criterion than the naïve rule, with over 70% of eggs correctly classified. Using both colour and texture information is better still, with human vision achieving perfect classification and outperforming that of birds, and both outperforming carnivore vision. In the saltmarsh habitat, the classification success of carnivore vision drops to that of the naïve rule; with hardly any eggs classified correctly but 98% of backgrounds correctly classified, the model is essentially matching the no-information rule of classifying all objects as backgrounds.

Table 2.4. Measures of classification success based on binomial mixed models with leave-one-out cross-validation. Separate analyses for beach and saltmarsh habitats.

	Accuracy		Sensitivity		Specificity	
Measure	Beach	Saltmarsh	Beach	Saltmarsh	Beach	Saltmarsh
Human colour	0.86	0.85	0.00	0.10	0.96	0.94
Avian colour	0.87	0.84	0.00	0.02	0.97	0.93
Carnivore colour	0.88	0.88	0.00	0.01	0.98	0.98
Pattern	0.94	0.95	0.71	0.69	0.96	0.98
Human both	0.98	1.00	0.90	1.00	0.98	1.00
Avian both	0.97	0.94	0.88	0.86	0.98	0.95
Carnivore both	0.96	0.88	0.80	0.01	0.98	0.98

Accuracy is the proportion of eggs and backgrounds classified correctly. Sensitivity is the proportion of eggs correctly classified as eggs, Specificity is the proportion of background samples correctly classified as backgrounds.

The classification accuracy discussed above assumes that the costs of failing to identify an egg correctly (Type II error: failed detection) is the same as failing to identify a background sample correctly (Type I error; false positive), which may not be true. Therefore it is helpful to look at the complete trade-off between type I and II errors as shown in ROC curves (Figure 2.12 and 2.13). Using both colour and texture information, as would be the case for a predator very close to the nest, the modelling predicts no trade-off for humans searching on a saltmarsh (no errors of either kind) and only a small trade-off on the beach (Figure 2.12a and Table 2.4). However, although classification performance for avian vision is also very high, an avian predator seeking to detect all eggs (sensitivity = 1) would have to accept a false positive rate over 20% (specificity < 0.8) in either habitat (Figure 2.12b). Carnivore classification performance on the saltmarsh is predicted to be poor: to achieve 100% egg detection, a false positive rate over 75% (specificity < 0.25) would be incurred (Figure 2.12c).

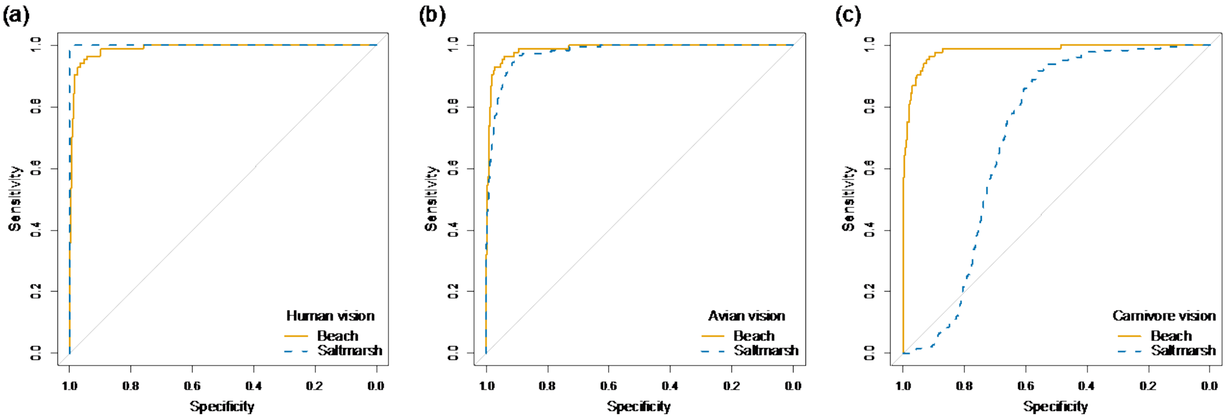

Figure 2.12. Receiver Operating Characteristic (ROC) curves for (a) humans, (b) avian and (c) mammalian carnivore predators, using both colour and texture information, separately plotted for beach (orange solid lines) and saltmarsh (blue dashed lines). Sensitivity is the proportion of eggs correctly classified as eggs; specificity is the proportion of background samples correctly classified as backgrounds.

The relative contributions of colour and texture information can be separated by calculating the ROC curves for each type of information (Figure 2.13). The role of colour alone is relevant for detection at a distance, i.e. at distances above which the patterns on the eggs and background sample of a similar size cannot be resolved. Using texture information alone, high sensitivity can be achieved at higher specificities than using colour alone, in either habitat for any of the three visual systems. Therefore it is texture that is the major contributor to the classification success seen in Figure 2.12, using all available information. On the beach, humans and birds face similar trade-offs when using colour alone, with a much steeper trade-off (the false positive rate for a given level of egg detection) for mammalian carnivore vision. On the saltmarsh, the strength of trade-off is human < avian < carnivore, and somewhat steeper than on the beach.

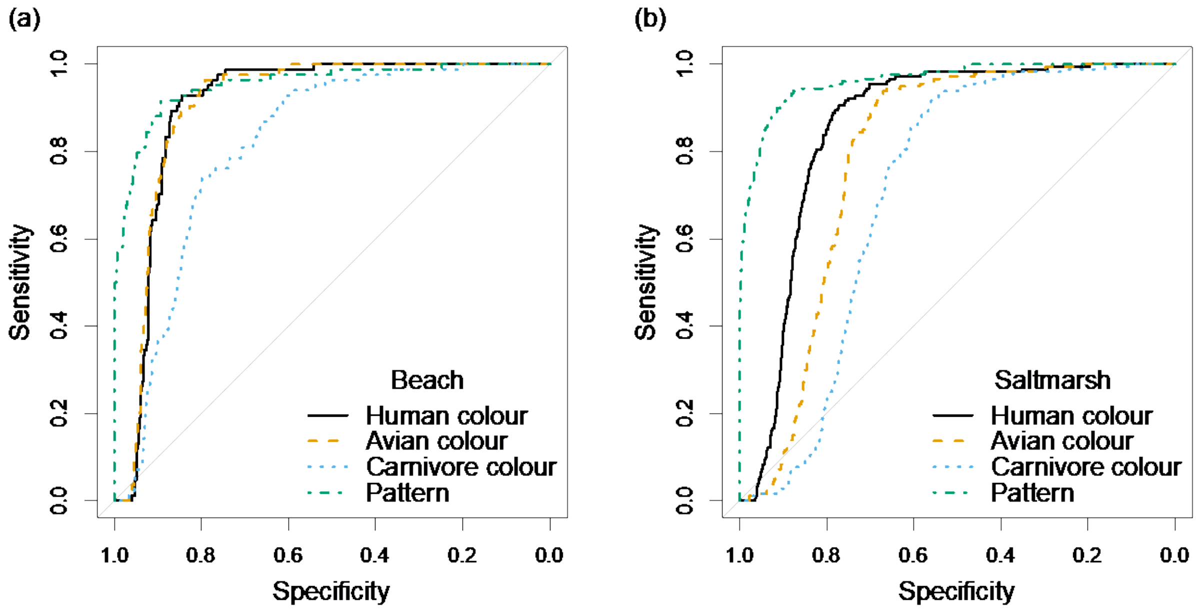

Figure 2.13. Receiver Operating Characteristic (ROC) curves using colour information only (human, avian and mammalian carnivore vision plotted separately), and texture, for (a) beach and (b) saltmarsh habitats. Sensitivity is the proportion of eggs correctly classified as eggs; specificity is the proportion of background samples correctly classified as backgrounds.

2.5 Discussion

Three main issues arising from the results will be discussed: whether and in what ways eggs are camouflaged, whether the eggs are better adapted (in terms of reduced visual detectability) to beach or saltmarsh habitats or whether they exhibit intermediate ‘compromise’ camouflage, and general messages about how best to study camouflage.

For an avian (or human) predator that is close enough to nests to see the surface patterning, plover eggs are easily distinguishable from the background in either the beach or saltmarsh habitats. Even without formal analysis showing noticeably higher values of PC2 (high spatial frequencies) in the eggs than backgrounds (Figure 2.10b,c), this could be anticipated because the egg patterns consist of small dark dots and wispy lines, unlike common small background objects like pebbles and bits of vegetation. I will return to why egg patterns do not closely match the background later. Conversely, at a distance beyond which egg patterns cannot be resolved and only average colour can be used by predators, the eggs are quite cryptic. While there is a statistically significant difference between the means of all colour metrics, for each visual system investigated, the distributions overlap considerably and so egg and background colours are readily confused. Because egg colours are less variable than background colours, there are a large number of background objects which could never be eggs (based on colour), but there are still a considerable number that could be. In technical terms, predator can set a colour-based threshold for classifying an object as ‘egg’ or ‘background’, but a high detection rate for eggs can only be achieved at the expense of a high false positive rate (backgrounds misclassified as eggs).

It must be emphasised that this study only investigated background matching: whether the surface colours and textures of eggs were similar to those of the background (Merilaita & Stevens, 2011). No aspects of egg shape were considered. Depending on the height of the sun and surrounding objects, the cast shadow on the adjacent ground or the shape-from-shading cues created by directional illumination could reveal an egg (Cott, 1940; Penacchio et al., 2015b). This is likely to be a greater problem in an open habitat like the beach, where vegetation does not create shading or its own cast shadows. Eggs are geometrically very regular objects, unlike stones of a similar size, and so the outline itself could be a cue to predators (Cott, 1940; Webster et al., 2015). This may be relevant to understanding the maculation on the eggs which, at face value, do not aid background matching when a predator is close. Previous studies have shown that eggs exhibiting a higher quantity of spots possess improved camouflage (Montevecchi, 1976; Kilner, 2006; Gómez et al., 2016; Troscianko et al., 2016a,b), but seemingly not in this study. However, as opposed to matching the background, the dark maculation could act as edge-disruptive colouration, shown by Lovell et al. (2013) to be a likely factor in the camouflage of quail eggs, or surface disruptive colouration to reduce the homogeneity of colour that might itself be revealing (Stevens et al., 2009). That said, if contrasting colour patches are there to create disruptive camouflage, why are they not larger? Larger colour patches would be more effective at edge-disruption because the true edge would be interrupted more and false edges would be more distinctive (Stevens & Cuthill, 2006; Espinosa & Cuthill, 2014). Also, disruptive colouration is most effective when combined with background matching (Stevens et al., 2006; Fraser et al., 2007). All this points to disruption being an unlikely function of the maculation on the eggs. Other possibilities are that larger dark patches, because of heat absorption, are too costly in terms of thermoregulation when a parent is off the nest (Wisocki et al, 2020). Having a mixture of lighter base colour and small maculation patches may achieve an average colour that is a good match to the background, but at lower cost than a darker, evenly coloured egg. This is speculation, but the combined thermal and visual consequences of different patterns of maculation (as opposed to average colour) should be investigated. The final possibility is that there is some other habitat, not investigated, to which the birds are better adapted, and that the sites in my study were peripheral, suboptimal, choices. This seems unlikely because other accounts of Kentish plover breeding ecology, across the world, discuss habitats very similar to the ones that I studied (Székely & Cuthill, 1999; Kosztolányi et al., 2003, 2007; AlRashidi et al., 2010, 2011; Mcdonald et al., 2022).

Although the two habitats studied, beach and saltmarsh, were superficially quite visually different (the former dominated by sand, the latter with muddy and vegetated areas), there was considerable overlap in both colour and texture: both contained sandy and pebbly areas. Furthermore, and importantly, it was the overlapping areas (in terms of colour and texture) which the plover eggs matched. Therefore, although based on overall subjective appearance of the habitats, we had predicted that the birds' eggs might display local adaptation, either diverging in egg appearance in the two habitats, or either specialise on matching one habitat or show intermediate (compromise) camouflage, the birds did none of these things. They specialised on the microhabitat characteristics which allowed successful camouflage (from a distance) in both habitats.

Stevens et al. (2017) presented two mechanisms to explain how birds might achieve nest camouflage. The first is adaptation through natural selection, whereby the better camouflaged eggs are the ones that survive predation and so these characteristics are transmitted and refined over successive generations. The second, and not mutually exclusive, hypothesis suggests that birds learn to recognize their own eggs over time, or there is some genetic correlation between egg appearance and nest-site-preference, enabling them to make informed decisions regarding their placement. Both processes are credible, as there are correlations between egg colouration and species-typical patterning in open-nesting birds (Kilner, 2006) and there is supporting evidence from previous studies of habitat choice (Rothstein, 1975; Gómez et al., 2021). Furthermore, Stevens et al. (2017) own study showed that female individuals had a preference for nesting places that closely resembled their own eggs and plumage, as opposed to those chosen by other members of their species. This suggests that their decision-making process was influenced by their own unique phenotype, rather than adhering to a more generalized strategy employed by the entire species. The extent to which this is true of Kentish plover site nest-choice remains to be investigated. Furthermore, no aspects of the appearance of the nest as a whole and the extent to which parents alter its appearance were investigated. While the nest scrape in which eggs are laid seems to have involved minimal effort, whether parents remove or add objects to the periphery (particularly when the background is more visually homogeneous, such as bare sand; e.g. Figure 2.3a) is unknown. In this respect, aspects of the background other than its component colours and texture *per se* may influence nest predation. Background complexity has been shown to reduce the detectability of objects independent of their degree of background matching, as long as they are moderately well camouflaged (Xiao & Cuthill, 2016; Rowe et al., 2021), as is the case for plover eggs.

To gain a comprehensive understanding of the role of egg camouflage in plover breeding success, it would have been advantageous to estimate the predation rate in both areas. This would have allowed us to determine whether colouration predicted egg predation, as in Troscianko et al. (2016a). It is reasonable to anticipate that nests on the beaches, being a more exposed habitat with less protective cover, would experience higher predation rates than saltmarsh eggs, but based on the similarity of egg colour in the two habitats and the apparent tendency of birds to place nests in parts of the habitat that are similar in colour (both to each other and to the birds' eggs), there may not be any habitat differences in the effect of egg colour on predation.

A final general point should be emphasised from the approach taken in this study. Most of the statistics that behavioural ecologists (and others) use are designed to test for differences between means, with great emphasis placed on significant differences between means in different groups or the effect of a covariate on the mean of some response variable (Nakagawa & Cuthill, 2007). Furthermore, in the study of animal colouration, great weight is often given to the perceptual discriminability of two colours, usually measured in 'just noticeable differences' on the assumption that receptor noise determines discriminability (Vorobyev & Osorio, 1998). For the study of camouflage in natural environments, this is inappropriate: a predator has to discriminate between multiple possible colours in a potential target and the background. It is confusability of distributions that matters, not the discriminability of any two points in a colour (or texture) space.

Chapter Three: Plover Chick Camouflage

3.1 Abstract

This chapter investigates the variations in colouration and patterning of plumage in Kittlitz Plover (*Charadrius pecuarius*) chicks. Of particular interest are potential disparities in these characteristics between males and females, because differences in the effectiveness of chick camouflage, and hence predation risk, could explain the male-biased operational sex ratio observed in many populations. The findings indicated that the plumage of plover chicks plays a significant role in their ability to remain inconspicuous, particularly in terms of colouration and patterning and that males and females do not have detectable differences in average plumage colour although there are some subtle differences in patterning. Moreover, there was a significant sex difference in the backgrounds of the locations at which chicks were found, such that male chick colours and patterns were less easily discriminated from their backgrounds than those of females. The inference is that male chicks are better camouflaged than females, but by virtue of microhabitat choice rather than their own plumage colouration.

3.2 Introduction

Camouflage enables organisms to increase their chances of survival by avoiding predators or capturing prey (Edmunds, 1974; Ruxton et al., 2018; Cuthill, 2019). For example, plovers (Charadriidae) are a subfamily of shorebirds that have long been used as examples of remarkable camouflage adaptations that, at least to human observers, enable them to blend in seamlessly with their coastal and beach habitats (Thayer, 1909; Cott, 1940). The colouration and pattering of the plumage of different plover species have been argued to contribute significantly to their ability to conceal themselves. However, given the vulnerability of eggs, and their incubating parents, in ground-nesting birds most research attention has focused on concealment when nesting.

Plovers use behavioural camouflage techniques in addition to their colouration to further enhance their camouflage when nesting. There is evidence of nest-site selection with respect to the individual's own plumage colour, such that it maximises its own camouflage when incubating on its nest (Stevens et al., 2017). Kittlitz plover (*Charadrius pecuarius*), the species studied in this chapter, and Kentish plovers cover their nests with vegetation and small stones to help conceal the eggs (Troscianko et al., 2016b; Gomez et al., 2018). Many species of plover, including the Kentish plover, display vigilance and distraction when potential predators approach their nest (Larsen, 1991; Colwell, 2010). By feigning injury or engaging in distracting behaviour, adult plovers divert predators' attention away from their nest or young, thereby increasing their possibilities of successfully rearing young. Nesting plovers fled their nests at a greater distance from a simulated predator (an approaching human) when their eggs were less well camouflaged against the background, indicating an awareness of their eggs' degree of background matching (Wilson-Aggarwal et al., 2016). These behavioural strategies, in combination with a bird's own appearance, enables them to take advantage of the visual characteristics of their habitat, thereby increasing their chances of survival on different backgrounds. The stage of breeding that has received less attention regarding to camouflage is post-hatching.

One would expect the colouration and behaviour of precocial chicks to be crucial to their survival and protection during their vulnerable early life stages. For example, juveniles of the golden plover (*Pluvialis apricaria*) have downy plumage that, to human eyes, closely resembles the colour and texture of the sandy or gravelly substrate on which they hatch and so potentially serves a crucial camouflage function (Gupta et al., 2022) (Figure 3.1). Whether such colouration actually enables chicks to blend in with their nesting environment, and so reduces their visibility to real predators, remains untested.

Fig 3.1. Chick of Golden plover showing its camouflage. Imaged supplied by Camilo Carneiro © with permission for reproduction in this thesis.

In addition to colouration, behavioural adaptations enhance the camouflage of both plover chicks and adults. When confronted with danger, many species employ a strategy of immobilisation (Orabona & Patla, 2013). In this behaviour, chicks adjust to the surrounding substrate by remaining still and ducking low to the ground. By maintaining a low profile and moving as little as possible, they likely reduce the likelihood of being discovered by predators. In addition, by virtue of being precocial (abandoning the nest shortly after hatching) and seeking shelter in adjacent vegetation or beneath objects (Colwell et al., 2007), this also serves as protection against prospective predators.

Despite the compelling anecdotal impression that plover chicks appear well camouflaged, there is a scarcity of hard evidence on the extent and mechanisms by which they actually achieve camouflage (or not) from real predators in their natural habitat. The forthcoming experiments outlined below will be dedicated to addressing this issue. I will also investigate the possibility of sex differences in chick plumage and hence the effectiveness of their camouflage. Because, like most birds, the chicks moult as they reach sexual maturity, possible differences between male and female chick appearance are not usually considered (and, prior to molecular sexing from blood or tissue samples, difficult to investigate). However, several plover species show pronounced biases in the operational sex ratio (i.e. at adulthood), which has profound effects on their mating and breeding systems (Szekely et al., 2006). Studies on Kentish plover have indicated that female chicks experience higher mortality in the days after leaving the nest, which might explain the male-biased operational sex ratio in this species. This could plausibly be due to sex differences in camouflage, whether in the plumage or in behaviour. Because differences in the proportion of breeding males and females affects mating behaviour (a male bias predisposes the species towards polyandry) and parental care (a male bias favours female desertion and male-only care), examining potential sex differences in chick camouflage is not simply a matter of descriptive morphology.

The camouflage properties of plover chicks were thus analysed in different ways to answer the following questions: how similar is their average colour and pattering is in relation to that of the background? Can a male or female chick be discriminated by the colours and patterns present in their plumage? Is the camouflage of male or female chicks like to be equally effective as deduced from their degree of background matching?

3.3 Methods

3.3.1 Study site

The research conducted in this chapter was based on photographs taken during fieldwork by other researchers on three plover species (Kittlitz plover, *Ch. pecuarius*, white-fronted plover, *Ch. marginatus*, Madagascar plover, *Ch. thoracicus)* in Madagascar. With a total of 170 *Ch. pecuarius* (79 males and 67 females sexed, 24 unsexed), 5 *Ch. thoracicus* (3 males, 2 females sexed) and 33 *Ch. marginatus* (8 males and 7 females sexed, 18 unsexed), a decision was made to limit the analyses to the Kittlitz plover, as only this species had sufficient numbers of sexed males and females to have the statistical power to detect sex differences.

3.3.2 Photography and image calibration

The image processing proceeded as for the eggs in Chapter 2 and much of the text below repeats information already provided. In order to perform the analysis, three steps were necessary: (i) calibrating the photographs such that they represented standardized measures of reflectance rather than camera- and illumination-dependent RGB pixel values; (ii) scaling the photographs to a standard size; (iii) extraction of measures of colour and pattern relevant to different predator visual systems (Stevens et al., 2007; Renoult et al., 2017). This was possible because all photographs contained a grey colour standard and a ruler. However, so that the analysis program could identify the relevant objects in the pictures, it was necessary to first create ‘masks’ manually, selecting by mouse certain areas of the photos. A ‘mask’ is a digital layer, equal in size to the photograph, that contains 1’s where the object is present and 0’s where it is not. For this process, an efficient approach was to create three masks (grey standard, ruler, chick or background) in one, each corresponding to a different ‘layer’ in a colour image: one red, one green and one blue (Figure 3.2). The freehand-select and rectangle-select tools in the GIMP-2.1O photo-editing program (www.gimp.org) was used to select and colour one area red for the grey card, one area green for a 40 mm length of the ruler, and one area blue for the chick or background. Then, using the red and green masks, the photos were standardized for colour and size based on the RGB values of the grey card (of which the correct values in sRGB colour space are known), and ruler respectively. So that samples of equivalent size and shape were used to characterize the background as for the chicks, for each photograph, the chick mask from each photo was used as a mask to select a series of chick-shaped samples of the background from within the rectangular area designated as ‘background’ (Figure 2.4b). The xy coordinates for each So that samples of equivalent size and shape were used to characterize the background as for the chicks, for each photograph, the chick mask was used as a mask to select a series of chick-shaped samples of the background from within the rectangular area designated as ‘background’ (Figure 2.4b). The xy coordinates for each chick-shaped sample were selected at random, using the R function runif. Nine random, chick-shaped, background samples were taken from each photograph, such that each photograph gave 10 samples: one chick and nine from the background. The number nine is somewhat arbitrary: large enough to get a better characterisation of each background's colour and pattern variation but making the calculation of the probability of correctly classifying a sample as 'chick at random straightforward (1 in 10, or 0.1). Lastly, the size-and-colour-calibrated photos were analysed to extract the colours and textures (pattern) of chicks and backgrounds for different visual systems, using mapping functions (matrix multiplication) previously determined when the camera was calibrated. The chosen visual systems were avian, as birds of prey (gulls and corvids are the most likely visual predators), and mammalian carnivore (e.g. canids such as red fox *Vulpes vulpes* or domestic dog *Canis domesticus*, and mustelids). Given the type of birds involved, a VS (violet-sensitive) rather than UVS (ultraviolet-sensitive) visual system was used, the cone sensitivities being that of the peacock *Pavo cristatus* (not because peacocks were likely predators but because it is a well characterised and widely used VS visual system for modelling; (Hart, 2002; Maia et al., 2019). Mammalian carnivores are dichromats and the visual system used was that of the ferret *Mustela furo* (Calderone & Jacobs, 2003). Colours were also modelled for human vision, purely for comparison and to provide a form of ground-truth (did the model outputs match what we could see in the photographs. All calibration and extraction of colour and pattern measures were done using a custom program, written by my supervisor, I. Cuthill, in R (R Core Team. (2023) and the package OpenImageR (Mouselimis, 2023) (Figure 3.2). Also, chicks had been previously sexed using molecular markers (e.g. Székely et al., 2004).

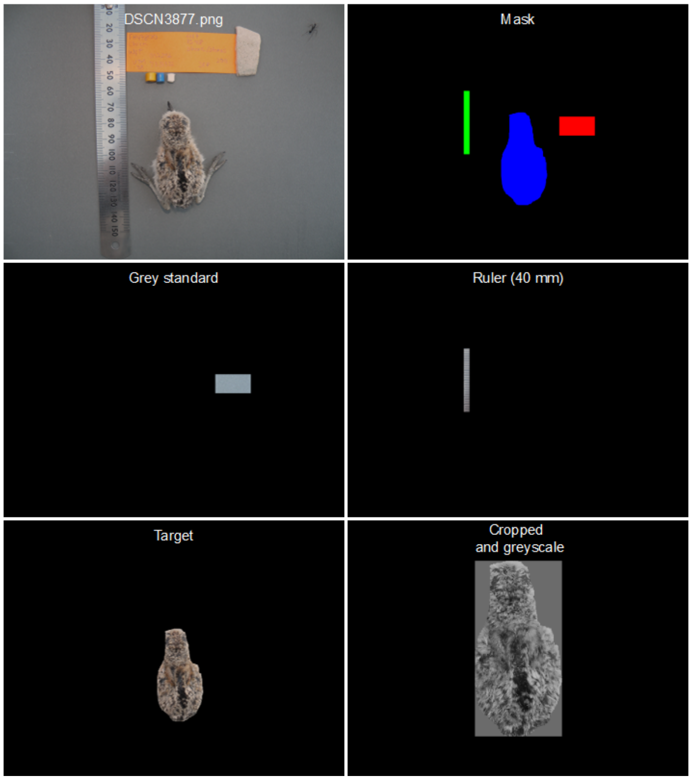

Figure 3.2. Images obtained from R program to perform the analysis. A: Image as it was taken, B: masks created manually to select sites of interest (red: greycard, green: 40 mm ruler, blue: chick or background), C: Piece of greycard used to standardize the image to sRGB colour space , D: Selected piece of 40 mm ruler to standardize size, E: Selection of target (chick or background), F: Target, in greyscale, after going through standardization.

3.3.3 Colour analysis

The colour and texture (pattern) analysis followed that in Michalis et al. (2017) and Barnett et al. (2018a,b). ‘Colour’ was defined by three variables: luminance (achromatic brightness), red-green chromatic contrast and yellow-blue chromatic contrast. For humans, the L*a*b* colour space is a well characterized representation of this type (L = luminance, a = red-green, b = yellow-blue) in which distances in this 3-dimensional colour space match perceived colour differences (CIE, 1976). An avian equivalent was also calculated, where luminance was represented by the calculated photon catches of the double-cone receptors, red-green by the contrast in photon catches of the long- and medium-wave single cones, and yellow-blue by the contrast in photon catches of the long- and medium-wave single cones combined compared to the short-wave cones (see discussion and justification in (Xiao & Cuthill, 2016). The VS cone was not used in calculations because, without a camera with distinct blue and violet (or ultraviolet) sensors, the values for VS and SWS cones are very highly correlated. That UV information can be ignored is an untested assumption, but the melanin that creates the brown colour of plover eggs also absorbs strongly in the UV (Kollias, 1995).

3.3.4 Texture analysis

As in Michalis et al. (2017) and Barnett et al., (2018a,b) and Talas et. al., (2017) texture was characterized by the output of a log-Gabor filter bank of six spatial scales and eight orientations, applied to the luminance plane of each image (Figure 3.3). The luminance signal was used as this is the main contributor to pattern vision for the species modelled (Kelber et al., 2003; Jones & Osorio, 2004). In practice, the same texture analysis was used for all three visual systems (avian, carnivore, humans) because the calculated luminance values for the images (chicks and backgrounds) were so highly correlated: avian-carnivore r = 0.972, avian-human r = 0.995, human-carnivore r = 0.987 (n = 1700; 10 samples from each of 170 chicks). Gabor filters are a standard tool in image processing, used to describe textures or detect visual structure. A single Gabor filter is a 2D sine or cosine wave of a given spatial frequency and orientation multiplied by a 2D Gaussian (normal) distribution of a given standard deviation. So, when multiplied by a patch of an image of the same size, the product will have the highest value when the pattern in the image-patch matches the structure of the Gabor filter. When you multiply a whole image by a given Gabor filter (by successively moving it, pixel-by-pixel, across all the rows and columns of the image), the largest values will show you the areas of the image where the orientation and spatial frequency (from coarse to fine grain) match that Gabor. If you repeat this process with a whole set of Gabor filters of different spatial frequencies and orientations, you get a comprehensive description of the patterns of light and dark, of given sizes and orientations, in that image. Rather than, for example, describing a 256x256 pixel image with 65536 numbers (the intensity values of the 65536 pixels), the pattern in the image is described with 48 numbers (6 spatial scales and 8 orientations) (Figure 3.3). Numerous vision specialists in the present era have concluded that the frequency and orientation representations exhibited by Gabor filters bear resemblance to the response properties of certain neurones in the human visual system (e.g. Field, 1987; Field & Olshausen, 1996; Olshausen & Field, 1996; Ruderman et al., 1998). The log of the Gabor output (hence 'log-Gabor filter') was used for statistical reasons: the output of a simple Gabor filter is always zero or positive, so correlated with mean luminance, while logged values can be negative.

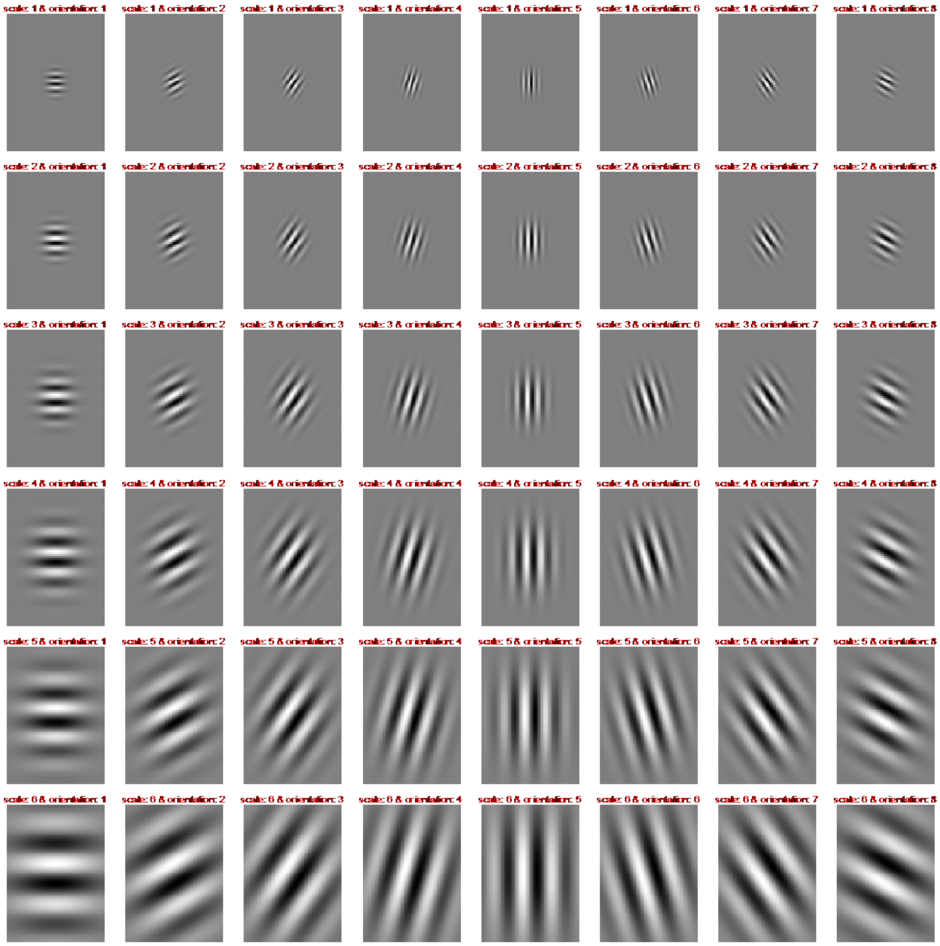

Figure 3.3. The Gabor filter is a linear filter employed in texture analysis. Its primary function is to quantify the presence of distinct frequency components inside a picture, specifically in predetermined directions within a localized area surrounding the point or region of investigation. Shown here are Gabor filter with 6 scales and 8 orientations, as used in this study.

The output of log-Gabor filters like this, when applied to natural images, are correlated because of the fractal nature (self-similarity) of natural scenes (Burton & Moorhead, 1987; Turiel et al., 2000; Párraga et al., 2002); for example, when there is high contrast at large spatial scales there tends to be high contrast at low spatial scales. Because of this, and to reduce the number of response variables to be analysed, Principal Component Analysis was carried out on the correlation matrix of the dataset using the *princomp* function in base R (the approach taken by (Talas et al., 2017). Four components had eigenvalues greater than 1 (i.e. explained more variation than any of the original variables) and captured 89% of the total variation in the 48 Gabor outputs (Figure 3.4a; 69, 11, 5 and 4% for PC1 to 4 respectively). We can understand what the components represent by examining their loadings: the contribution of the original variables to each component (Figure 3.4b). The first component (PC1) loads positively on all 48 original Gabor measures: it captures 'contrast' regardless of spatial scale (an image with a high value of PC1 would have areas of very light and very dark at both fine and coarse grain). PC2 loads positively on the Gabor filters capturing fine detail and negatively loaded on those capturing coarse detail; an image with a high positive value of PC1 would have more fine detail and few large objects (e.g. sand), while a high negative value would indicate mainly large objects (e.g. pebbles). PC3 and 4 together capture the orientation of edges in an image. The fact that they appear as 180 out-of-phase sine waves in Figure 3.4b is really an artifact of the method: by definition, principal components must be orthogonal (uncorrelated) so, if PC3 captures the relative importance of one set of orientations, PC4 is always likely to show the opposite pattern of loadings. The specific angles involved are not of interest for this study (these chicks and backgrounds are not striped), unlike the orientation of striped moths on striped tree bark (e.g. Kang et al., 2012, 2013b, 2014). Note that the analysis is at the level of 'chick-sized' objects and so any spatial variation in light and dark greater than this is not captured by our Gabor features or the principal components derived from them.

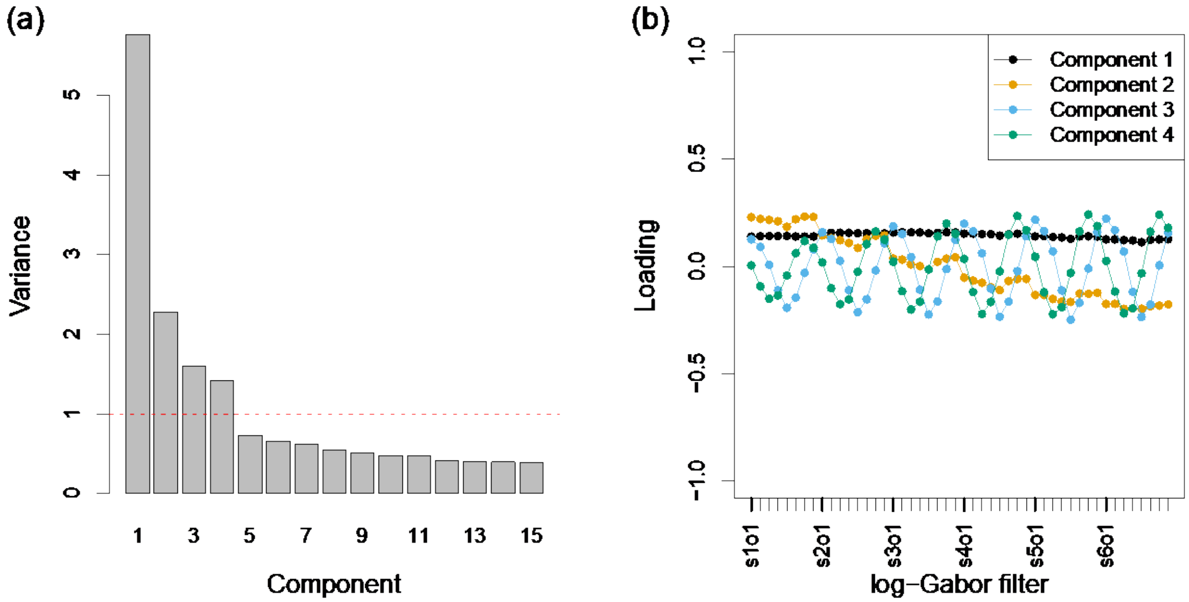

Figure 3.4. (a) The eigenvalues (variance) of the first 15 (of 48) principal components derived from Principal Component Analysis of the 48 log-Gabor filter outputs used to describe the texture (spatial pattern) of the chicks and backgrounds. (b) The loadings of the principal components on the original 48 variables: i.e. the contribution of the original variables to each component. The original Gabor variables (x-axis) are named such that the first two letters (s1, s2,…, s6) describe the spatial scale (1 is fine detail, 6 is the coarsest detail) and the second two letters (,o1, o2,… o8) describe the orientation of the filter, from horizontal (o1) turning anti-clockwise. For further help in interpretation, refer to Figure 3.2 for images of the filters themselves.

3.3.5 Statistical analysis

Analysis of the differences in the means of the response variables describing colour and texture was by linear mixed models, using the function lmer from the lme4 package (Bates et al., 2015). With multiple replicates (1 egg, 9 background samples) taken from each photograph, photograph was included as a random effect in all models. The predictors were either sex or object type (chick vs background) according to the question involved. The lmerTest package was used to obtain p-values from t- tests using Satterthwaite's method to calculate the appropriate degrees of freedom (Kuznetsova et al., 2017). For the texture measures based on PCA of the log-Gabor filter outputs, I also carried out Multivariate Analysis of Variance (MANOVA) on all four principal components as joint response variables, using Pillai's trace as both a test statistic and measure of effect size equivalent to R^2 (Pillai, 1955). This is a multivariate equivalent of R^2 in regression and is also equivalent to the partial eta^2 statistic provided by the widely used statistics package SPSS. To obtain a p-value I used the approximate F test provided by the MANOVA function in R, based on Pillai's trace and the ratio of the location variance to the between-photograph variance. The reason to use MANOVA to analyse the texture measures jointly was both as a protection against the elevated Type I (false positive) error rates of testing PC1 to PC4 separately but also, and more importantly, because these statistical measures of texture do not have the same perceptual interpretation as the colour measures. That is, the separate neural processing of luminance and colour (hue) is understood, but perceptual dimensions of texture ('pattern') are not (Stoddard & Osorio, 2019).

Of greater relevance to camouflage than differences between the mean colours or patterns of eggs and their backgrounds is their discriminability/confusability (Xiao & Cuthill, 2016; Michalis et al., 2017; Barnett et al., 2018b; Barnett et al., 2021). If one imagines chick colours and background colours as two clouds of points in a colour space, how much do the distributions overlap (Endler & Mielke, 2005)? This is a signal detection problem, with the chick features being the signal and the background features the noise (Merilaita et al., 2017). Unless the two distributions do not overlap, there is no single criterion that can perfectly distinguish one from the other: a threshold that classifies more chicks correctly will incorrectly classify more background features as belonging to chicks (false positives), and a threshold that classifies more backgrounds correctly will incorrectly classify more chick features as being part of the background (failed detections). That trade-off can be visualized as an ROC (Receiver Operating Characteristic) curve, where 'sensitivity' (correct classifications of chicks as chicks) is plotted against 'specificity' (correct classification of backgrounds as backgrounds) (Wickens, 2002). This is standard practice in machine learning, as is the procedure of "cross validation" of the discrimination model (Lantz, 2013). The goodness of fit of a model to a set of data will always be better than the success of that model when applied to new data of the same type, known as 'over-fitting'. This is because some of the variation in any one sample of data is random noise, so a model fitted to those data will not fit a new sample (with different random sampling variation) as well as it did the original data. In machine learning, the solution to this is to fit a model to one set of data ('training') but test it with a different set of data (Lantz, 2013). There are different ways you can do this (e.g. randomly divide the dataset in two, an approach taken by Barnett et al., (2021), when analysing camouflage in leaf-mimicking toads) but I used the computationally more intensive leave-one-out cross validation, because it makes fuller use of the data (Lantz, 2013). As the name suggest, the discrimination model is fitted to the data of all-but-one chick, then the model's success in correctly classifying the chick and background samples from the remaining photograph is assessed (the probability of the object being a chick, or background, is the output). The process is repeated for every photograph, each time training the model on the other photograph. The discrimination model used was a generalized linear mixed model with binomial error, fitted using the glmer function from the lme4 package. The response variable was object type (chick or background), the fixed effect predictors the colour or pattern metrics for different visual systems, and the random effect photograph (equivalent to chick ID). Classification errors were calculated using the confusionMatrix function from the caret package (Kuhn, 2008) and ROC curves were fitted using the pROC function from the package of the same name (Robin et al., 2011).

Classification performance was further analysed using mixed-model beta regression with R package and function glmmTMB (Brooks et al., 2017). The response variable was the probability of a sample being a chick (the converse being background) with the fixed effect sex and random effect of the ring number of the chick (matched for a given chick and its background in a photograph).

3.4 Results

A plot of the human-perceived sample averages gives the subjective impression that male and female chick colours are similar, and similar to their backgrounds (Figure 3.4). Statistical analysis, using linear mixed models, of the components of both avian and carnivore colour models matches this subjective view from human perception. Analysing all the data together with respect to both object type (chick/background) and sex (female/male), there are no significant type*sex interactions for all measures of colour, or main effect of sex (Table 3.1). The average chick and background colours do differ significantly (main effect of type; Table 3.1), with the chicks being very slightly darker and a redder shade of brown, although clearly the majority of chick colours fall within the centre of the distribution of background colours for either avian or carnivore visual systems (Figures 3.5 & 3.6). Considering texture (Table 3.1; Figure 3.7), there is a significant interaction between type and sex, with the difference between males and their background differing from the difference for females, but only with regard to PC3 and 4. As regards PC1 and 2, the chick-background difference is similar for males and females (no interaction) and the average values of PC1 and 2 do not differ (main effect of sex). We can explore the interaction for PC3 and 4 by analysing males and females separately (Table 3.2). The larger effect sizes for females indicates that the mismatch between chicks and backgrounds is greater for females than males (Table 3.2, Figure 3.7).

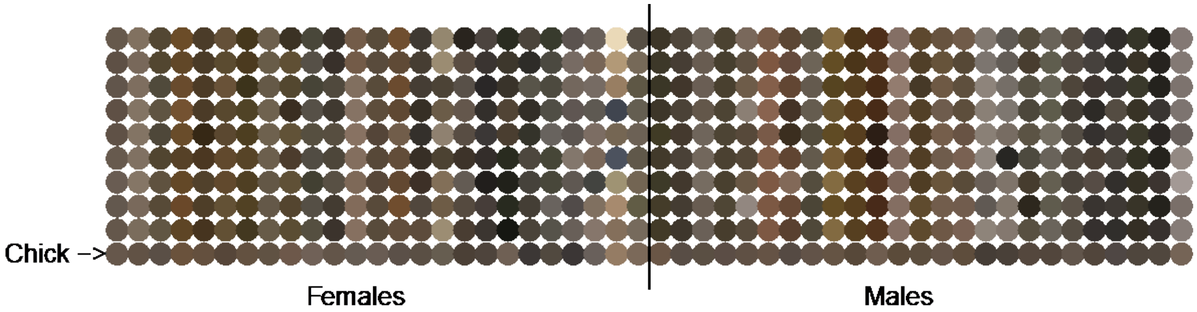

Figure 3.5. Examples of the average colours of female and male chicks and their respective nine background samples, based on a random sample of 20 chicks of each sex.

Table 3.1. Analysing chick and background colours and textures: tests of the effects of object type (chick/background) and sex (female/male) based on linear mixed models.

	Interaction			Type			Sex		
	t or F	df	p	t or F	df	p	t or F	df	p
Avian luminance	0.349	1312	0.727	2.801	1312	**0.005**	0.696	145.3	0.487
Avian RG	1.003	1312	0.316	9.381	1312	**<0.001**	0.672	145.3	0.503
Avian YB	1.269	1312	0.205	4.240	1312	**<0.001**	0.230	145.0	0.819
Carnivore luminance	0.792	1312	0.429	2.251	1312	**0.025**	0.387	145.4	0.770
Carnivore YB	0.972	1312	0.331	5.771	1312	**<0.001**	0.159	145.1	0.874
PC1-4 jointly (F)	3.870	4,1309	**0.004**	60.464	4,1309	**<0.001**	3.288	4, 141	**0.013**
PC1	1.187	1312	0.236	2.228	1312	**0.026**	0.274	145.6	0.784
PC2	0.376	1312	0.707	7.133	1312	**<0.001**	0.939	145.4	0.349
PC3	2.862	1312	**0.004**	2.838	1312	**0.005**	2.862	146.6	**0.004**
PC4	2.300	1312	**0.022**	3.541	1312	**<0.001**	2.497	148.7	**0.014**

The test statistic for all measures is Satterthwaite's t from linear mixed models, except for the joint analysis of the texture measures PC1 to 4, which is an approximate F-test from MANOVA.

Table 3.2. Comparison of mean texture measures between chicks and backgrounds, separately analysed for females and males.

	Females				Males			
	Effect	t or F	df	p	Effect	t or F	df	p
PC1-4 jointly (F)	0.224	43.309	4, 599	<0.001	0.110	21.949	4, 707	<0.001
PC1	-0.971	0.040	602	0.026	-0.268	0.667	710	0.505
PC2	1.159	7.004	602	<0.001	1.076	7.306	710	<0.001
PC3	1.338	9.624	602	<0.001	-0.792	6.096	710	<0.001
PC4	-0.514	3.648	602	<0.001	-0.060	0.439	710	0.661

With the exception of the joint analysis of the texture measures PC1 to PC4, where the effect measure is Pillai's trace from MANOVA, the effect size is the difference in standardised mean between chick and background (so a negative sign means a lower value for the chick than the background). The test statistic for all measures is Satterthwaite's t from linear mixed models, except for the joint analysis of the texture measures PC1 to 4, which is an approximate F-test from MANOVA.

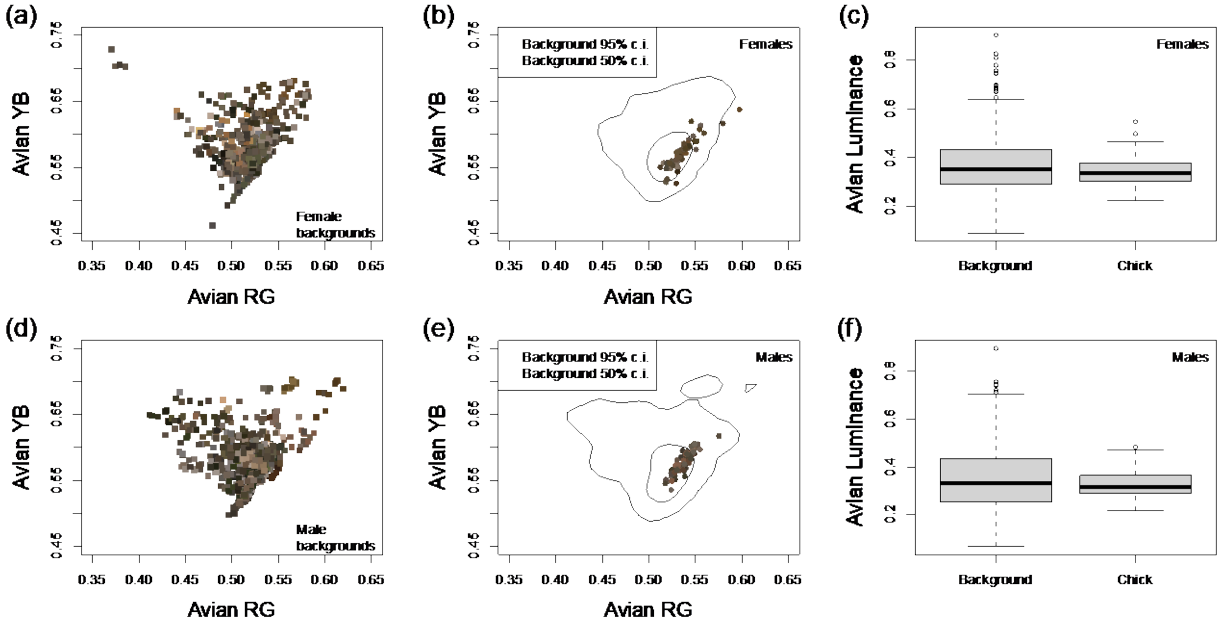

Figure 3.6. Avian-perceived colours of chicks and backgrounds separated by sex; females: top row, males: bottom row. (a) The hues of background samples (only) represented in avian red-green (RG) and yellow-blue (YB) opponent space. (b) The background distributions in panel (a) are summarised by their 95% and 50% kernels, with the hues of female superimposed as individual points. The point colours in both panels represent the colours as seen by humans. (c) The avian luminance (double cone catch) distribution of background samples and chicks, represented as boxplots. The thick horizontal line is the median; the box spans the lower to upper quartile; the 'whiskers' extend to the last data point within 1.5 inter-quartile ranges of the nearest quartile; the open circles are points outside the whiskers. Panels (d) to (f) are the equivalent plots for the male chicks.

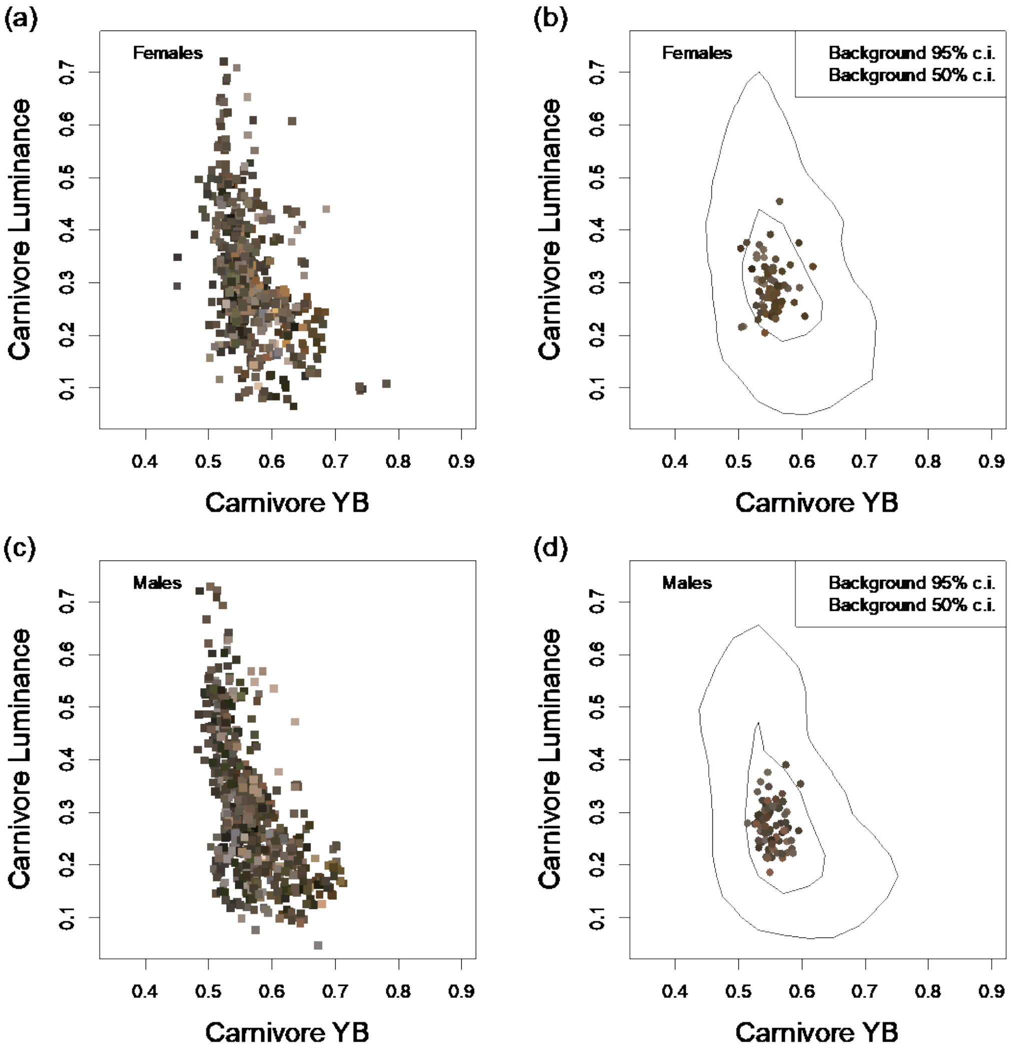

Figure 3.7. Colours of chicks and backgrounds in mammalian carnivore colour space; females: top row, males: bottom row. (a) Carnivores are dichromats, so the colours of background samples can be fully represented in a luminance and yellow-blue (YB) opponent colour space. (b) The background distributions in panel (a) are summarised by their 95% and 50% kernels, with the colours of female chicks superimposed as individual points. The point colours in both panels represent the colours as seen by humans. Panels (c) and (d) are the equivalent plots for male chicks.

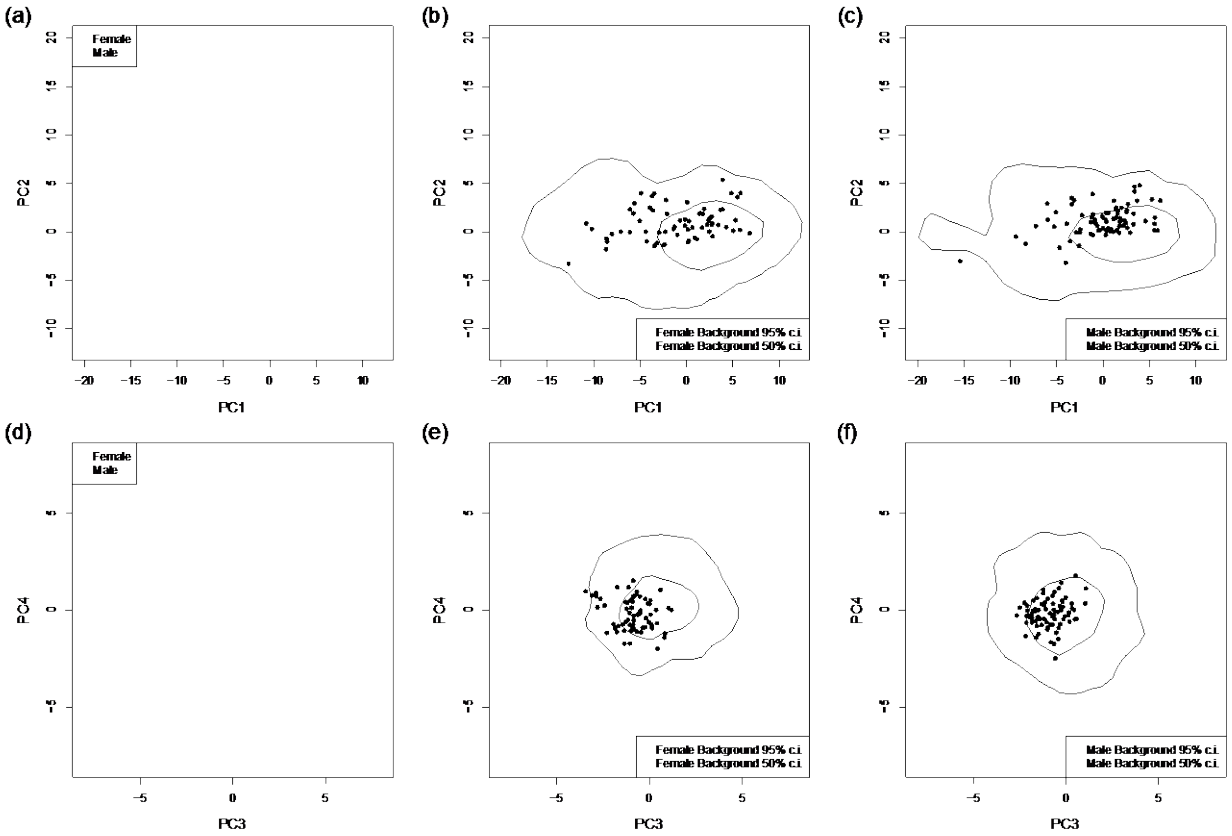

Figure 3.8. Differences between backgrounds and chicks for the principal components describing texture (top row: PC2 vs. PC1; bottom row: PC4 vs. PC3). (a) PC2 (relative amount of fine- to coarse-grain patterning) plotted against PC1 (overall contrast) for background samples for females (grey) and males (red). (b) Background data summarised by their 95% and 50% kernels, with the PC1 and 2 values of female chicks superimposed as individual points. (c) 95% and 50% kernels for the male backgrounds with the PC1 and 2 values of male chicks superimposed as individual points. (d) to (f) are the equivalent graphs for PC4 plotted against PC3; both PCs capture variation in line and edge orientations.

Although chicks and backgrounds differ in their mean values for all aspects of colour and texture, it is clear that the distributions overlap considerably for both avian and carnivore vision (Figures 3.6, 3.7). Furthermore, although there are significant sex differences in the average degree of match for the two principles components describing edge orientations, again there are considerable overlaps between chick and background distributions for both sexes (Figure 3.7).

Confusion matrices and ROC curves based on classification models with leave-one-out cross-validation quantify that overlap: the discriminability (converse: confusability) of the colours and textures (Table 3.3). Classification accuracy appears high, but it is important to remember that there were nine times as many background as chick samples (nine background samples and one chick per photograph), so the naïve rule of 'classify all objects as background' would have an accuracy of 0.9 (all backgrounds correct, all chicks incorrect). This is known as the 'no information rate' and the obtained accuracies using colour measures alone (for human, bird or carnivore vision) are lower than this. Few or no chicks are correctly classified based on colour alone. Incorporating texture information yields greater classification success, with pattern alone being a better criterion than the naïve rule, with 94% of chicks correctly classified. Using both colour and texture information is better still, with all visual systems at 96%+ accuracy and correctly classifying 98% of backgrounds, human vision only misclassifying 10% of chicks, avian vision 12%, and both outperforming carnivore vision (80% of chicks).

Table 3.3. Measures of classification success for different predator visual systems, based on binomial mixed models with leave-one-out cross-validation.

Measure	Accuracy	Sensitivity	Specificity
Human colour	0.86	0.00	0.96
Avian colour	0.87	0.00	0.97
Carnivore colour	0.88	0.00	0.98
Pattern	0.94	0.71	0.96
Human both	0.98	0.90	0.98
Avian both	0.97	0.88	0.98
Carnivore both	0.96	0.80	0.98

Accuracy is the proportion of chicks and backgrounds classified correctly. Sensitivity is the proportion of chicks correctly classified as chicks, Specificity is the proportion of background samples correctly classified as backgrounds.

The classification accuracy discussed above assumes that the costs of failing to identify a chick correctly (Type II error: failed detection) is the same as failing to identify a background sample correctly (Type I error; false positive), which may not be true. Therefore it is helpful to look at the complete trade-off between type I and II errors as shown in ROC curves (Figure 3.8). For example, if it was essential to find all chicks, all visual systems can achieve 100% classification accuracy for chicks (sensitivity = 1), but for humans and birds this would come at the cost of misclassifying more than half the background samples as being from chicks (specificity < 0.5) and, for carnivores, the cost would be around 90% of backgrounds misclassified (specificity < 0.1).

One can analyse the classification 'confidence' further, bearing in mind the greater average difference between female chicks and their backgrounds than for males and their backgrounds for the minor texture components PC3 and 4 (Table 3.1) and the difference in overlap of the distributions (Figure 3.7e,f). There is no sex difference in the probability of correctly classifying a sample as a chick, using all avian-perceived colour and texture information (beta regression coefficient 0.094, p = 0.557; Table 3.4). However, there is a significant sex difference in the probability of correctly classifying the backgrounds (as backgrounds) where male and female chicks are found (coefficient 0.297, p = 0.001; Table 3.4). That coefficient is a logit, or log (odds ratio), so this tells us that males are 35% more likely (exp(0.297) = 1.35) to be on backgrounds that can be misclassified as a chick, compared to females. The same conclusions hold for carnivore and human vision (Table 3.4).

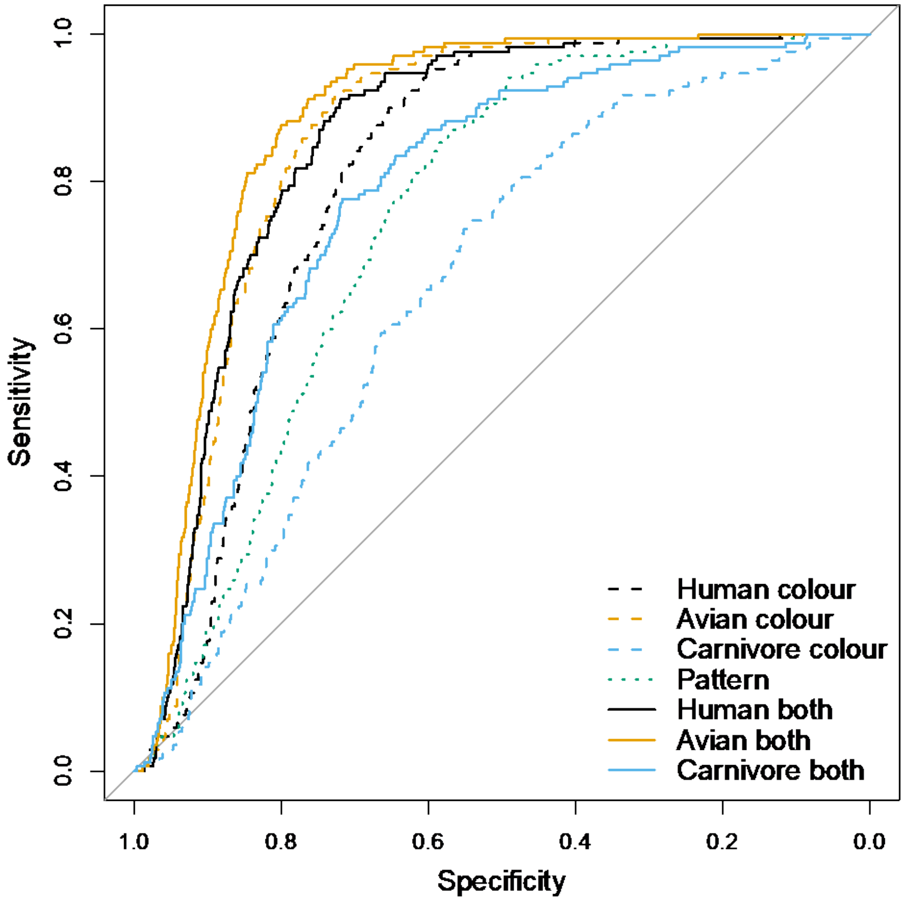

Figure 3.9. Receiver Operating Characteristic (ROC) curves for human (black), avian (orange) and mammalian carnivore (blue) predators, using both colour and texture information, and separately plotted for colour (dashed lines) and pattern (dotted green) information separately. Sensitivity is the proportion of chicks correctly classified as chicks; specificity is the proportion of background samples correctly classified as backgrounds.

Table 3.4. Sex differences in the probability of classifying a sample as a chick (= correct for chicks, incorrect for backgrounds), analysed separately for chicks and the backgrounds on which chicks were found.

	Chicks			Backgrounds		
Visual system	logit	z	p	logit	z	p
Human	0.089	0.617	0.537	0.346	3.924	<0.001
Avian	0.094	0.588	0.557	0.297	3.184	0.001
Carnivore	0.134	1.284	0.199	0.486	7.086	<0.001

The logits are the coefficients from mixed-model beta regression.

3.5 Discussion

Due to their precocial nature, plover chicks exhibit an early departure from their nest shortly after hatching. This may reduce their predation risk compared to remaining in the nest, but chicks nevertheless have a heightened susceptibility to mortality compared to adults, due to their limited mobility (Rohr et al., 2020). Concealment from predators through physical hiding in vegetation or camouflage at this developmental stage, coupled with appropriate behaviour such as freezing and remaining motionless until a threat has passed, is therefore essential. Nevertheless, there is limited knowledge regarding the nature of chick camouflage in precocial birds, so the findings in this study are novel with respect to the topic, as well as potential sexual dimorphism.

In broad terms, Kittlitz plover chicks tend to exhibit very similar colours to their surrounding environment. Indeed, at a distance, where the patterning of the plumage cannot be resolved and only average colour can be perceived, the chicks are indiscriminable from the colour of the background, whether to avian or mammalian predators. Matching the average colour of the background is likely to be more important than matching the detailed visual texture, because if you are visible at a distance then your camouflage has already failed (Michalis et al., 2017). However, at closer distances, where the plumage pattern of the chicks (and background) is visible, then chick and background can be reliably discriminated by avian and mammalian visual systems, although still with error. As the visual acuity of mammalian carnivores is liable to be much worse than that of avian predators (Kiltie, 2000; Veilleux & Kirk, 2014), what is “closer” will be nearer for carnivores than birds but, in any case, olfaction is likely to be more important for mammalian predators at close distances. Nevertheless, when colour and texture information are combined in the natural setting, the likelihood of correctly distinguishing a chick from its background or correctly identifying the background itself is high. However, If chicks are static and been able to settle on their chosen backgrounds, the ROC curves indicate that high rates of detection by predators can be achieved only by incurring two costs: getting close enough to discern texture, and approaching objects that turn out to be background, not a prey item. What is lacking, and a natural next area for future research, is the relative cost of false positives and failed detections for real predators in the course of natural foraging.

The findings pertaining to sex differences in plumage, and differences in camouflage effectiveness between male and female chicks were somewhat complex. The results indicated that there were no detectable disparities in terms of colour and the major components of pattern (contrast and the scale of patterning, as captured in PC1 and 2) in the plumage of males and females. However female chicks were less well matched to their backgrounds than males in some aspects of the distribution of the orientation of edges. The latter are not immediately apparent from subjective inspection of photographs, but whether there are detectable differences in male and female chick plumage is investigated directly in the next chapter. However, the major contributor to sex differences in discriminability of chicks from their backgrounds was not in the chick plumage, but in their backgrounds. Male and female chick colour patterns were equally likely to be misclassified as coming from the background (the hallmark of background matching camouflage). However, the backgrounds of localities where male chicks were captured had colour patterns that matched chick plumage better (35% more likely to be misclassified). Two things should be noted. First, this must be on the scale of a few metres: male and female chicks were caught in the same general location and, with a birth sex ratio close to 1, the broods that accompany a parent will usually be of mixed sex (Székely et al., 2004). Second, the photographs used in this study are not of chicks hiding *in situ*, on their exact chosen substrate, but next to where they were caught, photographed and measured. So we cannot distinguish between a capacity for specific background selection (as in the quail experiment of Lovell et al., (2013), discussed in the Introduction) or a more general preferences for a habitat type made by males in response to a predatory threat (the ornithologist) or their parents' alarm calls. Nevertheless, the obtained results potentially yield insights into a potential explanation for the higher mortality rate among female chicks at an early age (Stenzel et al., 2011; Eberhart-Phillips et al., 2017). An adult sex ratio exhibiting a bias towards males has been frequently documented in numerous species belonging to the plover family but whether a sex difference in the effectiveness of camouflage in the initial postnatal period can account for all, or any, of the difference remains to be established. We must not forget that there are other strategies for avoiding predators, such as hiding in vegetation, so poorer background matching in females may be compensated for in different ways. What the research in this chapter does show is that a sex difference in camouflage, as a possible result of microhabitat choice, is at least a plausible candidate explanation. Further research is needed to fully understand the mechanisms behind plover chick’s camouflage and how it is integrated with behaviour. By investigating the specific mechanisms employed by different precocial species, we can gain a deeper understanding of the evolutionary and ecological significance of camouflage at this crucial life-history stage.

Chapter Four: Plover Chick Detection in a Computer-Based Experiment

4.1 Abstract

Two visual search experiments utilizing humans as a model predator were conducted using computer-based technology. These tests aimed to investigate the perceptual ease or difficulty associated with the detection and identification of plovers' plumage and the plovers themselves in relation to their background. The first part involved replicating an unpublished experiment using photographs, taken in the field in Madagascar, of both male and female chicks of Kittlitz (*Ch*aradrius *pecuarius*) and white-fronted (*Ch. marginatus*) plovers. This study aimed to assess if there any difference in the effectiveness of male and female chicks' camouflage. A second experiment sought to establish how well chick plumage matched the background, utilizing square patches of plover plumage and comparable samples of different natural substrates (mud or vegetation). Because the task relied exclusively on colour and visual texture (pattern), the role of body shape and cues from the beak, legs or eyes could be eliminated. The results suggest that there was no noticeable difference in the detectability of male and female chicks and, in the second experiment, that the plumage is harder to discriminate from mud than vegetation. In addition, detecting chick plumage against background that contains one region of mud and one of vegetation is harder than the simple average of detection against these two substrates separately. The implications for habitat choice and anti-predator behaviour in plover chicks is discussed.

4.2 Introduction

An effective strategy to minimize the likelihood of being detected is to closely resemble the surrounding visual environment (Stevens & Merilaita, 2009a; Cuthill, 2019). This type of camouflage is referred to as background matching (Merilaita & Stevens, 2011), such that if the hues and geometry of a prey's colour pattern closely resemble the visual background in the eyes of a predator, it should be more challenging for the predator to spot the prey (Cott, 1940; Endler, 1978). The simplicity, or otherwise, of detection of the prey is therefore critical for the animal's survival and, for predators that rely on stealth or ambush to attack prey, avoiding detection is also critical (Smith & Ruxton, 2020). Birds, particularly females during nesting, have often been used as examples of 'concealing colouration' (Wallace, 1889; Thayer, 1909) but the degree to which plumage colouration functions as camouflage is still far from resolved (Marshall & Gluckman, 2015; Caro, 2017; Leveau & Ibáñez, 2022).

Plovers are a globally distributed species that use a wide range of habitats, including beaches, saltmarsh, tundra, and dunes, among others, for nesting purposes (Székely et al., 2014). Charadriidae, in general, exhibit nidifugous behaviour, their precocial chicks departing from the nest shortly after hatching, either in search of food or to find refuge. Furthermore, as time progresses, the fledglings gradually increase the distance they venture from the nest. Consequently, chicks may confront diverse settings to which they must blend in to avoid detection by predators, particularly until they acquire the ability to fly. Is a chick's colouration equally effective camouflage against the different backgrounds in which it finds itself, and does the plumage represent some form of generalist, or compromise, camouflage? Alternatively, would it be more efficacious if it specialised one of the options? In this chapter, I take a different approach to this question from the analysis of colouration used in chapters 2 and 3. Using humans as model predators, I investigate how easy it is to detect plover chicks against different types of background, with particular emphasis on (i) possible sex differences in camouflage, (ii) whether the inability to hide in vegetation on exposed mudflats drives plumage to match this substrate even at the expense of conspicuousness against vegetation, and (iii) the role of background complexity.

As I discussed in Chapter 3, certain plover species exhibit significant imbalances in the operational sex ratio during adulthood, leading to significant impacts on their mating and breeding systems (Szekely et al., 2006); for example, in Kentish plovers it has been shown that female chicks have a greater mortality rate in the weeks after leaving the nest. This could perhaps be attributed to sex-specific variations in camouflage, either in terms of physical appearance or behavioural patterns.

Examining potential sex differences in chick camouflage is therefore relevant to the understanding the mechanism behind variations in the proportion of breeding males and females, with consequences for mating behaviour and parental care. For example, a male bias predisposes a species towards polyandry and favours female desertion and male-only care (Szekely et al., 2006; Eberhart-Phillips et al., 2018). The approach taken here was inspired by an unpublished experiment carried out by a Ph.D. student, Jorge Parra, at the University of Bath, under the supervision of Prof. Tamas Székely. In that experiment, where participants had to search on a computer screen for plover chicks, male chicks took significantly longer to find, consistent with better camouflage and the observed higher survival rate than females. This sex difference was seen both when the images were of chicks as photographed on their natural backgrounds in Madagascar, or digitally inserted into a random location on natural backgrounds. The first step in my study was to replicate Jorge Parra's experiment, with a larger sample size and including a sub-sample of participants tested under tightly controlled laboratory conditions and a colour-calibrated monitor.

4.3 General methods

4.3.1 Experimental procedure

In the experiments that follow, experiments were created and run using the Python-based software PsychoPy in conjunction with the Pavlovia online experimental platform (Peirce et al., 2019). PsychoPy allows you to create computer-based experiments graphically, by linking a series of objects/actions in a flow diagram. Figure 4.1 shows the design for the experiments in this chapter, directly reflecting the experience of a participant doing the experiment. First, the participant would click through a series of instruction screens (Figure 4.2). Then, in the 'calibration loop', participants were asked to click the four corners of a yellow square in turn (Figure 4.3); this allowed subsequent calibration of the location of mouse-clicks during the experiment for participants using different monitors. After a screen indicating that practice trials would commence, participants would have eight practice trials on a representative set of images similar to those, but not actually used, in the experiment proper (Figure 4.4a). After each practice image, participants received feedback in the form of an identical image but with a yellow rectangle indicating the position of the target (Figure 4.4b). After an instruction that the practice was over and that the experiment was about to begin, the participants then started the experimental trials, grouped into blocks after each of which the participant was told they could take a short break if they wished. Clicking on an image, correctly on the target or otherwise, advanced to the next image. There was no feedback as to whether a target had been correctly identified by clicking but, at the end of the whole experiment participants were thanked.

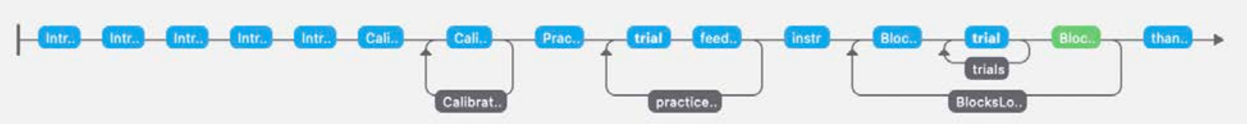

Figure 4.1. PsychoPy flow diagram representing the design of the experiments in this chapter.

Plover chicks are hard to spot

But how well does the plumage actually match the background?

CLICK ANYWHERE TO CONTINUE

Do they select backgrounds to which they are better matched?

CLICK ANYWHERE TO CONTINUE

We can compare their detectability on backgrounds they have chosen to random locations

CLICK ANYWHERE TO CONTINUE

Do male and female chicks differ in their detectability?

Could this explain why male chick mortality is higher than that of females?

CLICK ANYWHERE TO CONTINUE

Let's play Spot the Plover to find out...

Here it is

CLICK ANYWHERE TO CONTINUE

Figure 4.2. The five instruction screens for the first experiment, seen in turn and needing a mouse-click to advance to the next one.

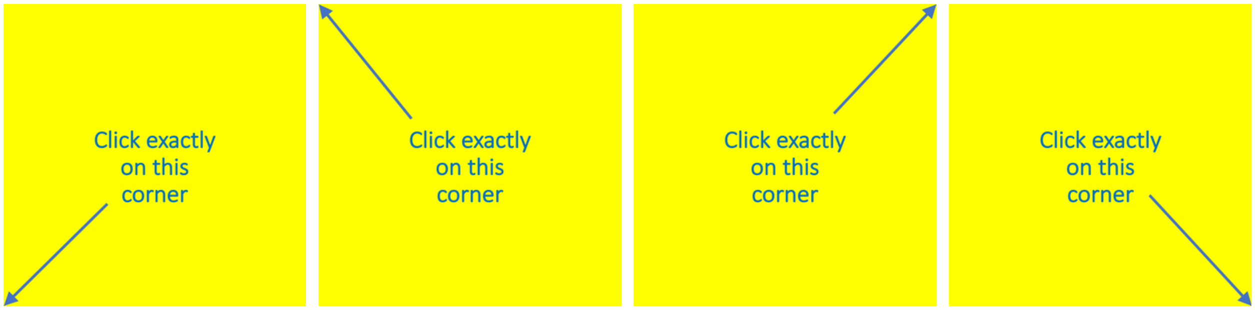

Figure 4.3. Images seen in turn for the purpose of calibration of screen size, each and needing a mouse-click to advance to the next one. No feedback on whether the click was accurate, but data were analysed subsequently to check whether plausible locations had been selected.

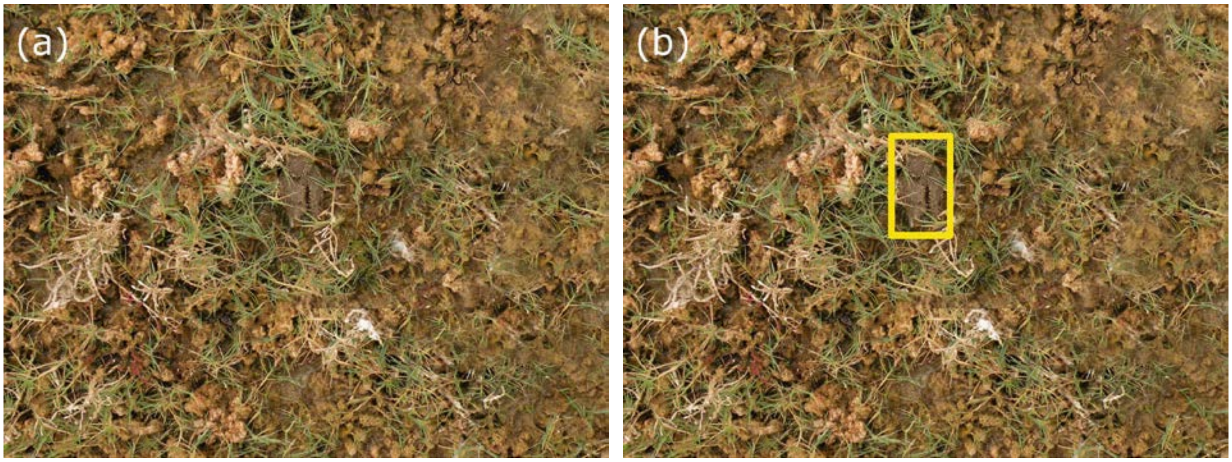

Figure 4.4. (a) Example practice trial for the first experiment. On clicking, a feedback screen (b) was shown with the location of the target.

One advantage of PsychoPy for experiments is that, apart from creating Python code (which can be edited directly if needed) from your diagram, it can translate the Python code into Javascript which, in turn, can be uploaded the Pavlovia website (https://pavlovia.org), developed by the same authors, for running online experiments. Pavlovia generates a URL which can be sent to participants, it stores the data collected, which can then be bulk downloaded as comma-separated values for analysis.

All participants had been briefed in line with the Declaration of Helsinki, with the right to withdraw from the experiment at any time without explanation and all names stripped from the datafiles prior to analysis, to ensure anonymity. Ethical approval was granted by the joint research ethics committee of the Faculties of Science and Life Sciences of the University of Bristol.

4.3.2 Data processing and statistical analysis

The experiments provided two response variables: response times (RT) in milliseconds and errors (binary: coded 0 for clicking on the target and 1 for clicking elsewhere). Errors rather than hits were analysed because both are affected in the same direction and this simplifies interpretation: increased difficulty in locating a target results in both longer RTs and more errors. Only the RTs for correct clicks on the target were analysed and, in both experiments, this comprised >95% of the data because errors were rare. The distribution of the RT data was first checked for the overall shape of the distribution (and hence any transformations required for analysis) and suspiciously short values resulting from clicking the mouse by mistake or failing to engage with the task (repeated clicking to finish the experiment quickly). As is typical for latency data, RTs were right-skewed and the two commonest transformations for such data were tried: logarithm and inverse (1/RT). Unusually fast mouse-clicks were very clear as outliers far from the approximately normal distributions obtained by either of those transformations, and were removed prior to analysis. Transformed data were analysed using Linear Mixed Models using the lmer function in the lme4 package (Bates et al., 2015) in R 4.3.1 (R Core Team, 2023). Errors were analysed with Generalized Linear Mixed Models and binomial error, using the glmer function in the same package. The relevant fixed and random effects, and means of model testing, are different for each experiment and are provided in the relevant section. Normality and homoscedasticity of residuals were tested by graphical inspection using histograms, quantile-quantile and residual vs fitted value plots. Pair-wise comparisons, where relevant, used the Tukey procedure implemented in the multcomp package (Hothorn et al., 2008).

4.4 Sex differences in detectability of plover chicks

4.4.1 Methods

4.4.1.1 Protocol

The experiment was a replication of Jorge Parra's experiment, using the same stimuli and presentation protocol. The photographs had been taken by Jorge Parra in 2011 with a Nikon Coolpix P80 digital camera (Nikon Corp., Tokyo, Japan) in natural lighting at coastal breeding sites near Andavadoaka, south-west Madagascar (latitude -22.073139301, longitude 43.2374177654), and saved as uncompressed TIFF files at 3648 × 2736 pixel resolution. The sample comprised eight female and ten male Kittlitz plover and four female and three male white-fronted plover chicks. Having taken a photograph of each chick as found *in situ*, the chick was captured for measuring and obtaining a blood sample for molecular sexing, then the same background was immediately photographed without the chick. Subsequently, each chick was digitally edited from its photograph and, using a custom Matlab program (The Mathworks, Natick, MA, USA) rotated a random number of degrees and inserted into the matching chick-absent photograph at random xy coordinates. Therefore, each chick appeared in two photographs: in its natural location and a random location on the same background (Figure 4.5 shows examples). All participants saw these two versions of all images, so 50 images in total, in a different random order for each participant. All the image manipulation had been carried out by Jorge Parra.

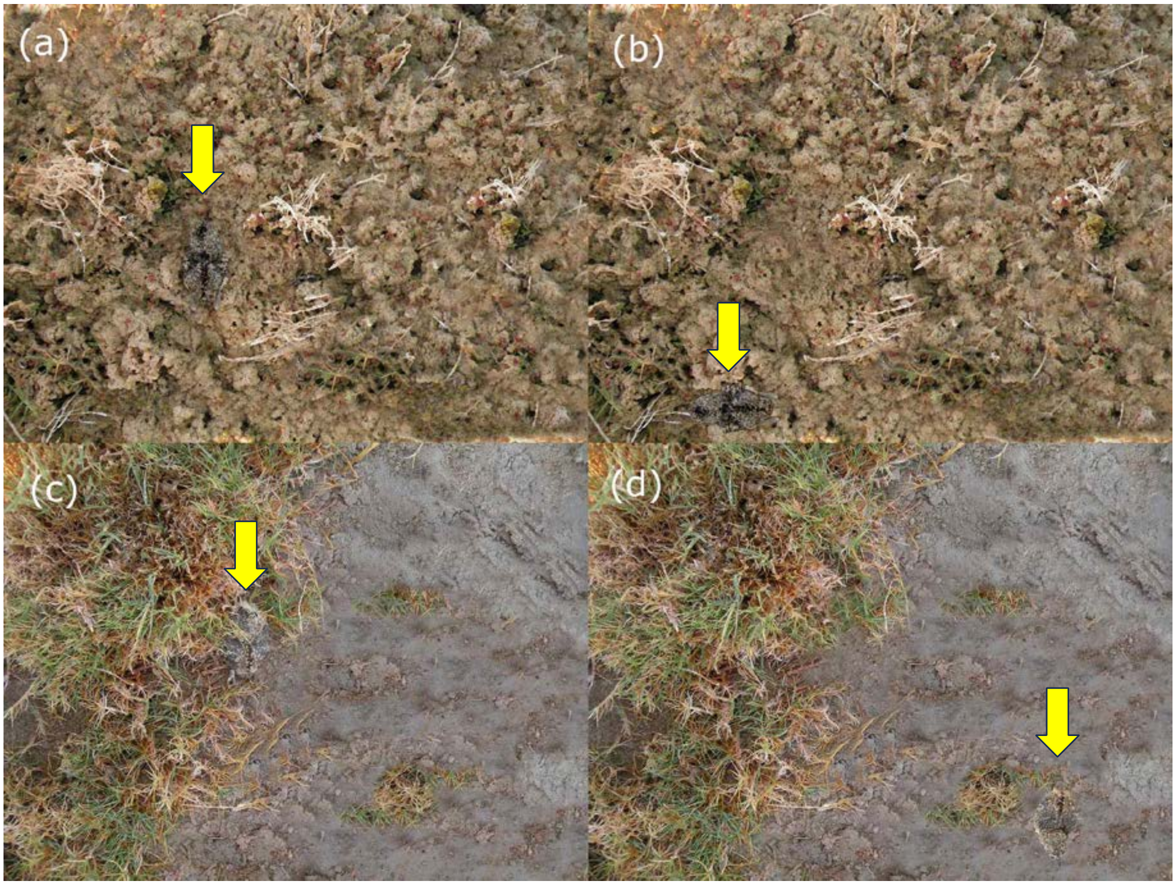

Figure 4.5. (a) and (c): examples of chicks in their original locations. (b) and (d): the same chicks digitally edited and randomly placed on the same backgrounds.

Sixty participants carried out the experiment as part of an undergraduate practical class at the University of Bristol; the briefing told them the task was to find a camouflaged plover chick, but not the object of the experiment.

4.4.1.2 Analysis

Initial checks on the RT data showed five values less than 300 ms (one of these less than 100 ms, the ‘false start’ criterion in Olympic sprint events), clearly differentiated from the rest of the distribution (Figure 4.6a,b). These were removed prior to analysis. The remaining data suggested that an inverse transformation might be best (Figure 4.6c,d) and analysis of the residuals from the main analysis indicated this was appropriate (Figure 4.7).

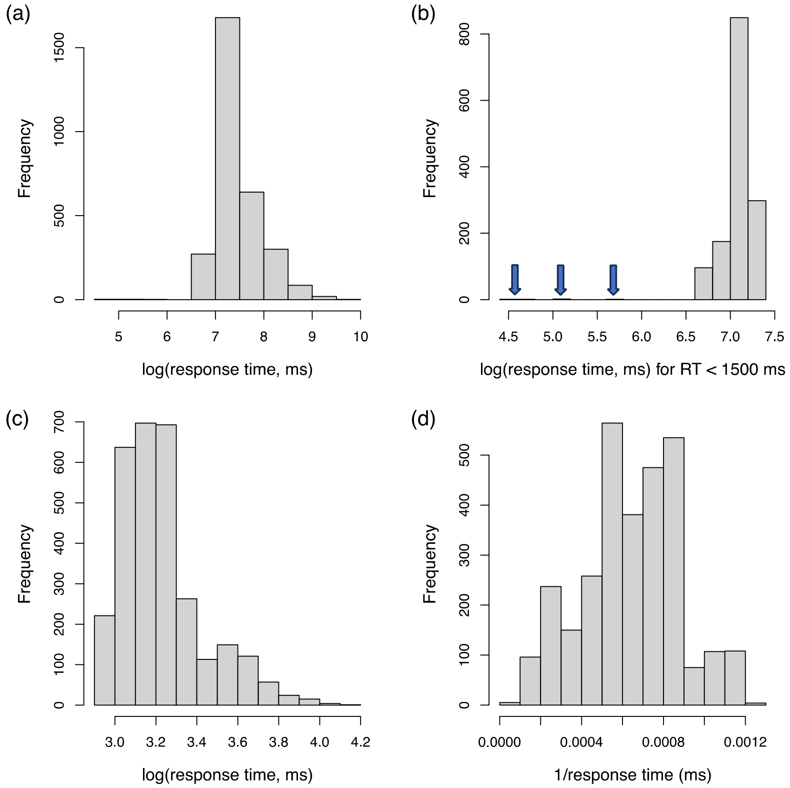

Figure 4.6. (a) Distribution of log-transformed response times (RTs). (b) Zooming in on the shorter values (< 1500 ms), the blue arrows indicate outliers far removed from the rest of the data, likely representing mouse-clicks in error as soon as an image was displayed. (c) Distribution of log-transformed RTs after the remove of these outliers (all < 300 ms). (d) Inverse (1/RT) transformation produces a less skewed distribution.

The experiment was designed (and originally analysed by Jorge Parra) solely with an interest in the effect of sex (male vs. female) and whether there was a difference in detectability depending on whether a chick was in the location it had chosen or in a random spot in the same photograph (factor ‘location’: original vs. random). However, although chicks from the two different species had been treated as identical/interchangeable, the possibility remains that plumage, and so the effectiveness of their camouflage, differs. Therefore, the factor ‘species’ in addition to sex and location were included as fixed effects, with both participant and ‘photograph’ (matched across each chick’s original and random location versions) as random effects. Because of the post hoc nature of the analysis, including multiple interaction terms, and the inflation of Type I errors (false positives) possible when testing many terms sequentially (Whittingham et al., 2006), an information-theoretic approach to model assessment was used, comparing the Akaike’s Information Criterion (AIC) of all models from one with the terms sex, location, species and all possible interactions, to a null model with only the intercept as a fixed effect. The model with the lowest AIC value is the ‘best’ model in terms of the trade-off between goodness of fit and complexity (number of parameters), with models within 2 AIC units of the best model being considered equally consistent with the data (Burnham & Anderson, 2002).

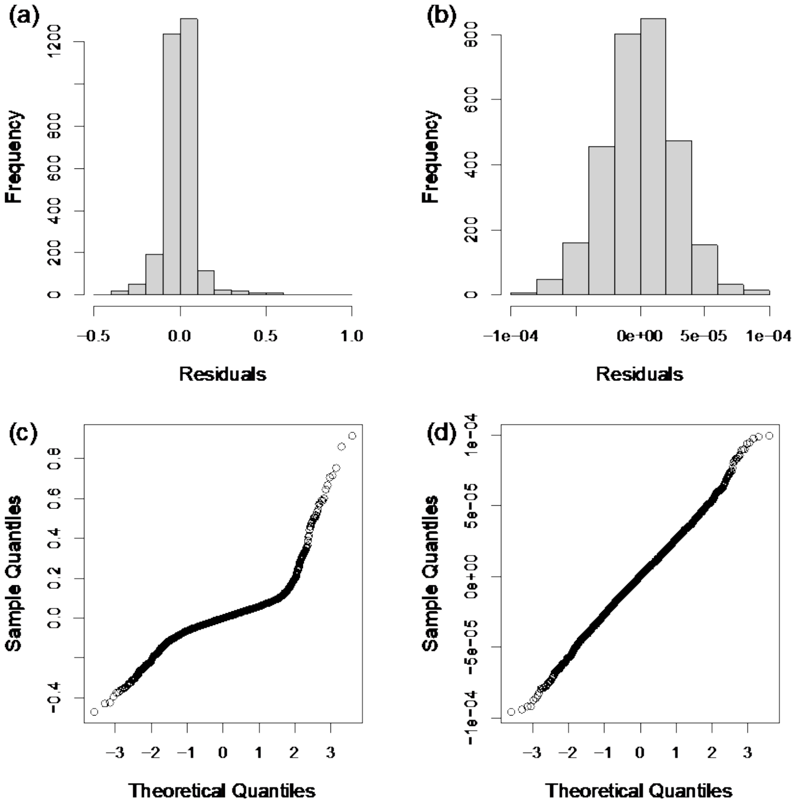

Figure 4.7. (a) Histogram of residuals from the full model applied to log(response time). (b) Equivalent histogram of residuals for an analysis of 1/(response time). (c) Quantile-quantile plot of the same residuals from the analysis of log(RT) and (d) 1/RT. The reduced skew in (b) and straighter line in (d) indicate that analysis of 1/RT better matches the assumption of normality.

4.4.2 Results

Inspection of the response time data (Figure 4.8) suggested that there might be an interaction between sex and species with male Kittlitz plover chicks harder to find than females but the opposite for white-fronted plovers, but comparison of the AIC values from the analyses of inverse-transformed response time shows that there is no evidence for any of the factors having an effect (the null model has the lowest – most negative – AIC value; Table 4.1). For comparison with the conclusion from Jorge Parra's original experiment, a model with only the effect of sex (plus the two random effects) was tested against the null model with a likelihood ratio test (Edwards, 1992). There was no sex difference (LRT = 1.643, d.f. = 1, $p = 0.200$). However, performing the same analysis but with only a random effect of participant did show a significantly longer search time for males than females (LRT = 190.28, d.f. = 1, $p < 0.001$). Suspecting that this second (incorrect) analysis might have been behind Jorge Parra's original conclusions, I reanalysed his data in the same way as mine (Figure 4.9, Table 4.2).

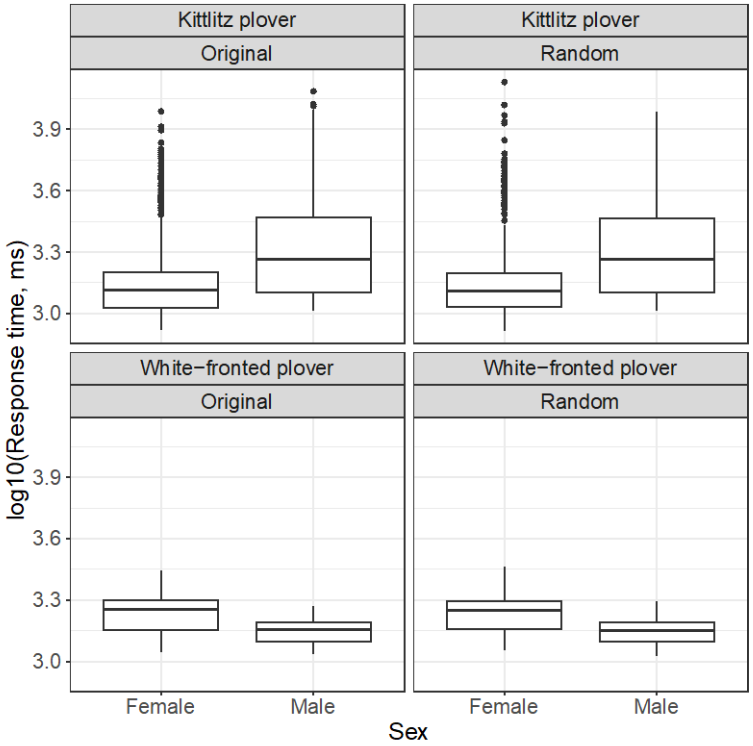

Figure 4.8. Response times ($\log_{10}$-transformed) for detecting plover chicks against the backgrounds against which they were found (‘original’) and random placement by digital insertion onto the background (‘random’). Data are split by species and sex. Although an inverse transform was used in the analyses, a $\log_{10}$ transformation is easier to interpret because the direction of differences matches that of the raw data.

Table 4.1. Akaike Information Criteria (AIC) values for the full set of statistical models of response time (inverse-transformed), ordered by number of parameters.

Fixed effects in model	df	AIC	∆AIC
sex * position * species	11	-53644.92	149.59
(sex + position + species)^2	10	-53669.51	125.01
(sex + position + species)^2 - sex:position	9	-53695.86	98.65
(sex + position + species)^2 - sex:species	9	-53684.10	110.41
(sex + position + species)^2 - species:position	9	-53692.11	102.40
sex * position + species	8	-53706.71	87.81
sex + position * species	8	-53710.45	84.06

sex * species + position	8	-53718.42	76.09
sex + position + species	7	-53733.01	61.50
sex + position	6	-53751.47	43.04
sex + species	6	-53758.90	35.61
position + species	6	-53750.18	44.33
sex	5	-53777.36	17.15
position	5	-53768.62	25.89
species	5	-53776.07	18.44
1	4	-53794.51	0.00

R notation for fixed effects is that A*B*C indicates a model with the A-by-B-by-C interaction, plus all two-way interactions and the main effects. (A + B + B)^2 indicates only the three possible two-way interactions between A, B and C, plus the main effects. A minus sign before a term removes that term from the model. A 1 indicates the null model with only the intercept. df = degrees of freedom. ΔAIC is the difference in AIC between a model and the best model (which is the intercept-only model).

In the original Parra analysis, the RT data were log-transformed and, in a model with the fixed effect of sex and random effect of participant (n=21, yielding 1050 data points), males took 20% longer to find than females (mean female RT = 1289 ms, mean male RT 1070 ms; $F_{1,1028} = 18.117$, $p < 0.001$). Visual assessment of the data split by sex, location and species (Figure 4.9), gives a very similar pattern to that in my replication (compare with Figure 4.8). However, I made the following changes to the analysis, based on the procedure for my own experiment. I checked for unreasonably fast RTs; there was one (214 ms) which I removed. Checking the residuals from the full model (analysis with fixed effects of sex, location and species, plus all interactions) showed that an inverse transformation of RT gave more normal residuals than a log-transform (Figure 4.10), just as in my experiment. The set of models from the most complex (all possible) to the simplest (only an intercept as the fixed effect) were fitted to 1/RT, including both participant and photograph as random effects, and compared using AIC (Table 4.2). As with my replication, the null model was the best supported, although a model with the main effect of location was within 2 AIC units of it (original location 914 ms, random location 1016 ms, using the model's parameter estimates). For completeness, testing a model with a main effect of sex against the null model showed no sex difference (LRT = 1.313, d.f. = 1, p = 0.252). However, performing the same analysis but with only a random effect of participant did show a significantly longer search time for males than females (LRT = 20.281, d.f. = 1, p < 0.001).

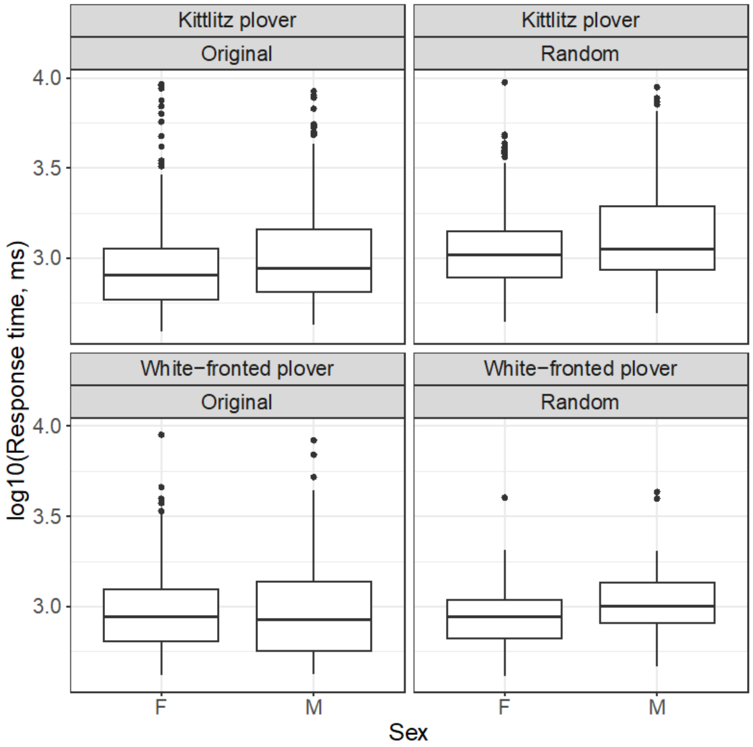

Figure 4.9. Response times ($\log_{10}$-transformed) in Jorge Parra's original experiment on the detection of plover chicks against the backgrounds against which they were found ('original') and random placement by digital insertion onto the background ('random'). Data are split by species and sex.

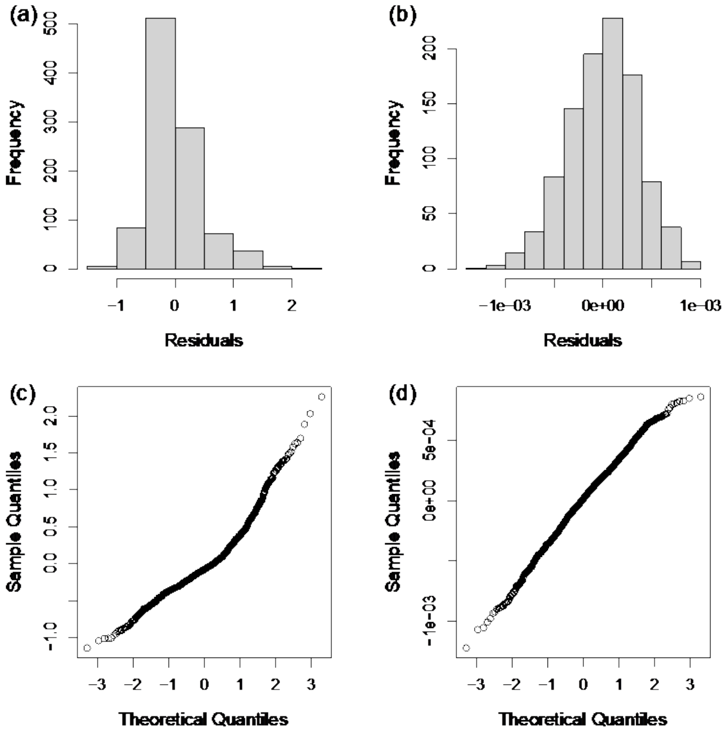

Figure 4.10. Reanalysis of Jorge Parra's original data. (a) Histogram of residuals from the full model applied to log(response time). (b) Equivalent histogram of residuals for an analysis of 1/(response time). (c) Quantile-quantile plot of the same residuals from the analysis of log(RT) and (d) 1/RT. The reduced skew in (b) and straighter line in (d) indicate that analysis of 1/RT better matches the assumption of normality.

Table 4.2. Reanalysis of Jorge Parra's original experiment: Akaike Information Criteria (AIC) values for the full set of statistical models of response time (inverse-transformed), ordered by number of parameters.

model	df	AIC	deltaAIC
sex * position * species	11	-13252.70	85.40
(sex + position + species)^2	10	-13270.80	67.30
(sex + position + species)^2 - sex:position	9	-13290.86	47.24
(sex + position + species)^2 - sex:species	9	-13287.27	50.83
(sex + position + species)^2 - species:position	9	-13267.04	71.06
sex * position + species	8	-13283.50	54.60

sex + position * species	8	-13307.33	30.77
sex * species + position	8	-13286.61	51.49
sex + position + species	7	-13303.07	35.03
sex + position	6	-13320.83	17.27
sex + species	6	-13303.38	34.72
position + species	6	-13320.16	17.94
sex	5	-13321.14	16.96
position	5	-13337.80	0.30
species	5	-13320.46	17.64
1	4	-13338.10	0.00

R notation for fixed effects is that A*B*C indicates a model with the A-by-B-by-C interaction, plus all two-way interactions and the main effects. (A + B + B)^2 indicates only the three possible two-way interactions between A, B and C, plus the main effects. A minus sign before a term removes that term from the model. A 1 indicates the null model with only the intercept. df = degrees of freedom. ∆AIC is the difference in AIC between a model and the best model (which is the intercept-only model).

4.5 Camouflage against different backgrounds

4.5.1 Logic

Plover chicks can physically hide in vegetation, occluding all or part of the body, but when on exposed mudflats or saltmarshes, they cannot. Therefore, although predators are likely to encounter them on both background types, I predicted that the selective pressure to match mud and saltmarsh substrates would be greater than on and in vegetation, so their plumage would be a better background match to the non-vegetated backgrounds (henceforth 'mud' for simplicity). To focus on background matching by the plumage alone, rather than detection through body shape (which would be affected by occlusion or any disruptive colouration in the plumage), and the fact that other body parts (beak, legs, eyes) might be a cue for detection, I abstracted the task to spotting one patch of plumage among same-sized patches of background. Those 'mosaics' of background could be composed of only mud or only vegetation. I also investigated the detectability of chick plumage on backgrounds that contained both types of substrate. The reason for this was that chicks were sometimes found, and photographed, at the boundary between mud and vegetation, and there is some evidence that objects are harder to detect near the boundaries between background patch types (Espinosa & Cuthill, 2014). I also included a random mixture of mud and vegetation squares as a control for there being two different types of background sample in a scene, rather than the scene containing a boundary *per se*.

4.5.2 Methods

4.5.2.1 Protocol

The experiment used small square patches of Kittlitz plover chick plumage. The images used in this experiment were from the same dataset that I have used for plumage analysis (Chapter 3). Using the masks that specified the location of chicks and backgrounds in photographs, a custom R script was used to randomly select 96x96 pixel tiles from within those regions: patches of chick plumage or background (the script was written by my supervisor, Prof. I. Cuthill). The same R script assembled the tiles into 8x8 mosaics (768x768 pixels), each containing one plumage square and 63 background squares (Figure 4.11). These mosaics were of four different types, corresponding to the experimental treatments: all mud, all vegetation, a random mixture of 50% mud squares and 50% vegetation squares, and a 'structured' 50:50 mixture (Figure 4.11). The structure was: top half vegetation, bottom half mud; the reverse of this; left side vegetation, right side mud; the reverse of this. The all-mud, all-vegetation and structured mixture represented different types of natural backgrounds a chick might be seen against (e.g. Figure 4.5c), the random mixture acting as a control, as explained in 4.4.1.

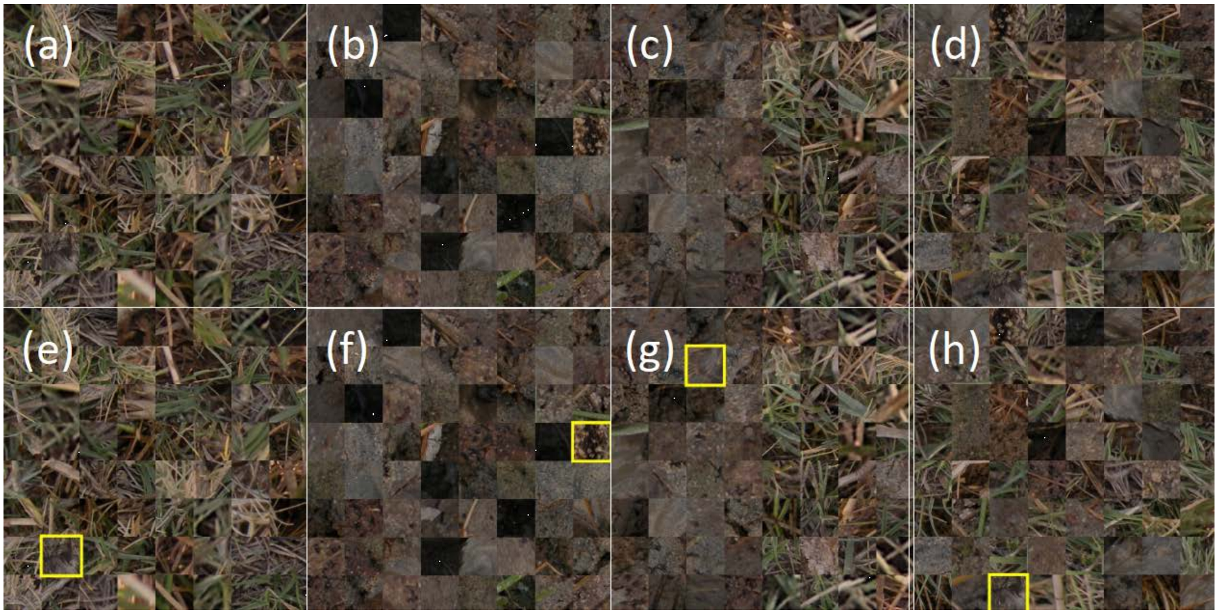

Figure 4.11. Examples of the four different treatments: (a) all-mud, (b) all-vegetation, (c) structured 50:50 mix and (d) random 50:50 mix. (e) to (h) indicate the location of the plumage square with a yellow rectangle. Participants were given (a) to (d), and a further four examples (one of each treatment) as practice trials at the start of the experiment, with the correct answer, (e) to (h) respectively, as feedback after they had clicked on a square, whether they were correct or not. No feedback on target location was provided in the experiment proper.

The experiment lasted approximately 20 minutes, with a total of four blocks of 25 different replicate images from each treatment, where the task was to search for the single tile of plumage among the mosaic of background tiles and click on it with the mouse. Because it was reasoned that predators would be likely to search on a particular background type for an extended period (or at least not randomly switch between background types), treatments were viewed in blocks of a single treatment. For example, a participant might see 25 images corresponding to background vegetation, followed by an opportunity to pause, then next block of 25 images of background mud, a pause, then 25 images of the structured 50:50 mix, a pause, then and the last block of 25 images of the randomly mixed mud-vegetation treatment. All participants saw the same 100 test stimuli (25 of each treatment), but every participant received a separately randomised sequence of blocks, and of replicates within blocks. There was a time-out criterion of

10 s (i.e. participants had a maximum of 10 s to click on the target, after which the experiment advanced to the next image).

The experiment was run in two formats: online, as part of an undergraduate practical class, using computers with Dell 24 Inch Video Conferencing (C2423H) monitors (Dell Inc., Round Rock, TX, USA), and under controlled conditions in a small, windowless, test room. The former had the advantage of a large sample size, but the latter provided confidence in how the stimuli were seen, in terms of colour rendition, and the rigour with which the experimental protocol was followed. The display in the tightly controlled calibrated-screen version of the experiment was a gamma-corrected (calibrated and linearised) 21.5" iiyama ProLite B2280HS monitor (iiyama; Hoofddorp, Netherlands) with a refresh rate of 60 Hz, a resolution of 1200 × 1080 pixels, a screen size of 27 by 48 cm and a mean luminance of 120 cd m^2) at a viewing distance of ca. 50 cm. The monitor was driven by a Macbook Pro (Apple Inc., Cupertino, CA, USA). The main room lights were turned off, and the participant was left alone, after briefing, to complete the experiment. In the mass-participation practical class version of the experiment, viewing conditions and computer/monitor type was uncontrolled (students could do the experiment online at home), but participants were asked to enter the viewing device, and self-identified sex and age (with no response signalled as allowed) at the start of the experiment as part of the PsychoPy protocol. A total of 191 participated in the entire experiment (104 female, 80 male, 7 undisclosed; the median age was 20, range 19-39, inter-quartile range 20-21). The sex ratio bias is typical of the Biological Sciences undergraduates at the University of Bristol. Of these, 171 were from the online version, with 10 males and 10 females (median age 20, range 19-23) taking part in the controlled calibrated-screen version.

4.5.2.2 Analysis

Checks for unusually fast response times were carried out and because, unlike in the previous experiment, participants frequently clicked on the wrong square, participants who made an unusually high number of errors (compared to the others) were identified. In the calibrated-screen version of the experiment, no unusually fast mouse-clicks or high error rates were found.

In the online version, one participant took 46 hours to find a target, compared to a median of 5.45 seconds (inter-quartile range 2.5 to 11.85 s); this data point was omitted but the rest of this participant's data were well within the range of most participants and so were retained. However, eight participants' data were omitted in their entirety because either they had a very low proportion of correct target detections (<5%, with others having a median of 60% and inter-quartile range of 52 to 68%) or a high proportion of very fast (< 300 ms) response times (> 25%, with others having very few or none: median of 0% and inter-quartile range of 0 to 0%). I concluded that these participants were not taking the task seriously or were using a very poor screen (for example, too small). This left a sample of 101 females, 75 males and 7 undisclosed sex for the entire experiment.

Response times were log-transformed prior to analysis, this producing closer to normal residuals than an inverse transformation. Linear Mixed Models were fitted with the fixed effect 'treatment' and random effects 'participant' and 'image'. The latter is because all participants saw the same 100 images (four replicates per treatment). Corresponding Generalized Linear Mixed Models with binomial error and logit links were used to analyse misses. A null hypothesis-testing approach, using likelihood ratio tests, was taken (as opposed to AIC) because there was one factor of interest, treatment, with a clear *a priori* hypothesis. The data for the 20 calibrated-screen participants were, in addition, analysed separately, the reasoning being that these should be the most reliable; then the pooled dataset of all 183 participants (including the calibrated-screen subjects) was analysed.

4.5.3 Results

4.5.3.1 All data

The proportion of misses (Figure 4.12; LRT = 761.77, d.f. = 3, $p < 0.001$) and response time (LRT = 208.51, d.f. = 3, $p < 0.001$) were significantly affected by treatment. Pair-wise comparisons suggest that detection on all-mud is hardest (more misses, slower RTs) and vegetation easiest, with the mixed treatments intermediate (Table 4.3). Interestingly, in terms of errors, the structured mix is harder than the random mix, although the response times are more similar to each other and to mud than any are to vegetation. We can investigate the data in more detail, by examining detection success and response time for the two halves of the structured mix separately (Figure 4.14). As one would expect, detection on the mud half is harder than on the vegetation (these two treatments analysed separately: misses LRT = 76.628, d.f. = 3, $p < 0.001$; RT LRT = 157.09, d.f. = 3, $p < 0.001$). Analysing all the data together, but splitting the structured mix data by background half (i.e. mud and vegetation separately, so five treatments in all) is very revealing. Taking the evidence from the misses and response times together, detection on the mud half of the structured mix is harder than detection on pure mud, and detection on the vegetation half of the structured mix is harder than detection on pure vegetation (Figure 4.14; Table 4.4). It is worth noting, in case it appears odd, that the mean response time for the structured mix treatment in Figure 4.12 is not halfway between the means of the vegetation and mud halves in Figure 4.13 because the analyses were done on log-transformed times and the means (and confidence intervals) back-transformed for plotting.

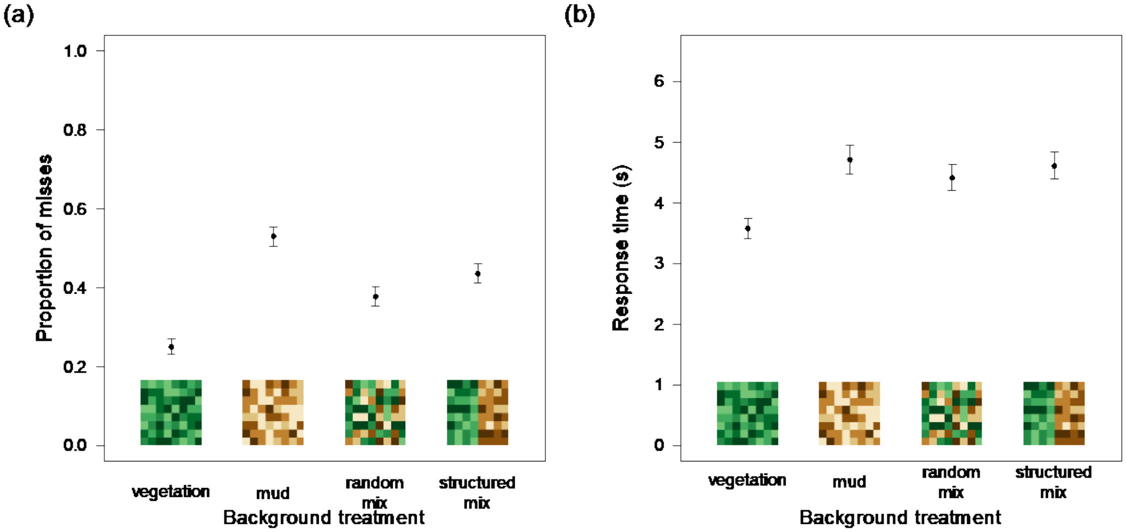

Figure 4.12. All data: (a) proportion of misses and (b) response times, means and 95% confidence intervals calculated from fitted models as described in the main text.

Table 4.3. Result of pair-wise comparisons, using the Tukey method, for the analyses of proportion of errors (logit link) and response time (log-transform).

Proportion of misses	Online				Calibrated			
Contrast	Estimate	SE	z	p	Estimate	SE	z	p
mud - vegetation == 0	1.219	0.046	26.281	**< 0.001**	1.255	0.144	8.723	**< 0.001**
random mix - vegetation == 0	0.597	0.047	12.764	**< 0.001**	0.810	0.145	5.592	**< 0.001**
structured mix - vegetation == 0	0.838	0.046	18.049	**< 0.001**	0.979	0.144	6.787	**< 0.001**
random mix - mud == 0	-0.622	0.044	-14.184	**< 0.001**	-0.445	0.133	-3.355	**0.004**
structured mix - mud == 0	-0.381	0.043	-8.791	**< 0.001**	-0.276	0.132	-2.101	0.153
structured mix - random mix == 0	0.241	0.044	5.476	**< 0.001**	0.168	0.133	1.265	0.585
Response time								
mud - vegetation == 0	0.274	0.023	12.100	**<0.001**	0.315	0.069	4.592	**<0.001**
random mix - vegetation == 0	0.209	0.021	9.940	**<0.001**	0.152	0.065	2.332	0.091
structured mix - vegetation == 0	0.252	0.022	11.716	**<0.001**	0.178	0.066	2.688	**0.036**
random mix - mud == 0	-0.065	0.023	-2.785	**0.028**	-0.163	0.072	-2.266	0.106
structured mix - mud == 0	-0.022	0.024	-0.907	0.801	-0.137	0.073	-1.870	0.241
structured mix - random mix == 0	0.044	0.022	1.948	0.207	0.026	0.070	0.379	0.981

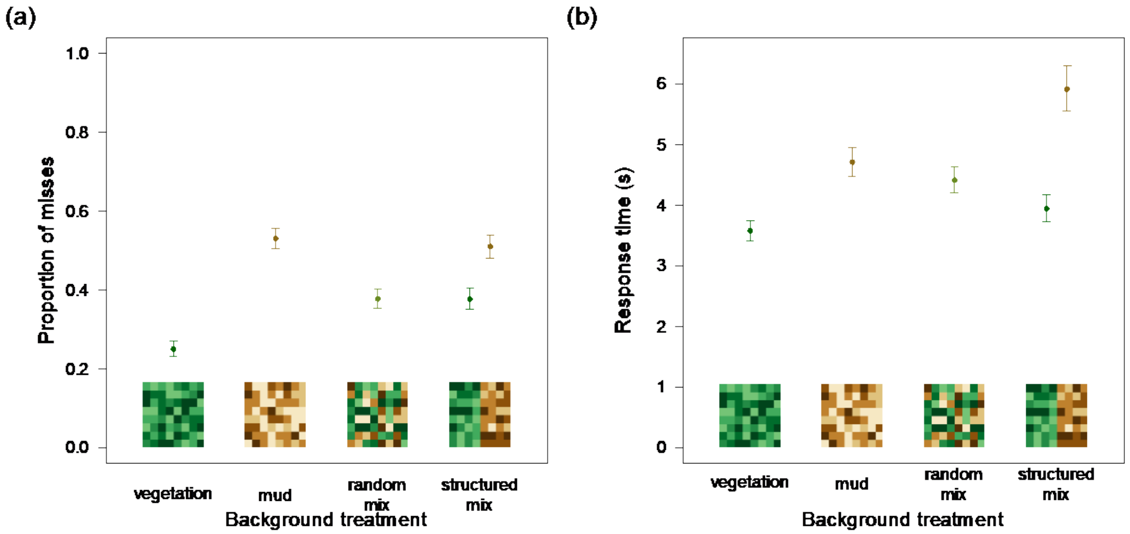

Figure 4.13. All data, analysing the two halves of the structured mix separately: (a) proportion of misses and (b) response times, means and 95% confidence intervals calculated from fitted models as described in the main text.

Table 4.4. Analysing participants' performance on the mud and vegetation halves of the structured mix treatment separately. Result of pair-wise comparisons, using the Tukey method, for the analyses of proportion of errors (logit link) and response time (log-transform).

	Proportion of misses				Response time			
Contrast	Estimate	SE	z	p	Estimate	SE	z	p
mud - vegetation == 0	1.220	0.046	26.288	**<0.001**	0.274	0.022	12.184	**<0.001**
random mix - vegetation == 0	0.597	0.047	12.768	**<0.001**	0.209	0.021	10.012	**<0.001**
structured mix (vegetation) - vegetation == 0	0.595	0.054	10.924	**<0.001**	0.097	0.025	3.880	**<0.001**
structured mix (mud) - vegetation == 0	1.139	0.058	19.719	**<0.001**	0.501	0.030	16.988	**<0.001**
random mix - mud == 0	-0.622	0.044	-14.187	**<0.001**	-0.065	0.023	-2.802	**0.039**
structured mix (vegetation) - mud == 0	-0.625	0.052	-12.026	**<0.001**	-0.178	0.027	-6.574	**<0.001**
structured mix (mud) - mud == 0	-0.081	0.055	-1.465	0.058	0.227	0.031	7.259	**<0.001**
structured mix (vegetation) - random mix == 0	-0.003	0.052	-0.048	1.000	-0.112	0.026	-4.376	**<0.001**
structured mix (mud) - random mix == 0	0.541	0.056	9.713	**<0.001**	0.293	0.030	9.710	**<0.001**
structured mix (mud) - structured mix (vegetation) == 0	0.544	0.062	8.729	**<0.001**	0.405	0.033	12.248	**<0.001**

4.5.3.2 Calibrated-screen participants

As a check against any biases created by the variation in viewing conditions and motivation of the online participants, I analysed separately the data for the participants doing the experiment under controlled conditions. The pattern of results was very similar to that of the whole dataset, with the proportion of misses and response time significantly affected by treatment (Figure 4.14; misses LRT = 87.369, d.f. = 3, $p < 0.001$; RT LRT = 21.777, d.f. = 3, $p < 0.001$). All the pair-wise comparisons showed similar directions and magnitudes of differences to the overall analysis, although not all were statistically significant (Table 4.3).

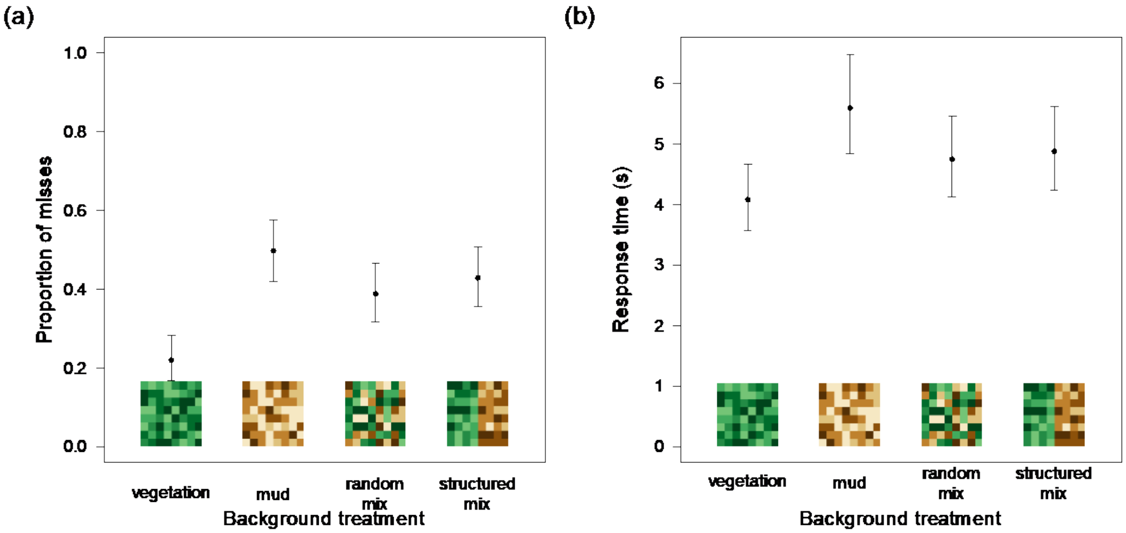

Figure 4.14. Calibrated-screen participants only: (a) proportion of misses and (b) response times, means and 95% confidence intervals calculated from fitted models as described in the main text.

4.6 Discussion

Although the experiment that inspired this research could be faithfully replicated (my results were fundamentally the same), Jorge Parra's conclusion that there was a sex difference in detectability of plover chicks turned out to be the result of a flawed analysis. While there were minor issues that my analysis improved upon (exclusion of implausibly fast responses and inverse rather than log-transformation of response times), the most important one was accounting for the fact that the same test images were seen by all participants. When this was included as an additional random effect (a well as participant) in the analyses of either my data or Dr Parra's original data there was no hint of a sex difference. (And when 'photograph' was not included as an additional random effect, sex was significant in my replicate experiment as well as the original Parra data.) This is an example of 'stimulus pseudoreplication' (Hurlbert, 1984; Kroodsma, 1989). Although a large number of participants may do an experiment (in my replication, 183 provided valid data), if there are insufficient replicate examples of the treatment of interest (here, individuals within sex, with only 13 female and 12 male chicks) then chance differences between the individuals within the female as opposed to the male group may be misinterpreted as a genuine sex difference. The 183 trials that result from every participant viewing any one chick are pseudoreplicates rather than real replicates: they represent variation in participants' ability to detect that chick, not variation in the detectability of chicks of that sex. This issue is magnified by the heterogeneity due to the sample chicks coming from two different species: eight female and ten male Kittlitz plover and four female and three male white-fronted plovers.

Given the small sample size and heterogeneity with respect to species in the stimulus set, I cannot conclude that there is no sex difference in detectability, just that none could be detected within these data. However, that there is no detectable sex difference in detectability of chicks, of which 18/25 were Kittlitz plover, is consistent with the lack of a sex difference in the colour and texture measures of Kittlitz plover chick plumage in chapter 3. In that chapter, there was a significant difference in the backgrounds on which males and females were found, so it might be natural to analyse the Parra photographs in the same way. However, I decided against this for the same reason that the detection data cannot conclusively show a lack of sex difference (or at least a difference, with tight confidence intervals, that is too small to affect detectability): the sample size of chicks, and backgrounds, is too small.

Stronger conclusions can be drawn from the experiment on camouflage against different backgrounds (section 4.4). The plumage of Kittlitz plover chicks is much harder to differentiate from mud than vegetation and, with identification error rates above 50% (Figure 4.12) for the all-mud treatment, it is reasonable to conclude that the plumage really does look like cracked and pock-marked mud, making the chicks very well camouflaged on this substrate. Although there was plenty of greenery in the vegetation treatment, and chicks are obviously not green, detection on this substrate was not trivially easy, with error rates around 25% (Figure 4.12). Just considering these two treatments, the hypothesis that chick plumage would better match mud because the alternative concealment tactic of physically hiding is not available, is supported. However, the fact that the camouflage still works quite effectively among vegetation would not necessarily have been obvious from either armchair theory (grass is green, chicks are not) or an experimental treatment like the random placement one in section 4.3 (and Parra's original), where chicks are superimposed on top of the substrate. In that type of experiment, additional cues such as the outline of the bird and features such as the beak, legs and eyes, are available, with the outline being particularly prominent when the animal is cut-and-pasted onto a background. My experiment involving a mosaic of background and plumage patches isolates background matching by the plumage, with these other cues absent. It may seem divorced from reality, but it needs to be to do this. However, I would also argue that it does capture a real-world task. When partially occluded by vegetation, patches of plumage may be all that is visible of a bird, and so is the cue that must be minimised by the bird's camouflage.

The ecological motivation for including the structured 50:50 mixture of mud and vegetation is that the natural habitat in which the fledged plovers of this and many other species is a mosaic of different background types, and chicks were often photographed near boundaries of mud and vegetation. This may be because they prefer to forage near the protective cover of vegetation, but I thought it would be worthwhile investigating the purely visual effect of having to search for a fairly well camouflaged object against two background types. So, not whether the plumage is a compromise between matching mud or vegetation (it seems, from the analysis as discussed above, it is a much better match to mud), but whether the search task for a predator, with humans as a model, is harder. The null expectation would be that participants would search either the vegetation side first and then switch to the mud half next, or vice versa, with search efficiency on each half matching that on the pure substrate of that type. In fact, while error rates on the mud half of the structured mix were similar to error rates on pure mud, response times were much longer, and both error rates and response times were high on the grass half of the structured mix than on pure grass. The effect is not simply because the background is more complex, because error rates were lower on the random mix than the structured mix. Indeed, in terms of complexity, one would have expected the random mix to be the hardest substrate to search on, because multiple field and lab experiments, both in biology and perceptual psychology, have shown that the higher variance in background features within complex environments impedes visual search (Duncan & Humphreys, 1989; Rosenholtz et al., 2007; Dimitrova & Merilaita, 2010; Xiao & Cuthill, 2016; Rowe et al., 2021). Instead, there is something about having divide attention between searching two visually different substrates that makes the task harder. This is an area that should be investigated further, perhaps using eye-trackers to see whether participants search each half systematically or, as the results might suggest, they switch between sides and the change reduces search efficiency. The consequence for prey species, such as young plovers, might be that there are advantages of living in a mosaic-type habitat purely in terms of detectability by visual predators, such as birds of prey, that need to search both background type for targets.

Chapter Five: Compromise Camouflage using an Artificial Moth Experiment

5.1 Abstract

Many animals rely on camouflage as a defence against predators but, for those that are active in more than one habitat, is it better to specialize on matching one type of background well or to have some form of generalist or ‘compromise’ camouflage? This chapter concerns a field experiment aimed at assessing the efficacy of compromise camouflage using artificial moth-like prey with free-living birds as predators. The experiment specifically focuses on prey viewed against two distinct natural backgrounds, characterized by variations in both colour and visual texture: the bark of oak (*Quercus robur*) and beech (*Fagus sylvatica*) trees. The oak bark is characterized by a dark brown-grey colour and prominent ribbing, while the beech bark is light grey to greenish-grey in hue and has a smooth texture. There were nine treatments: the factorial combination of three colours (oak, beech or an averaged ‘hybrid’ of the two) and three textures (again oak, beech and hybrid, the latter created by a Fourier-domain blend of the two ‘parent’ species), placed on both oak and beech trees. By independently manipulating visual colours and textures, the relative significance of these two elements in background matching was revealed. Compromise camouflage prey (hybrid blends) had lower average survival (across both oak and beech backgrounds) than specialists (prey oak or beech) but colour mismatches tended to have a bigger negative impact on camouflage effectiveness compared to texture mismatches. This is likely because colour mismatches are always detectable but at greater viewing distances, textural information is lost. However, the relationship across oak and beech backgrounds was asymmetric, with oak being more ‘forgiving’ of mismatches than beech, probably because of its higher visual complexity.

5.2 Introduction

Camouflage is the most widespread form of protective colouration, and also used effectively by many predators (Stevens & Merilaita, 2011; Cuthill, 2019; Smith & Ruxton, 2020). A correlation between the colouration of species and their habitats suggests that background matching is a common strategy (Endler, 1984; Merilaita & Stevens, 2011) but many animals live in heterogeneous environments or move between habitats. Therefore, a question arises, is it better to match one background very well or have generalist camouflage that is a compromise between different backgrounds (Merilaita et al., 1999, 2001; Houston et al., 2007; Hughes et al., 2019)?

In general, if an animal that can be seen on different backgrounds needs to hide, the benefits of matching one are likely to be offset by greater visibility on others (Merilaita et al., 1999). However, if the latter costs do not outweigh the former, then a compromise camouflage that works reasonably well on multiple backgrounds can be favoured (Merilaita et al., 2001; Houston et al., 2007). This is one explanation for "imperfect camouflage" (Hughes et al., 2019), just as matching multiple models is a potential explanation for what appears to be imperfect mimicry (Howse & Allen, 1994; Edmunds, 2000; Sherratt, 2002).

Merilaita et al. (1999) modelled when it is best to have a specialist or generalist camouflage, an approach extended by Houston et al. (2007). The key driver was the shape of the trade-off curve between survival (as affected by detectability) on one background versus the other; if convex, a generalist camouflage was favoured, if concave then specialists should prevail. Empirically, Merilaita et al. (2001), working with captive great tits (*Parus major*) searching for artificial prey, demonstrated that such a convex trade-off curve could exist for two backgrounds of identical texture (spatial pattern) but differing in spatial scale. Toh and Todd (2017), in experiments with humans searching on patterned backgrounds, manipulated the sizes of the geometric elements that constituted the patterns, and thus the perceptual difference between background types. When the elements in different backgrounds were more similar in size, targets with intermediate-sized elements had longer detection times, averaged across both background types; that is, the compromise strategy did best overall. However, when the pattern elements were very different in size, with the prediction that the intermediate compromise strategy would do poorly on both backgrounds, in fact average detection times for generalist and specialist patterns were similar. This indicates that, under some conditions, a compromise colouration could be the best strategy, but not how often these conditions might be met in nature nor, for backgrounds that vary in multiple attributes (e.g. lightness, colour, texture), along which dimensions compromises might be effective. Hughes et al. (2019) discuss some of these possibilities, proposing, for example, that compromise patterns may be some form of average of the different backgrounds, or consist of a mixture of discrete elements from each.

I present an experiment designed to determine whether a compromise camouflage can be effective against free-living avian predators, for prey encountered on two natural backgrounds that differ in both their colour and texture. By 'texture', I mean spatial variation in reflected light intensity (which underlies the visual perception of physical texture) or, more colloquially, 'pattern'. The two backgrounds are oak (*Quercus robur*) and beech (*Fagus sylvatica*) bark, the former dark brown-grey and heavily grooved, the latter light grey to greenish-grey and smooth. Manipulating matches in colour and visual texture separately allows us to assess the relative importance of these two components of background matching. All things being equal, because spatial detail is lost at greater distances (Endler, 1990; Barnett & Cuthill, 2014; Barnett et al., 2016), mismatches in colour are likely to be more deleterious to concealment than mismatches in texture (Michalis et al., 2017). However, a complex texture, by virtue of the fact that visual search on such backgrounds is more difficult (Dimitrova & Merilaita, 2010, 2012; Xiao & Cuthill, 2016; Rowe et al., 2021), may itself be more forgiving of mismatches in average colour (Merilaita, 2003; Toh & Todd, 2017).

5.3 Methods

5.3.1 Stimuli

The two types of background that targets were placed on were common oak and common beech tree bark. Targets were right-angled triangles of base 45 mm: notionally moth-shaped coloured paper as the 'wings' and a dead mealworm (*Tenebrio molitor* larvae frozen at −80 ° C then thawed), pinned underneath the paper but with a few mm protruding, as the edible 'body' (Cuthill et al., 2005). These triangles were made from calibrated photographs of 60 oak and 60 beech trees in the study site of Leigh Woods National Nature Reserve (North Somerset, UK, 2 ° 38.60 W, 51 ° 27.80 N). Images were taken at a distance of ca. 1 m with a Nikon Coolpix 5700 digital camera (Nikon Corp., Tokyo, Japan), at an aperture of f8 and the appropriate integration time for correct exposure. A Gretag-Macbeth Minicolorchecker chart (X-Rite Inc., Grand Rapids, MI, USA) was held against the bark, using the chart in the photograph to scale the images for size and to linearise the relationship between RGB pixel value and reflectance (Párraga et al., 2002; Stevens et al., 2007). While such photographs lack ultraviolet information, which birds are sensitive to (Cuthill, 2006), the bark of these trees has minimal UV reflection (Majerus et al., 2000; Cuthill et al., 2006a). RGB values were transformed to the estimated short-, medium-, long-wave and double cone photo catches of one of the main avian predators in the study site, the blue tit *Cyanistes caeruleu*s (Hart et al., 2000), viewed under a standard daylight illuminant, D65 (CIE, 2003). The photon catches were then transformed to a three-dimensional avian colour space (i.e. lacking UV) equivalent to the luminance, red-green and blue-yellow opponent channels in human vision. The luminance equivalent was the intensity variation in photon catches of the double cones, which are either the mediator of detailed spatial vision in birds, or very highly spectrally correlated with that mechanism (Kelber et al., 2003; Jones & Osorio, 2004). Following Michalis et al., (2017) and Xiao & Cuthill (2016), the red-green opponent measure was defined as the ratio of (L – M) to (M + L); the yellow-blue opponent measure as the ratio of (M + L – 2*S) to (M + L + 2*S). The luminance and colour opponent metrics were scaled to lie between 0 and 1.

There were nine treatments, the factorial combination of three colour classes and three pattern classes (Figure 3.1). We refer to these as 'classes' because there was natural variation between replicates within each treatment, in both pattern and colour. When we refer to pattern, or 'visual texture', we mean spatial variation in intensity only; any one replicate was monochromatic in terms of hue (as defined by the red-green and blue-yellow opponent metrics). This was done for convenience of stimulus design, but there are two reasons that it is a reasonable approximation. First, for a target-sized sample of the bark of a single tree, most of the variation is indeed in intensity (shades of brown for oak, shades of olive-brown for beech). Second, detection at a distance (where the detail cannot be resolved) is a function of contrast, with the background, in average colour (Michalis et al., 2017; Barnett et al., 2018b). Any one replicate within these nine treatments was a blend of two bark samples/images, either two of oak, two of beech, or one oak and one beech. That blend could be an averaging of colours, of patterns, or both. Henceforth I term oak-beech blends as the 'hybrid' (or compromise) treatment, but all replicates were blends of two images, including oak and oak or beech and beech, so that any advantage or disadvantage of the beech-oak hybrid over the 'specialist' beech or oak treatments was not confounded with blending per se. Blended colours were the means of the means of the colours, in the 3D avian colour space described above, of the two blended images. The blending of pattern was carried out in Fourier space, rather than an averaging of pixel values (Figure 5.1). The advantage of a 'Fourier blend' (Tolhurst & Tadmor, 2000) is that two otherwise identical patterns that are out of phase are not 'averaged out' (otherwise black-and-white stripes combined with, 180° out of phase, white-and-black stripes would produce homogeneous grey). Instead, the spatial variation in amplitude is maintained, with the phase being the average of the phase of the two originals (e.g. black-and-white stripes combined with their out-of-phase equivalent would produce black-and-white stripes phase-shifted by 90°). The targets were printed onto waterproof paper (Rite-In-The-Rain, JL Darling LLC, Tacoma, WA, USA) using a using a calibrated printer (Canon imageRUNNER ADVANCE C5535i; Canon Inc., Tokyo, Japan). Examples of each treatment are provided in Figure 5.2.

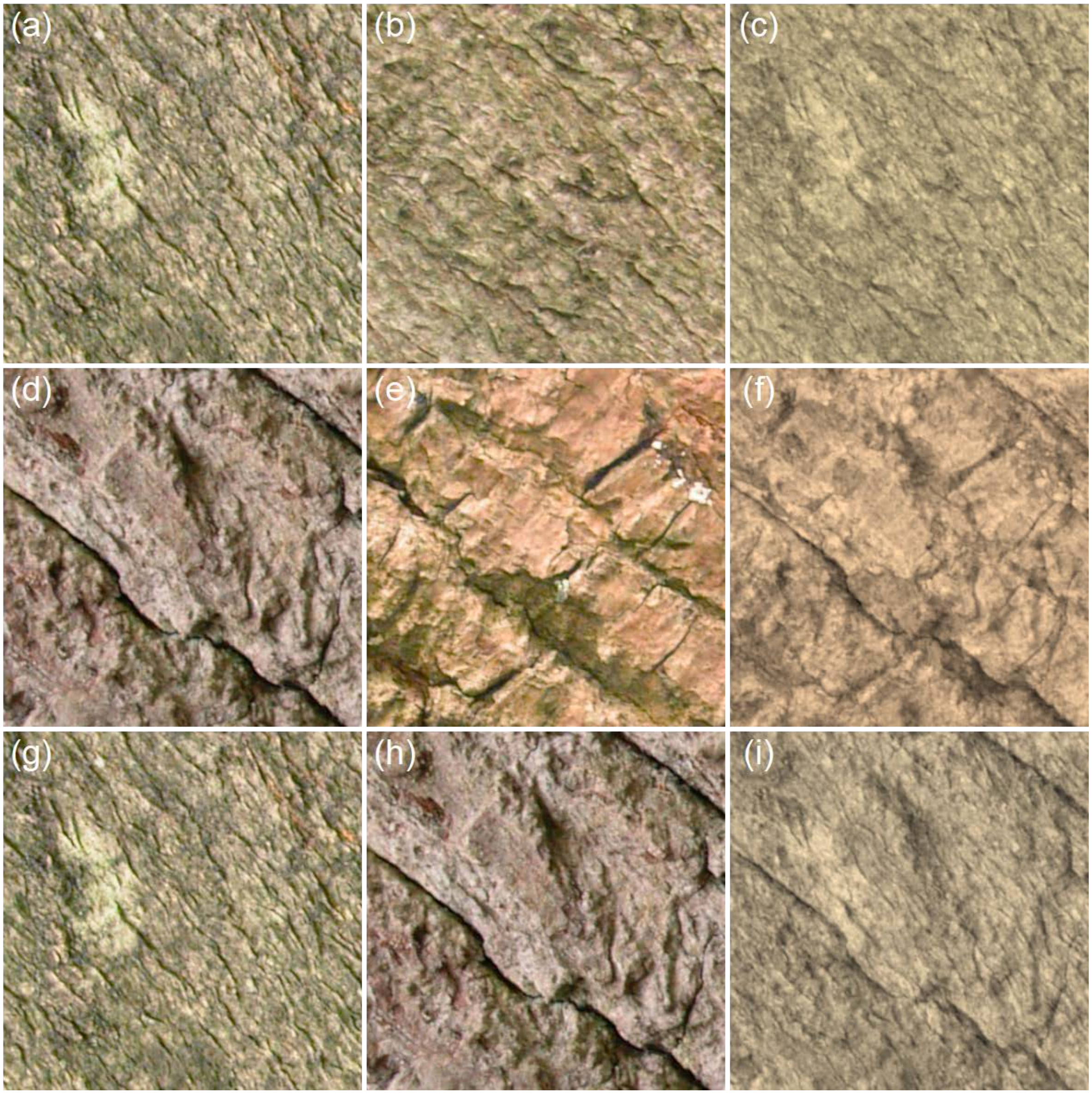

Figure 5.1. Blending images in Fourier space (separate averaging of amplitude and phase components of the two constituent images). (a) beech image 1; (b) beech image 2; (c) Fourier blend of beech images 1 and 2; (d) oak image 1; (e) oak image 2; (f) Fourier blend of oak images 1 and 2; (g) beech image 1; (h) oak image 1; (i) Fourier blend of beech image 1 and beech image 1.

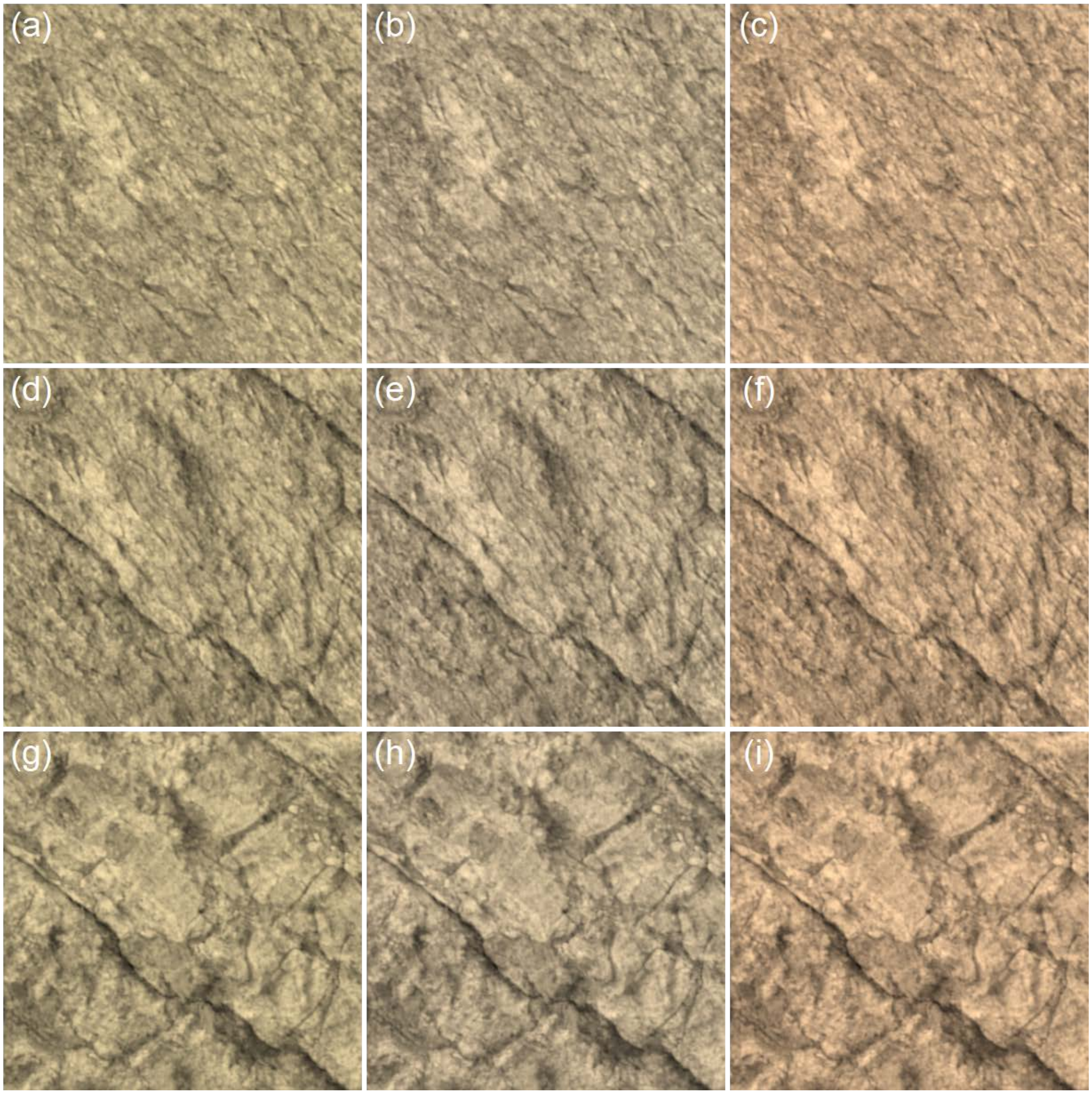

Figure 5.2. Examples of the nine treatments. (a) BB (beech texture + beech colour); (b) BX (beech texture + hybrid colour); (c) BO (beech texture + oak colour); (d) XB (hybrid texture + beech colour); (e) XX (hybrid texture + hybrid colour); (f) XO (hybrid texture + oak colour); (g) OB (oak texture + beech colour); (h) OX (oak texture + hybrid colour); (i) OO (oak texture + oak colour). 'Hybrid' indicates a blend of the beech and oak components, either colour or texture or both. Every replicate involved different samples from different trees, varying in both colour and visual texture. The colours were designed to match natural oak or beech in avian colour space when printed on waterproof paper, not as printed here as viewed by humans.

5.3.2 Procedure

The experiment took place at the study site where the bark photographs were taken, following a randomized block design. The blocks had 10 replicates of each of the nine treatments pinned, one per tree, to 90 mature beech and 90 mature oak trees in a given part of the woods. Ten blocks were carried out, for a total of 1800 targets. Each block was carried out in a different area in a different week, and consisted of a meandering transect of 1 to 1.5 km, following minor paths. I cannot rule out the possibility of a single bird consuming more than one prey, but the elongated nature of each transect, and the spatial separation of blocks, meant that any one bird would have had a negligible impact on the results. To simplify relocation, targets were pinned at head-height and, to reduce chances of interference by the public, on the side facing away from the trail.

Having put out targets for a block at the start of the week, checks were made at 24, 48, 72 and 96 h intervals. The 'survival' of each artificial moth was determined by the presence or absence of the mealworm, with the paper still intact and attached to the tree. Targets were marked as 'censored' if they were could not be found (n=2), if there was evidence of non-avian predation (n=55; *in situ* invertebrate predators or indirect evidence: slime trails of slugs, or only the hollow exoskeleton of the mealworm remaining, following spider predation) or they 'survived' predation to the end of the week (n=90). Avian predators that have been observed taking similar artificial prey in the study site (Cuthill et al., 2006a), and frequently seen throughout this experiment, were blue tits (*Cyanistes caeruleus*), great tits (*Parus major*), European robins (*Erithacus rubecula*), wrens (*Troglodytes troglodytes*), and chaffinches (*Fringilla coelebs*). Predated targets were removed immediately, surviving targets at the week's end.

5.3.3 Analysis

A mixed effects Cox regression was used to perform survival analysis using the coxme function of the coxme package (Therneau, 2020) in R 4.0.2 (R Core Team, 2023). The full model has three fixed effects -- target colour and pattern, each with three levels (beech, oak and hybrid), and tree background, with two levels (beech, oak) -- with experimental block as a random effect. The effect of the treatment was tested with analysis of deviance, comparing the log-likelihoods of a model with and without the factor in question, tested against a χ^2 distribution. Significant main effects were tested with the glht function in the R package multcomp, using the Tukey procedure to control Type I error rate (Hothorn et al., 2008). Effects are displayed as odds ratios: the odds of predation compared to survival for each treatment, in relation to the oak-coloured, oak-patterned treatment when placed on oak bark. This treatment was chosen solely for convenience of graphical display, because it was expected to have the lowest mortality: matching its background in both colour and pattern, with the complexity of oak bark further reducing detectability (Xiao & Cuthill, 2016). Expected average survival times were estimated using the package coxed (Kropko & Harden, 2020).

5.4 Results

The interaction between tree, pattern and colour was significant ($\chi^2 = 12.29$, d.f. = 4, $p = 0.015$), with the dissection of the effects summarized in Figure 5.3. For both beech and oak backgrounds, the target pattern by colour was significant, but the nature of the interaction differed. On beech trees, if the target colour was oak, mortality was uniformly high and did not differ between patterns. If the target colour was the beech-oak hybrid, mortality was high for oak and beech patterns (and similar to the mortality of oak-coloured targets) but mortality was lower for the beech patterned targets. When the target colour matched beech, oak patterns had higher than beech or hybrid patterns. On oak trees, when the target colour was beech or hybrid, both beech and hybrid pattern had similar high mortality, significantly greater than oak patterned targets. However, when the target colour was oak, both oak and hybrid patterns had the lowest mortality, each lower than beech pattern.

Overall, there is higher average mortality on beech backgrounds, the effect of colour is greater than that of pattern and, if there is a mismatch in colour, a matching pattern does little to reduce mortality. However, if the colour matches the background, the hybrid pattern survives similarly to the background-matching pattern.

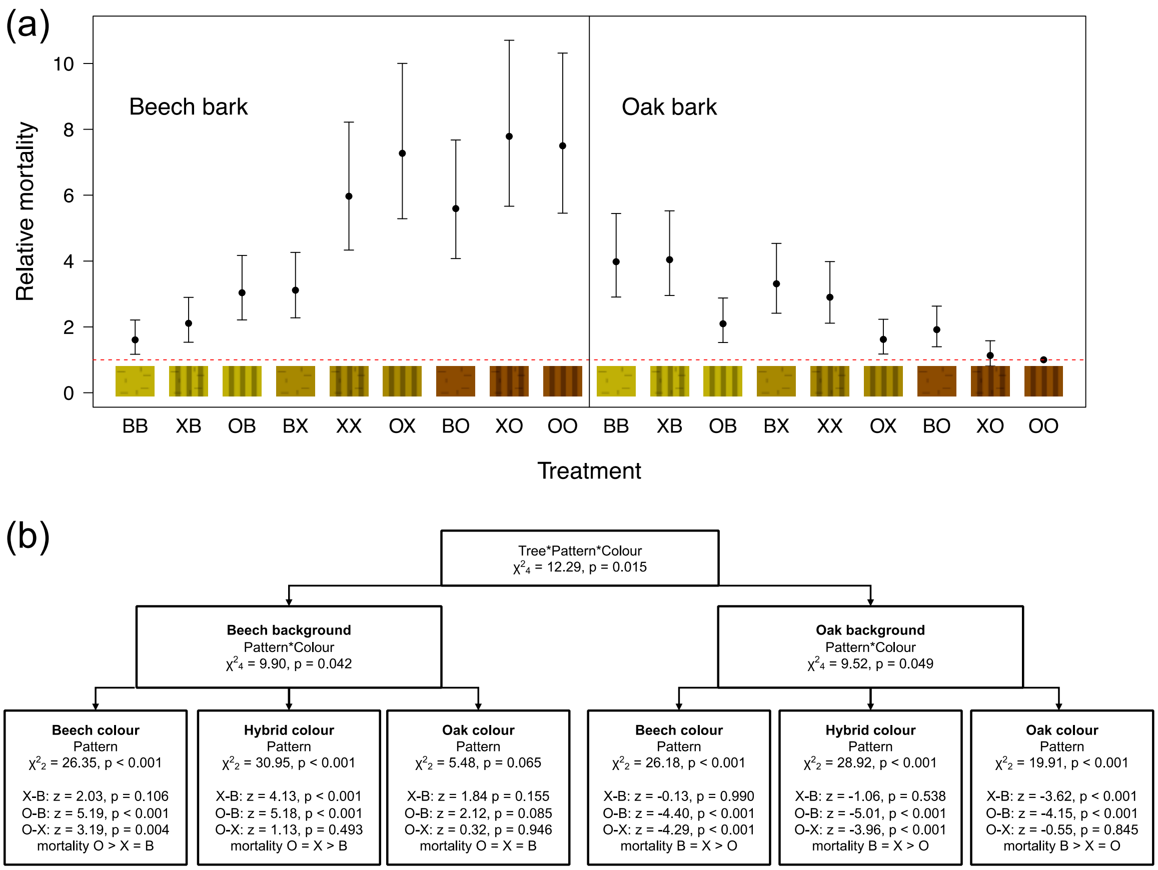

Figure 5.3. (a) Relative mortality expressed as odds ratios and 95% confidence intervals, estimated from a mixed model Cox regression using the oak-patterned oak-coloured treatment on oak bark as the baseline for comparison. The first letter of each treatment code denotes the pattern, and the second letter the colour, of the target (B = beech, X = beech-oak hybrid, O = oak). The relative mortalities of the nine treatments are separated with respect to the background (beech or oak) they were placed on. (b) Breakdown of the statistical analysis of treatment effects, with the three-way Tree*Pattern*Colour interaction at the top then, successively, separate analyses of the two-way Pattern*Colour interactions for beech and oak; then separate one-way analyses of the effect of Pattern for each of the three colours.

Figure 5.4 reproduces the same data but visualised as a trade-off curve of the same type used by Merilaita et al. (2001; Figure 2) to analyse the latency of blue tits to find prey against two different backgrounds. A prey type that matches oak is expected to survive for longer when placed on oak backgrounds, but survive less well on beech, and vice versa for beech-coloured prey. The fitness measure is the average survival across both backgrounds, so the critical issue is whether compromise prey (blends in the colour or texture domain, or both) have an average survival higher or lower than ‘specialists’ on either background. The general concave nature of the curve indicates that compromise camouflage fares worse, on average (e.g. hybrid treatment XX in Figure 5.4), than the specialist oak- and beech-matching prey (BB and OO) although, when oak-coloured, hybrid texture (XO) survives as well on oak as oak texture (OO). Colour mismatch seems more costly than texture mismatch, backed up by the fact that hybrid colours (which match neither beech nor oak well) tend to survive poorly on average.

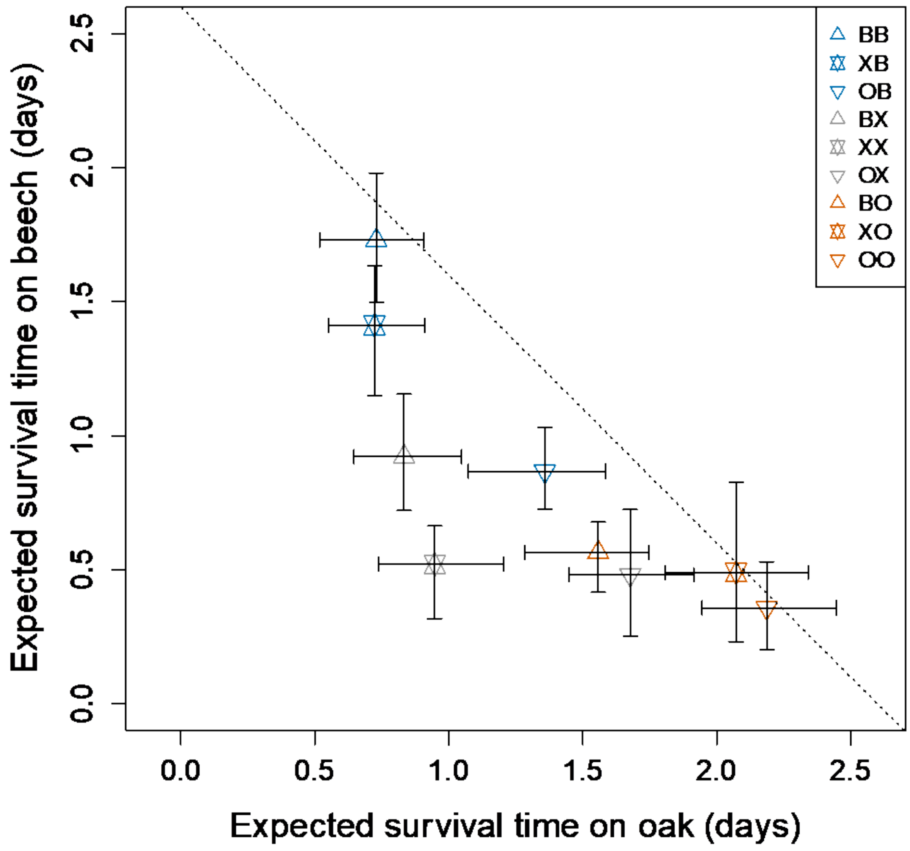

Figure 5.4. The expected survival, in days (with 95% confidence intervals), of the nine treatments on beech backgrounds plotted against their respective survival on oak backgrounds. The dotted line represents the highest average survival observed against both backgrounds combined. Thus, oak or hybrid beech-oak patterns, both coloured as oak, would be the optimal camouflage, on average across both backgrounds. The first letter of each treatment code denotes the pattern, and the second letter the colour, of the target (B = beech, X = beech-oak hybrid, O = oak).

5.5 Discussion

Both theory and several lab experiments on humans and other animals suggest that a generalist, compromise, camouflage performs less well than a specialist camouflage when the multiple backgrounds to be matched are "very different" (reviewed by Hughes et al., 2019). This is not always the case; for example, Toh and Todd (2017) found that, although generalist camouflage had the predicted advantage over specialist forms when the two background types were similar, when the two background were very different, specialist and generalist camouflages were equally hard to find. There were also asymmetries: targets with large pattern elements were, on average, harder to find on small-element backgrounds than vice versa. So, not all types of 'compromise' camouflage necessarily provide the intermediate performance predicted. As Hughes et al. have noted, the next steps should be to identify which aspects of visual differences matter, and whether predicted effects hold true in the field, with complex backgrounds and complex illuminants contributing to concealment. My study takes that step, with natural backgrounds and free-living predators, but using synthetic prey to allow us to manipulate the targets in such a way that we achieve different mixtures between average colour and pattern.

In general, compromise camouflage (a hybrid in terms of colour and pattern) is far less effective than being a full specialist on either. Looking at Figure 5.4, even though oak-coloured/patterned prey had an average 'life expectance' of only 0.4 days on beech bark compared to around 2.4 days on oak (and the converse for beech-coloured/patterned prey: 1.8 days on beech vs 0.7 on oak), both had higher average survival than the colour+pattern hybrid (0.5 days on beech and 1.5 on oak). Those figures also illustrate that average survival of any prey type on beech was lower than on oak, probably because the latter has a far more complex texture. Background complexity has been shown to reduce detection success in other studies (Dimitrova & Merilaita, 2010, 2012; Toh & Todd, 2017), including 'artificial moth' experiments similar to mine (Xiao & Cuthill, 2016; Rowe et al., 2021). The higher complexity of oak bark is also the most plausible explanation for why the hybrid-patterned-oak-coloured treatment survives as well as the oak-patterned-oak-coloured treatment, which one would have expected to be optimal for that background. Beech, having a far simpler, relatively homogeneous, texture is a background against which differences are much more obvious. While, at face value, these results seem to contradict those of Merilaita and Lind (2006) where compromise camouflage outperformed specialist camouflage (on average, across both background types), their backgrounds were identical in colour (black symbols on a white background) and the textures were simple size-transformations of each other. That is, their 'fine-texture' background was enlarged on a photocopier to produce the 'coarse-texture' pattern, with the compromise treatment intermediate in scale. Theory would predict that compromise camouflage is likely to be most successful when the alternative backgrounds are fairly similar (Cuthill & Troscianko, 2009). In addition, the results matched predictions based on theory (Endler, 1990) and previous empirical research (Barnett & Cuthill, 2014; Michalis et al., 2017) that, all other things being equal, mismatches in average colour are likely to be more detrimental to concealment than mismatches in texture.

My experiment does not take into account effects of predator learning; indeed, the spatial separation of prey within blocks, and between blocks in both space and time, was designed to minimise the possibility of individuals forming search images for prey features (Tinbergen, 1960; Lawrence & Allen, 1983). Computer-based visual search experiments on humans searching show that variability in camouflage patterns interferes with effective search image formation, and some types of camouflage, notably disruptive patterns, seem particularly effective (Troscianko et al., 2018; Troscianko et al., 2021). Search image formation by predators could act differentially against average colour and pattern, depending on which feature was most variable. Whether because of this, or for independent reasons related to memorability, experiments on mimicry have shown that avian predators preferentially learn colour over shape or pattern, even when both are equally predictive of prey palatability (Kazemi et al., 2015a,b). In the context of camouflage, we might predict that this might enhance the importance of matching the average colour of the background, if this is the cue that predators are predators are more likely to learn and memorise. Furthermore, it is likely that predators not only learn characteristics of their prey, but also likely that they learn the characteristic background features of the substrates on they feed and non-prey items they can ignore. The latter has been shown, in the context of masquerade, in laboratory experiments on domestic chicks (Skelhorn et al., 2010b; 2011), but what features were learnt was not investigated. This should affect the type and effectiveness of compromise camouflage just as much as features of the prey themselves. However, what features of general backgrounds are learnt by wild animals in natural foraging situations is completely unresearched.

In summary, this study provides evidence that when backgrounds vary markedly in both colour and pattern, compromise camouflage is generally disfavoured. A prey item that is equally likely to be viewed against either background type has higher fitness if it specialises on just one of these backgrounds (even though it is readily found on the other). However, because matching the average colour of the background is more important in terms of camouflage than matching the pattern, this can allow a particular form of compromise camouflage to succeed: a hybrid texture. There is a bias, however: that hybrid beech-oak texture was only successful when its average colour matched that of oak trees, not beech. At viewing distances where the texture can be resolved, the hybrid texture is more easily discriminated from the relatively simple beech bark than it is from complex oak bark. If we translate these findings to what one might observe in real camouflaged moths, one would observe a beech-specialist species which is a very close match to both the colour and texture of beech bark, and an oak-specialist species that is a good match to the colour of oak bark but a less perfect match in texture. So, even while the scenario in my experiments is one in which compromise camouflage is generally disfavoured, the observed bias in which prey features are most important supports one of the proposed evolutionary routes to successful 'imperfect camouflage' (Hughes et al., 2019).

Chapter Six: General Discussion

6.1 Synthesis of Thesis Findings

The results of this thesis contribute not only fundamental knowledge about camouflage, but also information relevant to understanding the life-history of precocial birds such as plovers, and as a basis for conservation strategies for ground-nesting species. The first chapter offers a succinct overview of the significance of colouration in animals, with a specific emphasis on camouflage. The chapter commences by examining the many strategies employed by animals to employ camouflage as a means of evading notice, whether they are potential prey or predators themselves. Subsequently, it proceeds to present a concise account of the historical progression of camouflage research, encompassing the contributions of early trailblazers such as Abbott Thayer and Hugh Cott. The chapter also discusses several forms of camouflage, including background matching, disruptive colouration, and countershading. The text explores the various strategies employed by animals to utilize different forms of camouflage, enabling them to seamlessly blend into their environment and evade detection by both predators and prey. The chapter not only covers camouflage but also explores other roles of colouration in animals, including communication, thermoregulation, and UV protection, because the colouration of any one species is likely to represent a trade-off between multiple fitness components. The text presents illustrations of how animals employ colouration for these objectives and, because it is essential to understanding the mechanisms of protective colouration, examines the various methods through which animals perceive colour. Chapter 1 therefore lays the foundation for subsequent chapters that delve into camouflage from an empirical perspective.

Chapter 2 investigated the mechanisms underlying egg camouflage in the Kentish plover, based on my own fieldwork in south-west Spain. A particular focus was the relative effectiveness of egg camouflage, assessed through visual modelling, in the two main habitats where nests were found: beach and saltmarsh. Were the ages better adapted to one of those habitats, with nesting at the other site a suboptimal choice by, perhaps, inexperienced or subdominant birds, or was the colouration a compromise across both types of background? According to local ornithologists, the beach-nesting birds primarily consist of young or inexperienced breeders, whereas the saltmarsh birds tend to consist of older individuals. Re-encountering and visually identifying the same individuals from year to year, by means of their leg-rings, is infrequent on the beach, whereas in the saltmarsh the recapture rate is high every year. Despite the expectation that this might lead to poorer camouflage in the beach nests, in fact the eggs were equally well camouflaged on both sites and there was no difference between them. Although the backgrounds of the beach and saltmarsh differed in both colour and pattern on average, eggs were found on the type of background colouration that overlapped between the sites. This suggests nest-site choice with respect to the background, which would agree with the conclusions of Stevens et. al. (2017) for different plover species and other ground-nesters in Zambia. In my study, background matching was only modelled, and nest detection will depend on other factors, such as background complexity (Dimitrova & Merilaita, 2010; Xiao & Cuthill 2016; Rowe et al., 2021) and occlusion by other objects (Hancock et al., 2023). In order to establish the extent to which the camouflage aids concealment, it would naturally have been advantageous to quantify the predation rate in both habitats.

Previous experimental work in the field and lab, for both birds and humans, has established that matching the average colour of a background is more important than matching the visual texture, because the latter only becomes important when the viewer is close enough to resolve the pattern (Michalis et al., 2017). While the average egg colour was significantly different from the average background colour in both saltmarsh and beach, the distributions overlapped considerably. For this reason, high rates of correct egg classification could only be achieved (for either avian or carnivore, or indeed human, vision), by accepting a very high rate of false positives (background samples classified as eggs). This is an important general message: when it comes to understanding the effectiveness of camouflage, examining differences from the background in terms of mean colour parameters is not the most relevant statistic: confusability is. Plover eggs were well matched to their backgrounds and, at a distance, would be hard to discriminate from the background. Not so for the visual textures; the fine spidery lines and speckles on eggs being readily discriminable from the backgrounds of either saltmarsh or beach. This raises the question of what the egg patterning is for and why it isn't a closer match. In the discussion of chapter 2, I speculated that it might result from constraints in either pattern production or trade-offs with other factors such as thermoregulation. This deserves further investigation, as does whether the patterns on eggs are better (in terms of camouflage) than no maculation at all, for example contributing to surface disruption (Cott, 1940; Stevens et al., 2009b) or edge disruption, as suggested for quail egg patterns (Lovell et al., 2013).

Chapter 3 elucidated the importance of camouflage in the detectability of plover chicks, using photographs previously collected in Madagascar and involving a different species, Kittlitz plover. As with all plovers, the chicks exhibit early nest departure and are particularly vulnerable to predation as a result of their limited mobility. This focus on precocial chicks is novel, as the current body of literature on avian camouflage centres on nests and adults. It provides original perspectives on the topics of plumage colour and pattern, and investigated the possibility of sexual dimorphism in these avian offspring. The conclusion was that both average colour and texture overlap considerably with those of the background and, as with eggs, colour is a better match than pattern. Indeed, using colour alone, classification success is very poor. Patterning is a closer match to the background than was seen in eggs in the previous chapter, although we cannot treat this as a general difference between camouflage in eggs and chicks because the species and localities were different in chapters 2 and 3. Nevertheless, the results suggest that the colour and pattern are likely to be critical factors in the ability of these birds to avoid detection by predators. Males and females differed slightly in their discriminability from the background, with male colouration more readily confused with the background than that of female chicks. However, this is not because of a sex difference in colouration: males and females did not have significant differences in their plumage, but there was a difference in the backgrounds of the locations they were found in. The conclusion was that male chicks are better camouflaged than females, but because of microhabitat choice rather than their plumage colouration. Investigation of sex differences in chick behaviour, whether that is in their average location (unlikely perhaps, as chicks tend to follow a parent) or where they seek cover when threatened, is an important future challenge. This reinforces the message that camouflage and behaviour need to be studied together (Stevens & Ruxton, 2019).

The findings in chapters 2 and 3 could have important implications for conservation efforts aimed at protecting plover populations in the wild. Specifically, the study suggests that habitat management strategies should take into account the specific colouration and patterning needs of these birds, both at the nesting stage and post fledging. My results indicate that plover eggs and chicks frequently exhibit colouration that corresponds to their environment, so augmenting their capacity to blend in and avoid detection. Nevertheless, the correlation between chick plumage patterns and background patterns is not straightforward, as background patterns alone are not a unique determinant of detection by predators. The reduction of detection errors is attributed to the combination of chick plumage and background features, which in turn are influenced by behaviour.

Chapter 4 took a different approach to evaluating the efficacy of plover plumage camouflage across various environmental contexts, using a visual search paradigm with humans as the 'predators'. The study employed detection time and errors as metrics for assessing the degree of resemblance between plumage and backgrounds. The motivation for the study (in fact, the whole thesis) was an unpublished experiment by Dr. Jorge Parra and Prof. Tamas Szekely of the University of Bath, as part of Dr. Parra's doctoral thesis. In that experiment, in which participants searched for plover chicks on natural backgrounds, a sex difference in detection times was found, with male chicks taking longer to find than females. I first replicated the experiment using the exact same stimuli and three times the sample size of participants. Analysing the data in the same way as Dr Parra, I got the same result. However, there were several aspects of the experiment that suggested a different analysis was more appropriate. An inverse transform of response times produced more normal (Gaussian) residuals, including species as a factor was necessary because the sample of chicks was a mixture of Kittlitz and white-fronted plovers and, most importantly, because participants saw the same images, image ID needed to be included as a random effect as well as participant. Analysed this way, there was no evidence of an effect of sex; the null model had as low or lower an Akaike Information Criterion as any other model. I also reanalysed Dr.

Parra's data in the same way and also found that those data were also consistent with the null model. Although it seems ironic that the experiment that motivated my study of sex differences in plover camouflage actually, when analysed correctly, showed no effect of sex, this is actually consistent with the results of chapter 3, where no sex difference in plumage was found. One might have expected a sex difference in chick detection in the *in situ* photographs, as a result of the sex difference in backgrounds found in chapter 3, but the sample is too small and heterogeneous to be confident of detecting such effects: there were 8 female and 10 male Kittlitz plovers, and 4 female and 3 male white-fronted plovers. Indeed, within the detection data, there is the hint that the reverse pattern (females harder to find) is seen in the white-fronted plovers but, again, the sample size is very small. Investigation of sex differences in detectability of the chicks of different plover species, in different habitats, is clearly a possible direction for future research.

In chapter 4 I also investigated camouflage of plover chicks using a different experimental approach which isolated the degree of background-matching of the plumage *per se*. In the experiments above, and the task faced by a predator in the field, plumage certainly contributes to detectability, but there are also other cues: the beak, legs and eyes of the bird. Also, any mismatch between the chick and background at the body's edge can reveal its outline and so shape; disruptive camouflage acts against such cues, which are as much to do with recognition as detection (reviewed by Stevens & Merilaita, 2009a; see also Egan et al., 2016; Sharman et al., 2018). In order to isolate the effectiveness of background matching by the plumage itself, I presented participants with mosaics of square patches, one of which was a sample of chick plumage and the rest (63 out of 64) samples of background. The task was therefore discrimination of one patch of chick plumage among similar patches of background. I also investigated the difficulty of detecting the patch of plover plumage with respect to the two different substrates on which they were found, and photographed, in Madagascar: mud and grass. In addition to mosaics of all-mud and all-grass, chick plumage was also presented within random 50:50 mixtures of grass and mud patches and 'structured' 50:50 mixtures, with samples in the top half of the screen and mud samples at the bottom, or vice versa, or one set on the left and one on the right, or vice versa. The reason for this was that chicks were sometimes found, and photographed, at the boundary between mud and vegetation, and there is some evidence that objects are harder to detect near the boundaries between background patch types (Espinosa & Cuthill, 2014). The random mixture served as a control for there being two different types of background sample in a scene, rather than the scene containing a boundary *per se*. Chick plumage patches were more often missed and took longer to detect on mud backgrounds than grass, which is not particularly surprising given the differences in colour (although many grass samples did actually contain brown, dead, vegetation and so the task was not as trivial as one might think). However, vegetation provides opportunities for physically hiding that mud does not allow. Therefore the colouration of the chicks seems adapted for background matching on the part of the background where physical hiding is not possible; they are camouflage 'specialists' on mud, even though they are frequently found on other backgrounds. This accords with the latter part of Endler's definition that "a colour pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat, where the prey is most vulnerable to visually hunting predators" (Endler, 1978; my underlining).

Interestingly, chick plumage patches were as hard to find on the structured 50:50 mix as pure mud, so searching a scene with two background types is harder than you would predict from averaging detections on the grass and mud halves. The random mixture of grass and mud background samples was nearly as difficult as (but not in fact more difficult than) the structured mixture. This is consistent with background complexity making visual search more difficult (e.g. Rowe et al., 2021, and other works discussed in earlier chapters), but it is interesting that even a structured scene, where you could imagine a viewer searching one half systematically and then the other, can be 'complex' in its effect on search. The real-world implication is that plover chicks, and prey species in general, might be safer in visually complex habitats, even when they are not particularly well camouflaged on some of the substrates.

The utilization of human participants in computer research has played a crucial role in the comprehension of animal camouflage methods because, although such experiments lack ecological validity (neither the predator nor the context is natural), they allow precise control over exactly what is seen and what the task is. Even in field experiments such as those described in chapter 5, the distance, angle of viewing and exact lighting conditions at the time of detecting (or failing to detect) a prey item are unknown. Also unknown is the predator's motivational state, its knowledge and past experience of encounters with similar prey. In the laboratory, apart from the ease of manipulating prey and background features (colour, texture, size, positioning) with digital images, the distance from viewer to screen, the screen's illumination and resolution, and the sequency of encounters are under experimental control. The participants have also been given explicit instructions on what the task is (although the goals of the experiment and exact nature of the treatments are typically not revealed in order to avoid biases in the participants' behaviour). In my study, I took the additional step of replicating each experiment as both a mass-participation online exercise, in which the participants' computer hardware and viewing conditions were uncontrolled, and a laboratory experiment with a calibrated computer monitor and precisely regulated viewing conditions. Interestingly, the results were very similar across these two contexts but, particularly because online prey detection 'games' are becoming more common, it would be unwise to conclude that controlled viewing and screen calibration are unnecessary. Indeed, by collecting the necessary data and screening all the data carefully, it was possible to exclude participants with anomalous behaviour, such as clicking the mouse as soon as the test image appeared or exceptionally high error rates through using an inappropriate viewing device (e.g. small screen) or seemingly not taking the task seriously. Such anomalous behaviour was not detected in the controlled laboratory versions of the experiments. It is also the case that some tasks (of a type I did not use) really demand a high specification, calibrated, monitor with a high refresh rate, notably tasks in which objects move (see Scott-Samuel et al., 2023, for a discussion in relation to experiments on 'dazzle' colouration and distortions of perceived velocity).

Chapter 5 continued the theme of camouflage against multiple backgrounds but using a very different system: artificial moths on trees. Several major conclusions resulted from this experimental investigation on artificial camouflage, which focused on utilizing two species of trees as backgrounds, beech and oak. The findings of the study indicate that achieving a match between the background colour, particularly in the context of the more homogeneous, visually simple, bark of the beech tree, is of greater importance in ensuring good camouflage than matching the visual texture. Furthermore, it was found that possessing specialized characteristics, namely closely resembling both colour and pattern to the surrounding environment, generally proves to be more effective in terms of camouflage on these two backgrounds than hybrid traits that exhibit compromises (blends) in colouring and pattern. This makes intuitive sense when two backgrounds are 'very different' (as in the simple model of Cuthill & Troscianko, 2009), although how large the difference needs to be to disfavour compromise camouflage has yet to be operationally defined for real backgrounds. The importance of average colour over texture is consistent with previous research (Endler, 1990; Barnett & Cuthill, 2014; Michalis et al., 2017), suggesting that discrepancies in colouring have a stronger negative impact on concealment compared to discrepancies in texture, particularly when observed from longer distances. This might also explain the findings of experiments where, even though multiple cues are equally predictive, birds show a tendency to prioritize colour over shape or texture when discriminating between aposematic and Batesian mimetic prey (Kazemi et al., 2015 a,b). There was a notable exception to the conclusion that specialist camouflage is best when a prey can be viewed on very different backgrounds: as long as the average colour matched oak, the hybrid texture survived as well as the pure oak specialist. The more complex texture of oak bark is more 'forgiving' of mismatches than the texturally simple beech bark. This is consistent with the emphasis on discrimination between distributions of prey and background features, explored in chapters 2 and 3, as opposed to examining differences in means.

In a general sense, we can understand the thesis presented here as follows. Chapters 2, 3, and 5 explore the concept of camouflage in various natural settings. The first two chapters focus on camouflage in plover eggs and chicks, while the last chapter explores the background matching of a model insect in its native habitat. All show that that selecting the appropriate location for nesting, feeding, or seeking shelter is crucial for the individual. To elaborate further, particularly regarding the chapters that focus on experiments conducted with real animals in natural environments (chapters 2 and 3), it is evident that the selection of the background plays a significant role, albeit in distinct manners for each case. Chapter 2 discusses eggs, which lack mobility. Consequently, it is the female's responsibility to select the most suitable location for laying them. In addition, other studies have shown that in many instances, once the eggs are laid, the female or male (or both, depending on the species' form of parental care) choose to supplement the eggs with additional substrate. This is done to enhance their camouflage and serve other purposes such as thermoregulation. In contrast, chapter 3 explores the consequences of the chick's capacity to move shortly after hatching, meaning that it can be viewed against different background types. The selection of where to move is an individual choice that might vary during the day, including whether to follow their parents, search for food, or seek warmth from their parents. Chicks presumably possess the capacity to not only select the background based on colour and texture, but they can also choose locations with plants, so providing themselves with the heightened safety of a physical refuge. However, because of the need to search of food, there is no guarantee that they will always be in suitable locations for effective camouflage. Therefore, in these instances, the constraints and issues vary, and therefore, the tactics for survival differ in each circumstance. I predict that the next stage of camouflage research will move beyond establishing the different mechanisms at play (background matching, disruptive colouration, mimicry, etc.), but start to integrate the role of behaviour and trade-offs with other effects of colouration (e.g. thermoreulation) and competing demands on time and habitat utilisation.

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