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Countershading in Seabirds

Douglas John Sands

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Biological Sciences MSc (R) in the Faculty of Life Sciences.

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18913 words

Abstract

The functional significance of the dorso-ventral gradient in plumage pigmentation ('countershading') in seabirds has remained unclear since the topic first received interest over 100 years ago. A range of hypotheses have been proposed to explain this, including thermoregulation, abrasion resistance, camouflage and social signalling; however, in no case has a firm conclusion been reached. The aim of this thesis was to ascertain if white ventral coloration could function as hunting camouflage in marine birds, and under which environmental conditions would white plumage be least visible against the sky, from the perspective of aquatic prey. I recorded videos of white spherical targets suspended above, and resting on, the water surface from an underwater perspective. I measured the luminance contrast ratios between the target and the background (sky) and compared ratios across different environmental conditions. I also executed two detection experiments with human participants: one in a realistic simulated pelagic environment, and one where participants were shown frames from the videos taken in the field. Of the video frames taken when it was sunny, 79% had targets with low visibility (<5% luminance contrast), compared to only 0.3% when it was cloudy. More than 90% of frames taken when it was sunny and windy had low visibility targets. In 23% of the frames analysed the target was totally undetectable; wind then cloud cover explained the most variance in undetectability. In the detection experiments, participants generally took longer to detect targets and were less accurate when it was sunny compared to cloudy. Direct sunlight causes glare, obscuring nearby objects from view, potentially causing undetectability of targets. Higher wind speed causes increased surface rippling and wave height, which affects refraction at the water surface and can lead to distortion of the above water image. Contrary to the conclusions in published papers using light-field modelling, white ventral plumage can potentially conceal seabirds from their prey under some conditions.

This thesis is dedicated to my parents, whose unwavering support was critical to the development and completion of this work.

I would like to thank the following people for their invaluable assistance in many aspects of this thesis: Firstly, my supervisors: Profs. Innes Cuthill & Nick Scott-Samuel; friends and colleagues in the CamoLab research group: Callum McLellan, Leah Costello, Benito Wainwright, Ioan Smart, Dr Karin Kjernsmo and Dr Bryony Sands. I would like to especially thank Dr Sam Matchette, who provided invaluable help and guidance with the development and execution of my simulated detection experiment. Thanks also go to Henleaze Swimming Club for granting access to the lake for data collection.

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.

SIGNED  DATE: 26/05/2020

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1 Introduction

1.1 Animal Camouflage

This thesis concerns countershading, a widespread form of animal coloration that has been commonly proposed to function as camouflage, but not without contention (Thayer 1896; Kiltie 1988; Ruxton *et al.* 2004; Rowland 2009). However, to understand how countershading might aid concealment, it is first necessary to examine the general principles of camouflage.

The ubiquity of visual concealment and the mechanisms by which different camouflage strategies function has been studied and described by naturalists and scientists for over a century (Thayer 1896; 1909; Cott 1940). Both predators and prey can often benefit from utilising visual camouflage strategies, including background-matching, disruptive coloration, countershading and masquerade (Stevens & Merilaita 2009; Ruxton *et al.* 2018; Cuthill 2019).

Camouflage strategies make detection or recognition of the individual more difficult for an observer (Merilaita *et al.* 2017; Cuthill 2019). The evolution of camouflage coloration in animals drives an ongoing evolutionary battle in which predators and prey evolve unique strategies to conceal themselves in response to adaptation of the other. All types of visual camouflage have evolved under the selection pressure resulting from the visual system, and perception of the predator or prey that the individual is trying to elude (Endler 1978; 1990; Bennett *et al.* 1994; Cuthill & Troscianko 2011; Merilaita *et al.* 2017; Cuthill 2019). This pressure to evade recognition as a predator or prey item (driven by the need to not be killed or to consume food) can lead to some extraordinary examples of camouflage and other anti-predator coloration (Stevens & Merilaita 2009). For example, the caterpillars of some moth species (*Macrauzata maxima*, *Apochima juglansiararia* and *Acronicta alni*) masquerade as bird droppings through both coloration and the adoption of a bent posture (Suzuki & Sakurai, 2015). Furthermore, the larvae of the alder moth *Acronicta alni* strongly resemble bird droppings in early instars, but in the final instar their coloration changes to conspicuous black and yellow stripes; this reflects the need to move from foliage to pupation sites

during the final instar, when masquerade would not be advantageous (Valkonen *et al.* 2014).

Some species of caterpillar appear to masquerade as small twigs, and this has been shown to cause misidentification of the prey item after detection by the predator (Skelhorn *et al.* 2010). Predators use aggressive masquerade to gain access to prey: for example, ghost mantises (*Phyllocrania paradoxa*) strongly resemble dead leaves, allowing them to attack and catch their prey (who misidentify them as leaves) more efficiently (Skelhorn 2018).

Disruptive coloration, a different but widely accepted camouflage mechanism, interferes with shape and feature recognition (Thayer 1909; Cott 1940; Merilaita 1998; Cuthill *et al.* 2005; Stevens & Cuthill 2006). An animal that matches its background perfectly displays no clear cues to its edges. However, very slight differences in surface properties between the animal and its background generate conspicuous edge information which reveals both its location and identity. Disruptive coloration employs strongly contrasting patches on the interior of the animal's body to create false edges, whilst minimising the signal of the true body outline through the placement of background matching patches at the edge of the animal's body (Merilaita *et al.* 2017).

While the impressive examples discussed above concern mimicry: false cues of identity, and disruptive coloration which interferes with shape recognition, the conceptually simplest form of camouflage is matching the background.

1.1.1 Background matching

Background matching was amongst the first strategies of concealment to be reported in the early literature – Poulton (1890) described it as 'generalised resemblance' and it was recognised by Darwin and Wallace as a key adaptation in their explanations of natural selection (Darwin 1859; Wallace 1877; 1889). Background matching involves the coloration of the prey matching hues, patterns and levels of luminance present in the background, and can be very effective camouflage on a motionless individual (Thayer 1909; Cott 1940). Cott (1940) pointed out that, though exceptions exist, most

species inhabiting a given environment are clad in hues that accurately mimic its surroundings. Endler (1978; 1984) defined crypsis as an animal's appearance matching a random sample of the background where and at what time predation risk is highest. This definition of crypsis has often been considered synonymous with background matching but, more recently, others have defined crypsis to include all traits that reduce the animal's risk of being detected when it is possibly visible to an observer (Stevens & Merilaita 2009).

There is good evidence against Endler's (1978) crypsis definition, despite it being widely adopted. Merilaita & Lind (2005) performed detection experiments using artificial prey and great tits (*Parus major*) as predators. Their three prey types consisted of two randomly sampled background matching types (classified by human observers and pilot trials as easy or hard to detect) and a disruptive type. They found that the effective search time of great tits was significantly longer for background matching prey classified as more difficult to detect, signalling that different samples of the background do not provide the same level of concealment from predators and that matching a random sample of the background is not sufficient to minimise detection by predators, as postulated by Endler (1978). The fact that the disruptive prey types and the difficult background matching types were equally well concealed suggests that the best camouflage strategy for a given background might not necessarily be a random sample of that background. The most powerful evidence against Endler's (1978) random sample of the background definition of crypsis is from Michalis *et al.* (2017). The experimenters predicted that the statistically most common background sample (in terms of both colour and texture) would, on average, be the most cryptic. This prediction was supported by robust evidence from field experiments using artificial prey and avian predators, as well as tightly controlled human detection trials. This research shows that the most cryptic camouflage pattern is the most probable background sample for heterogeneous backgrounds, not a random sample.

Achieving effective crypsis in visually dissimilar microhabitats presents a challenge for animals. In a homogeneous environment, better camouflage through crypsis can be achieved simply by increasing the degree of similarity between an animal's body and the background. Actually, there are two possible solutions (for non-colour changing

animals) to background matching in heterogeneous environments: maximise crypsis in the microhabitat where the predation risk is greatest (Endler 1978) or have coloration that is an optimal compromise of crypsis across the microhabitats frequented by the individual. Merilaita *et al.* (1999) used a theoretical model habitat consisting of two visually dissimilar microhabitats to study the optimal compromise crypsis that maximises the overall probability of avoiding detection when prey experience all the microhabitats in its heterogeneous environment. The results of this study contradicted the idea that optimal coloration should always be that which maximises crypsis in the highest predation risk area (Endler 1978). Merilaita *et al.* (1999) found that the shape of the trade-off curve between crypsis in the two microhabitats determines whether compromise or specialist crypsis is optimal – when the curve is convex then compromise is optimal, and when it is concave the optimal strategy tends towards maximisation of crypsis in the habitat with the highest predation risk. The shape of the trade-off curve is, in turn, affected by the physical and biological constraints associated with the production of a cryptic coloration, and the visual acuity of the predator. Similarity between visual elements of the two backgrounds leads to a more convex trade-off function and a combination of their requirements is optimal. However, a compromise between the two backgrounds may be physically possible but biologically constrained by a lack of genetic variation, high production costs or sexual selection, for example (Endler 1978; Belk & Smith 1996). If the visual acuity of a predator is high then detection of deviations from the background is much more likely and any compromise between backgrounds is far less cryptic; hence, poor predator visual acuity could be predicted for situations where compromise is optimal for crypsis. This has never been tested. Other strategies for avoiding detection when living in visually heterogeneous environments include reducing background specificity (by using disruptive coloration, for example), active substrate choice, or using dynamic camouflage in response to the current background (Merilaita *et al.* 1999; Hughes *et al.* 2019).

Some animals have been shown to undergo colour and pattern change in response to the background on which they are resting (Umbers *et al.* 2014; Duarte *et al.* 2017). Colour change can take place over minutes and seconds or much longer temporal

scales, depending on the organism and underlying mechanism. The European common cuttlefish *Sepia officinalis* uses chromatophore organs and two types of reflecting elements, leucophores and iridophores, to dynamically control its body pattern, which can change in fractions of seconds (Hanlon 2007). The body patterns that can be produced by chromatophores range through uniform, stippled, mottled and disruptive patterns (Hanlon & Messenger 1988). Chromatophores are cytoelastic sacs of pigment with radial muscles attached to control dilation, and the direct motor-neuronal control of these radial muscles facilitates the rapid pattern changing ability of cephalopods (Hanlon 2007). The diverse range of substrates matched by cephalopods, and the visual capabilities of their natural predators demonstrate their impressive camouflage abilities and may offer deeper insight into the general principles of visual camouflage (Hanlon *et al.* 2009). Cuttlefish *Sepia officinalis* have a single visual pigment with a maximum absorption wavelength of 492 nm (green). This begs the question of how they camouflage themselves despite being colour blind. Marshall & Messenger (1996) tested the patterns produced by *S. officinalis* on different combinations of coloured gravel substrates. When they rested on a blue gravel background with scattered yellow gravel, they produced a low contrast stipple body pattern, despite the striking high contrast background as it appears to humans. As expected, the cuttlefish produced a high contrast coarse mottle pattern when on a high contrast white background with red gravel. Photographs were taken using a green interference filter (λ_{\max} 490nm) to simulate how the backgrounds would appear to the visual system of *S. officinalis*, revealing that the yellow and blue gravel appear very similar, whereas the red gravel contrasts strongly with white. This showed that cuttlefish do not respond to wavelength differences in the substrate but produce their patterns based on intensity contrast information.

Achieving crypsis in a pelagic environment is difficult due to the featureless nature of the background. This has led to the evolution of a range of interesting adaptations for camouflage in this ecosystem, including whole body transparency, mirrored sides, countershading and counterillumination. Johnsen (2002) calculated the optimally cryptic and conspicuous coloration in pelagic environments by modelling the underwater radiance distribution. Viewing angle and depth had the greatest effects on

the predictions for optimal crypticity and conspicuousness, and showed that red coloration was most cryptic at depth.

1.1.2 Countershading

In terrestrial mammals and birds, dorsal pigmentary darkening (or countershading) has been proposed to remove cues to the three-dimensional form to aid concealment – a function originally described as ‘obliterative shading’ but now referred to as self-shadow concealment (Thayer 1896; Caro 2009; 2014; Rowland 2009). The functions of countershading coloration across the wide range of animals that exemplify it have been debated at length (Kiltie 1988; Ruxton *et al.* 2004; Rowland 2009). Some non-camouflage functions have been hypothesised, of which protection from ultraviolet radiation has the most compelling evidence (Lowe & Goodman-Lowe 1996). The mechanism by which countershading might provide camouflage for animals seems to vary depending on the context. Countershading may result from the requirement of some animals to match multiple backgrounds from different viewing positions, or it may remove cues to three-dimensional shape from shading. When an object of uniform reflectance is lit from above, it will appear lighter on the top surfaces and darker on the lower surfaces due to shadows. If the object has a gradation of reflectance that is the inverse of the self-shadow, then they cancel each other out and the object appears to have constant luminance and be two dimensional (fig. 1.1). This hypothesis of self-shadow concealment is both controversial and long-standing, first proposed and described in early camouflage literature as countershading to obliterate shape-from-shading cues (Poulton 1890; Thayer 1896; Cott 1940).

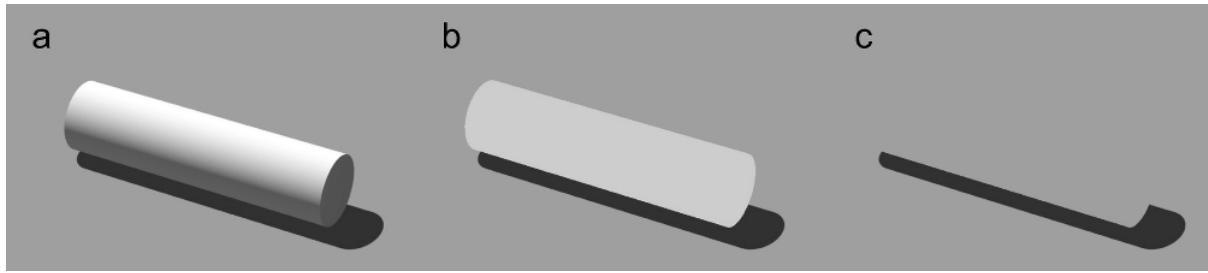


Figure 1.1. A: A uniformly shaded object lit from above casts shadows on itself. B: When the reflectance of the object is the inverse of the shading gradient the two cancel. C: Reflectance chosen to produce self-shadow concealment and background matching. Reproduced with permission from Penacchio *et al.* (2015b). Licence ID: 1035392-1.

Kiltie (1988) pointed out that Thayer's (1896) description of countershading as an adaptation to remove cues to three-dimensional shape from shading had led to the problematic conflation of a proposed camouflage function of countershading coloration (self-shadow concealment) with the pigment distribution that the term is often used to describe (dorsal pigmentary darkening). This lack of clarity leads to the assumption that self-shadow concealment is always the function when dorsal pigmentary darkening is present. Kiltie (1988) goes on to describe Craik's (1944a) theory that seabirds with a white ventrum are less detectable from below than those with a black ventrum, and how this seems plausible when the bird is in flight over water as the reflected light may be enough to confer an advantage, unlike underwater where there is very little upwelling light. He likened this situation to Thayer's (1896) idea of shadow obliteration except in that, with seabirds, the entire silhouette is supposed to be concealed, a two-dimensional version of self-shadow concealment. He also points out several issues associated with self-shadow concealment for terrestrial animals, namely that Thayer (1896) and Cott's (1940) descriptions of how self-shadow concealment works crucially depend upon the light source being directly above the animal, which is in fact rarely the case. This issue was addressed in later theoretical work involving light-field modelling (e.g. Penacchio *et al.* 2015a; 2015b; see later). The following year, Kiltie (1989) used an image-processing approach to show that the dorso-ventral gradient of brightness for grey squirrels was steeper in uniformly coloured individuals (specimens photographed with their dorsal surface facing the camera) than in countershaded individuals (correct horizontal orientation), supporting Thayer's (1896) hypothesis. Kiltie remained sceptical, however, because his analysis

revealed that pigmentary countershading did not completely remove brightness gradients, and because the squirrel must be orientated horizontally for the brightness gradient to be minimised by countershading.

More recently, there has been a growth in empirical study of the function of countershading, using artificial prey experiments and modelling. For example, Edmunds & Dewhirst (1994) showed that countershaded artificial pastry caterpillars were eaten by birds significantly less than uniform dark green, uniform light green and reverse-shaded artificial prey; however, this work was criticised because of the possibility of post-detection bias of the birds explaining the difference in predation rate, rather than differences in detection (Ruxton *et al.* 2004). Later, these experiments with artificial caterpillars were repeated, but with the addition of more controlled trials with prey presented on green boards to individual blackbirds (Rowland *et al.* 2007). This study showed that countershaded artificial prey experienced significantly lower rates of predation than plain background matching prey, both on lawns (as in Edmunds & Dewhirst 1994) and in a laboratory setting. These results contrast somewhat with those of Speed *et al.* (2005) who found that the advantage of countershading was inconsistent across different prey species. It has been suggested that this may be attributable to long sampling periods and associated habituation of predators obscuring the survival advantage of countershaded prey (Rowland *et al.* 2007). Rowland *et al.* (2008) performed similar detection experiments with artificial prey but in a woodland, the results of which were in agreement with the previous work. Countershaded prey survived for significantly longer than uniform background matching prey when placed on beech tree branches and the undersides of leaves (the natural resting position of many arboreal caterpillars).

Evidence for countershading as camouflage from comparative studies using subjective classification of countershading coloration (Stoner *et al.* 2003; Kamilar 2009; Kamilar *et al.* 2011) is less strong than the results of empirical work previously discussed. Stoner *et al.* (2003) constructed a weighted phylogenetic supertree to study associations between coloration and variables including behaviour and habitat in Lagomorphs. Species with white ventral surfaces (i.e. countershading coloration) were only marginally associated with diurnal activity, and were not associated with open

habitats. In a similar analysis, Kamilar (2009) used a comparative approach to test whether countershading coloration was associated with diurnal activity patterns and whether countershading coloration was associated with lower body mass and associated increased predation threat in primates. In contrast to Stoner *et al.* (2003), countershading was given a numerical score for each species included in the analysis: the ratio of average luminance values on the dorsal and ventral surfaces from digital images of specimens. Kamilar (2009) found that countershading was negatively associated with body mass as predicted, but countershading was equally prevalent in diurnal and nocturnal primates, perhaps due to advantages of countershading under moonlight. In a later study, Kamilar *et al.* (2011) found that the degree of countershading is negatively associated with the frequency of adopting a vertical posture in primates. This supports the hypothesis that countershading functions to reduce conspicuousness because dorsoventral countershading can only be effective as camouflage when an animal adopts a horizontal posture.

Building on earlier comparative analysis involving subjective assessment of countershading (e.g. Stoner *et al.* 2003), Allen *et al.* (2012) determined the optimal countershading coloration for self-shadow concealment using a model ruminant photographed in natural light environments. The predictions were then compared to calibrated images of 114 species of ruminant (museum skins). They found that generally, optimal countershading for self-shadow concealment (henceforth SSC) in different light environments, as predicted from the model ruminant, was well matched with the observed strength of countershading shown by calibrated images of the museum specimens. Comparative phylogenetic analyses confirmed that the lighting environment tends to explain variation in countershading strength. In closed habitats with more diffuse lighting, a smooth dorsoventral gradation is common whereas in open habitats where direct overhead illumination dominates, a sharp dark to light transition is observed. Comparison between modelling of optimal countershading for SSC and an organism's actual patterning has even been used to investigate countershading in an ornithischian dinosaur. A fossil of *Psittacosaurus sp.* which had extremely well-preserved melanin was used to reconstruct the animal's coloration. The resulting pattern was projected onto an accurate life-size model and compared to

models of optimal countershading for SSC in open and closed habitats, leading to the conclusion that *Psittacosaurus sp.* inhabited dense forest habitats (Vinther *et al.* 2016). This methodology was also used to determine the habitat of another dinosaur *Sinosauropteryx* (Smithwick *et al.* 2017).

Cuthill *et al.* (2016) combined modelling of the optical environment to predict optimal countershading coloration with predation experiments in the field to confirm the predictions. To test the illumination dependence of countershading, they measured predation rates of artificial caterpillar prey by birds for different putative countershaded patterns on sunny and cloudy days. Two of the artificial prey were designed to counterbalance either direct sunlight (sharp transition from light to dark) or diffuse light (gradual transition), so each of these designs should be predated significantly less in only its own appropriate light environment. The results confirmed the predictions. The sharp transition from dark dorsal surface to light ventral surface is only optimal under direct solar illumination; under diffuse illumination this treatment survived only as well as the dark green control. Similarly, the smoother gradation between dark dorsum and light ventrum was optimal under cloudy sky and shade.

Investigations of countershading have also been conducted in relation to aquatic animals, the results of which have yielded evidence for a different mechanism by which countershading affords camouflage. Kelley & Merilaita (2015) looked for variation in dorsal pigmentary darkening (henceforth DPD) in wild caught populations of the western rainbowfish (*Melanotaenia australis*) to test the assumptions of different explanations for countershading. They found that fish collected from sites with high downwelling irradiance had significantly paler dorsal skin pigmentation. Fish from low predation risk areas also had paler overall coloration. *M. australis* can also change its coloration over a period of days to weeks. When males were allocated to tanks that were surrounded by brown paper and dark brown substrate, their level of DPD increased. Males which were allocated to cream (light) tanks showed a reduction in the level of DPD. This result suggests that *M. australis* changes its countershading coloration for the function of background matching, as opposed to self-shadow concealment, as males in dark tanks darkened their dorsal surface to match the darker substrate (background). Kelley *et al.* (2017) used clay models of *M. australis* to

determine the optimal countershading pattern for self-shadow concealment by photographing the models under two different lighting conditions with different visual backgrounds, a procedure similar to that of Allen *et al.* (2012). Inversion of the mean reflectance profile of the photographs was used to predict the optimal coloration for self-shadow concealment in the two environments. Live *M. australis* were kept in these same two light environment and visual background treatments for two weeks to allow for body coloration adjustment. When images of the fish were compared with the images of models for optimal self-shadow concealment, the reflectance profiles did not match, suggesting that the fish adjusted their body pattern to match the visual background and not to conceal ventral shadowing. These findings support the idea that the different light environments in air and water and the different typical predatory viewing angles resulted in the evolution of similar coloration phenotypes but divergent mechanisms of concealment.

Penacchio *et al.* (2015b) used a computational model to formally test whether proposed mechanisms of countershading camouflage are mutually exclusive. The model simulated a three-dimensional environment with controlled and realistic lighting conditions and allowed the optimal coloration for concealment of 3D shape to be determined. They found that the optimal coloration of an animal in an open environment depends on weather: under sunny conditions, perfect background matching may not always be possible and the gradient of irradiance (and hence the compensating gradient of reflectance) is steep (as found by Allen *et al.* 2012 and Cuthill *et al.* 2016). This is because the reflectance of a surface cannot be greater than 1, meaning that some parts of an animal's body that receive little irradiance (such as the belly) may have a lower outgoing radiance than the background, even when these surfaces are maximally reflective (white). Thus, background matching is incomplete and the shading resulting from areas receiving little irradiance provide some cues to the animal's shape. They also found that orientation of the animal with respect to the sun has the largest influence on crypsis achieved through countershading. Except at midday in the tropics, the animal must face towards or away from the sun to achieve a matching pattern of shadow on both sides of its body and hence compensate for that irradiance distribution with an almost always bilaterally symmetrical pattern of

reflectance. The importance of facing the sun is relaxed for animals that live predominantly in shady or cloudy environments, or at high latitudes or if they are only active in open environments at dawn and dusk. Orientation with respect to the sun is surprisingly common in animals, but this may be attributable to optimising countershading camouflage, ultraviolet protection, thermoregulation or a combination thereof. Mostly the requirements for these three functions of coloration and orientation coincide, suggesting that the selective pressures for body orientation associated with coloration are not mutually exclusive (Penacchio *et al.* 2015a). Later work on countershading requirements has shown that deviations from the appropriate orientation beyond 15 degrees drastically increases the salience of countershaded targets, and that countershaded targets that are optimised for the actual lighting of the scene (cloudy or sunny) take significantly longer to detect than sub-optimally countershaded or uniform targets. Both of these studies were computer-based detection experiments using virtual prey in realistic, but synthetic, light fields, and human participants as predators (Penacchio *et al.* 2017; 2018).

1.1.3 Countershading in sea birds

The plumage of sea birds has received attention for over a century, and yet the functional significance of their countershading coloration remains unclear. It seems likely that countershading and white ventral coloration evolved in seabirds for multiple non-exclusive functions, including aggressive camouflage and social signalling (Simmons 1972; Siegfried *et al.* 1975; Andersson *et al.* 1981; Götmark *et al.* 1986; Götmark 1987). It has also been argued that in many cases white feathers are the default (the colour without pigmentation) and we must accept a lack of adaptive function (Tickell 2003).

Dwight (1920) described in great detail the plumage changes in seabirds through consecutive moults as they mature. He noted that larger species such as *Larus marinus* and *L. argentatus* take a greater number of years to attain mature adult plumage than species of smaller size (for example *Chroicocephalus ridibundus*). He also described however that this rate of plumage maturation is inconsistent within species, and some individuals (which he called laggards) develop at a much slower

rate, generating confusion in estimation of age of individuals. Despite this confusion it seems clear that gulls gain mature adult plumage after their first post-nuptial moult, which for smaller species is at the beginning of their second year, and for larger species the beginning of their fourth year. Also, since the flight feathers of the wings are moulted once per year, whereas the body plumage undergoes two annual moults, the immaturity of younger individuals may be evident through their flight feathers but not body plumage (Dwight 1920).

Dwight (1920) also described the plumage appearance through consecutive moults for a number of species, including *L. argentatus*, describing the body plumage of juvenile individuals as “mostly grayish or sooty brown irregularly mottled and barred with buff, the markings coarsest on the upper surface, the lower parts being of a more uniform grayish brown”. A gradual transition from this juvenile plumage is described through consecutive pre- and post-nuptial moults until *L. argentatus* gains full adult plumage by their fourth winter (fig. 1.2).

The plumage of juvenile gulls as described by Dwight (1920) appears cryptic against typical nesting sites, for example rocky shorelines and coastal littoral zones where immature gulls tend to forage. This cryptic coloration may also afford them protection from interference by skuas and other gulls (defensive camouflage) (Philips 1962). Mature individuals may spend more time in pelagic oceanic environments foraging for food. This begs the question concerning the adaptive function of seemingly conspicuous black, grey and white adult plumage in many seabirds. Adult gulls, and indeed most seabirds have DPD – a white ventrum and grey or black dorsum. The reason for this coloration pattern in gulls remains contentious, as it does for many other countershaded animals. Cott (1940) described the coloration of gulls to be conspicuous in any environment, suggesting that they are aggressive and hardy enough to protect themselves.



Figure 1.2. An adult *Larus argentatus* in flight, against a clear sky. Pamart, M. T., 2018, licenced under the creative commons attribution 4.0 international licence (<https://creativecommons.org/licenses/by/4.0/deed.en>).

There is good evidence that the melanic pigmentation of bird feathers serves functions other than camouflage or signalling, for example, melanism increases abrasion resistance in keratin (Bonser & Witter 1993; Bonser 1995). Bonser (1995) showed that melanic keratin from willow ptarmigan (*Lagopus lagopus* race *scoticus*) primaries was significantly harder, and hence more resistant to abrasion and fracture, than non-melanic keratin. Non-melanic keratin would need to be 39% thicker than melanic keratin to resist the same amount of abrasion. This suggests that the typically black wing tips of seabirds are an adaptation to abrasion resistance. It has also been found that melanized feathers are more resistant to feather-degrading bacteria (e.g. *Bacillus licheniformis*) than unmelanized feathers (Goldstein *et al.* 2004; Gunderson *et al.* 2008).

In 1944, a series of letters to Nature were published, the first of which by Craik (1944a) introduced his idea of the white ventral coloration of seabirds functioning as aggressive

or hunting camouflage. He likened his proposed scenario of sea birds being able to approach aquatic prey at closer range before detection to that of military aircraft being painted white on the undersides to decrease the critical range of visibility, a strategy devised by William Ralph Merton during the Second World War (The Telegraph 2014). An obvious objection to this theory is that any natural object, even if it is pure white, would be less bright than the sky and will as a result appear dark when viewed from below (Penacchio *et al.* 2015b), but Craik argued that when viewed from a distance, the scattering of atmospheric skylight would reduce this effect. Similarly, when viewed from close range above water, the skylight reflected from the water surface may illuminate the underside of a white object, conferring decreased contrast against the sky (Kiltie 1988). Even though the reduction in contrast against the sky of a white object compared with a black one is relatively small, Craik theorised that it may still confer an advantage to foraging seabirds as the visual acuity of fish is generally poor (Caves *et al.* 2018) and this small decrease in threshold detection distance may be enough for the foraging bird to capture its prey before it can dive to safety.

Craik's letter to Nature was met with some opposition, presented in replies later in the publication, from both an optical physics and an ornithological standpoint (Pirenne & Crombie 1944; Armstrong 1944). Pirenne & Crombie (1944) described a simple experiment conducted on the roof of the Zoology building at Cambridge University, where a human observer looked upwards through a glass trough filled with water. When presented with three-by-five inch cardboard stimuli, coloured black or white, the two were indistinguishable when the sky was overcast. However, when the sky was clear and the sunlight fell directly on the observer and stimuli, the black and white stimuli were easily distinguishable. Importantly, they also noted that the observer's field of view through the water was heavily distorted when the water was agitated by wind. The above water image, through Snell's window, becomes increasingly distorted as the wave action increases, eventually resulting in total internal reflection and complete disintegration of the above-water field of view (Johnsen 2012). Pirenne & Crombie (1944) calculated that under cloudy conditions, given that the reflection coefficient of water is 0.02 at normal angle of incidence, a white horizontal surface lit solely by sky light reflected from the water surface will have a contrast against the sky

of about 0.9, compared with 1.0 for a uniform black object. However, the contrast of a white object against the sky would be reduced further by scattered atmospheric light. The authors calculated that considering the sole effect of scattered atmospheric illumination, and assuming the intensity of scattered light is proportional to the viewing distance, a white object would be invisible at a distance 10% shorter than a black one. One might assume that these two effects, scattered atmospheric illumination and reflected illumination, might reduce the contrast of incoming seabirds against the sky sufficiently for white plumage to be advantageous over black for catching aquatic prey. However, Pirene & Crombie argued that since the visual acuity and range of vision of fish is poor, it is unlikely that their threshold of visibility will be affected by atmospheric scattering. When the sky is clear however, the authors calculated that white plumage lit by direct sunlight would be several times brighter than the blue sky background, rendering white birds very conspicuous under these conditions. Perhaps this is not relevant to the predation of fish by seabirds, however, because the ventral surfaces of a seabird in flight will be lit by reflected light from the water, not by direct sunlight, and therefore the brightness of the bird's ventrum will be less than Pirene & Crombie's estimate.

At the end of this letter, the authors made reference to the observations of Francis Ward, recorded in his 1920 book 'Animal Life Under Water'. Ward considered the white ventral plumage of gulls to be "aggressive rather than protective". He described the optical manhole effect, as predicted by Snell's Law, stating that a white breasted bird swimming on the water surface is masked by reflection from a fish's perspective until it enters the underwater viewer's 'window'. Even then, it is likely that the ripples at the edge of Snell's window conceal the bird from view until it is very close to the viewer. Ward also observed, through photographs presented in his book, that "only a suggestion of the body of the bird can be detected". The photograph he is referring to is one of a Gull floating on shallow water, taken from below – the body of the gull appears to match the background well, with the legs being the main distinguishable cue to the bird's presence. He went on to theorise that the image of the grey and white body of the bird from an underwater perspective is compressed at the edge of Snell's window, and lost in the ripples. The bird's head, being just visible at the edge of the

window (given its slight elevation above the water surface), is coloured white which intuitively seems the most appropriate colour for reducing conspicuousness against the sky. In an earlier chapter, Ward also described how, in the case of wading piscivorous birds, the head and shoulders of the bird, visible at the edge of Snell's window, appear on the same plane as reeds and trees in the background and hence blend into the visual scene and are relatively well concealed from an underwater viewpoint. Ward argued that this effect allows waders, such as herons, to catch fish easily whilst standing in clear water. One could assume this effect would extend to gulls floating on the water surface if they are close enough to the shore for objects such as trees and cliffs to be present in the background.

In response to the letter to Nature by Pirenne & Crombie, Craik (1944b) provided a counterargument which was published in the same issue immediately following Pirenne & Crombie's contribution to the debate. He claimed there was still a significant reduction in threshold detection distance for sea birds, and that a clear blue sky without any cloud cover was rare in the temperate regions that Laridae predominantly occupy. Further to this, he stated that if the sun was shining through breaks in the cloud, then there may be no or minimal contrast in brightness between the bird's ventrum and the sky. In this communication, Craik also provided details of an experiment using grey and black paper disks mounted on white card, presented in the peripheral vision of human observers, to add support to his theory. He showed that at long range (3.8 to 4.2 metres), participants failed to report the presence of a grey spot much more than they did for a black spot on the white card.

A final response to Craik's theory was printed directly after Craik's second letter. In this correspondence: Armstrong (1944) detailed three main objections to Craik's hypothesis. Firstly, he stated that most of the prey relevant to the system in question do not have sufficient visual acuity for the coloration of the bird to be relevant; for example, albatrosses and shearwaters that feed on cephalopods, crustaceans, molluscs and krill. Also, he stated that most white sea birds do not use feeding methods where white coloration would be useful in the manner described; gulls are scavengers. Secondly, Armstrong found it unlikely that dark coloration would be disadvantageous to species such as gannets, diving and catching fish at high speeds.

I find this second point to be irrelevant, as the plunge diving feeding technique of a gannet is very different from the varied methods employed by many sea birds, such as gulls. His final objection was simply that many diving piscivorous birds are “brilliantly coloured or dark” such as kingfishers, mergansers and cormorants. However, if the coloration of these species mentioned by Armstrong are examined, one finds that they all show some degree of countershading (that is, a gradation to lighter coloration towards the ventrum), the ultimate causes of which remain to be explained.

Two years later (after Craik’s death), Armstrong (1946) published a paper detailing his theory explaining the white plumage of seabirds. Armstrong argued that since his objections to Craik’s hypothesis were conclusive, namely that the coloration of sea birds is not relevant to eluding prey or predators, then it must be relevant to conspecifics if it is not arbitrary. His reasoning was that signalling is generally an important function of bird plumage; however, the coloration of seabirds does not come under the explanations of aposematism, camouflage or common signalling interactions. The ocean is a much more visually homogeneous environment, so there is much narrower diversity in adaptive coloration; however, this does not explain why they look the way they do. Similarly, one might attempt to explain their coloration in terms of a lack of natural enemies for many large seabirds, meaning they can afford to be conspicuous – again, Armstrong acknowledged the weakness of this explanation in that one cannot explain a trait simply by asking why it should not exist. Armstrong also made reference to *Pachyptila desolata* (the Antarctic prion) as an example of a seabird that apparently does utilise ‘obliterative’ coloration (i.e. camouflage); he used this as evidence for his point that the conspicuous coloration of seabirds is not due to there not being an effective camouflage strategy for birds in a pelagic marine habitat. However, there are few differences in colouration between images I have seen of *P. desolata* and gulls – the visual texture of the dorsal surfaces is admittedly more complex, perhaps increasing the effectiveness of crypsis. But overall, they look similar.

Armstrong’s (1946) theory of the function of white seabird plumage was that it is advantageous for them to be able to see each other at great distances, as they consequentially attract each other to food sources. He described how this function seemed peculiar to him – as it suggests that this plumage evolved as a result of social

benefit to the species as a whole, not because it is beneficial in increasing the survival of individual birds. This smacks of group selection, but was published sixteen years before Wynne-Edwards' (1962) book 'Animal Dispersion in Relation to Social Behaviour', the initial significant suggestion of group selection. Anecdotally, Armstrong went on to describe how gulls are visible (at least to humans) at great distances, that they appear to 'watch' conspecifics and follow their movements, and that those sea birds that are predominantly coloured white tend to be those that rely on spatially and temporally transient food sources. Hence if the food supply is unreliable in the sense that it will be plentiful for a short time frame, then it must be advantageous for white sea birds (for instance gannets – plunge diving on shoals of fish, or stilts – feeding at shallow pools that are liable to rapid evaporation) to be conspicuously coloured so that the discovery of a food source by one individual is clearly (albeit unwittingly) signalled to nearby conspecifics, to their benefit. Another clear issue with the social signalling hypothesis is that if true it would predict totally white coloration, not just a white ventrum, especially if one considers how the observation of feeding conspecifics would typically be from above, not below. Armstrong's further explanations of examples reinforcing his theory seem hyperbolic or tenuous. Examples include that within groups of seabirds, those species that do not rely primarily on patchy or transient food sources are those which diverge from white conspicuous plumage, for example black terns which feed on insects, and the skuas which are kleptoparasitic. Perhaps the most unlikely evidence he stated was that immature gulls have cryptic plumage because it prevents flocking of conspecifics to unsuitable feeding grounds discovered by immature birds. This seems improbable given the existence of far simpler explanations and a lack of evidence presented.

Finally, Armstrong theorised that the evolution of white plumage in gulls occurred concomitantly with the development of increased sociality. Social interactions are common in gull colonies, but Armstrong's claim that adult sandwich terns engage in altruistic feeding of creches of young, many of which are not their offspring, is simply not true. This was reported to be incorrect 15 years prior by Steinbacher (1931), and by Smith (1975) who confirmed through a colour-ringing study that although young sandwich terns do indeed form creches, individuals are fed by their parents alone.

Following this spate of interest in the topic, the debate around sea bird coloration slowed down for some time. The main contributions up until the 1970s were both works by Niko Tinbergen (1953; 1964) – his book: *The Herring Gull's World*, and a paper on adaptive radiation in gulls. The paper (Tinbergen 1964) paid attention to, among other things, white coloration as an adaptive feature. The first question dealt with actually concerns the phylogeny of the gulls (tribe Larini). Tinbergen concluded that they are monophyletic, because of the uniformity and consistency in social signalling or display behaviours throughout the group. These behaviours are more reliable indications of phylogenetic relatedness compared to feeding behaviours for example, which are affected by environmental factors to a greater extent.

When he addressed the adaptive nature of white coloration of gulls in front and underneath, Tinbergen described work conducted by Phillips (1962). Firstly, that some three-spined sticklebacks (*Gasterosteus aculeatus*) in an experimental tank fled more quickly and intensely when a black model gull was moved overhead, compared to a white corresponding model. Secondly, after reviewing literature, that a good correlation existed between reports of species plunge-diving to feed on live fish (making up a major dietary component) and those species being coloured white ventrally. Finally, Tinbergen (1964) discussed how Phillips (1962) observed that one-year-old herring gulls (*Larus argentatus*) are dark in colour and appear cryptic, leading to the assumption that they must employ alternative feeding methods to those used by their white coloured adult counterparts. Phillips (1962) found that young gulls feed much more along the coast in the littoral zone. Phillips verified this observation by counting the numbers of young and adult gulls feeding along the coast and in a pelagic environment, over 15 sea crossings between England and Europe. An average of 30% of birds in coastal flocks in both the UK and Europe were dark coloured, but only 3% of birds in open ocean were dark. Tinbergen (1964) briefly considered the plumage of the young, mentioning that the apparent crypsis may afford protection from Skuas along the coast. Potentially it may aid in concealing young gulls nesting from terrestrial predators, such as many mustelids.

Phillips (1962) also examined the fine structure of gull feathers. Unlike white feathers of domesticated birds that have simply lost pigment, the barbs of gull feathers contain

large air chambers, and highly refractile material. This could potentially increase the perceived brightness of the white plumage of gulls, reducing contrast against the sky. Furthermore – those gulls which have a dark mantle, such as the greater and lesser black-backed gulls (*Larus marinus* and *Larus fuscus*) actually have a white border around the frontal wing edge, which could function to remove any possibility of the dark mantle and wings breaking camouflage during approach to prey. In addition to this, Black headed gulls (*Chroicocephalus ridibundus*) (amongst others) change habitat in late summer and undergo a corresponding moult after which the head is white. It was reported anecdotally that fish form a larger component of their diet during winter, which is consistent with the change in coloration (Tinbergen 1964).

Subsequently, Murton (1971) described his own observations of foraging strategies and seemingly corresponding plumage polymorphisms in Ardeidae (herons). He proposed that the polymorphism was maintained through advantages to the light and dark morphs under different foraging conditions. Temporal partitioning of foraging between morphs, as in dark-coloured marsh terns (*Anous* spp.) and light-coloured *Sterna* spp. feeding during the night and day respectively, seems not to apply in the case of Ardeidae. Instead, Murton observed how the light and dark morphs of herons forage in different environments and employ different hunting techniques. Specifically, when a single species occupies a habitat in isolation from closely-related conspecifics that may otherwise partition the resources, plumage polymorphism may evolve. This seems most likely to occur in coastal environments, where tide cycles facilitate and promote the use of distinct feeding methods by altering the environment. Dark morphs seem to employ active pursuit methods, whereby prey are scared from refugia in deep water and are subsequently caught by the herons, whereas light morphs seem to rely on stand-and-wait predation methods, their white plumage apparently providing adequate concealment for this strategy to be effective (see Ward 1920). Recher (1972) provided an alternative explanation for colour dimorphism in herons based on his own observations: that the dimorphism in herons is mainly limited to subtropical and tropical species, and that white morphs may be adapted to hunting on open and hot coastal flats and reefs as they are better able to regulate body temperature.

Armstrong (1971) responded to Murton's observations, conceding that social signalling and cryptic functions of white plumage need not be inconsistent or mutually exclusive.

The first published experiment for white plumage reducing undersides' contrast against the sky was from Cowan (1972), who made mounts of gulls that were ventrally white, partially white, and black. He photographed these mounts in pairs (e.g. white and black, white and partially-white) at the same time, held six feet above water. The pairs of images were then suspended side by side and drawn towards a human participant (actually Cowan himself), and the relative distances at which the two mounts in the photographs were detected was recorded. This is clearly a methodology with flaws; however, at the time no photoelectric method of measuring brightness existed, and the effect of subconscious observer bias was probably not widely recognised. The white mount was detected later (and therefore had a smaller contrast against the sky) than black under all weather conditions and repeats of pairs. The frequencies of earlier detection in the white versus partially-white mounts were equal, suggesting there was no difference in detectability.

It seems unlikely that the white coloration of gulls could evolve as a conspicuous signal simply due to feeding benefits to whole species groups, as hypothesised by Armstrong (1944; 1946), when it at first seems detrimental to the fitness of individuals. However, experiments reported by Götmark *et al.* (1986) confirmed that individual gulls (including the individual that first finds the food source) consume more fish when foraging in increasing group sizes. If this is true, then the plumage of gulls may indeed have evolved to aid in the signalling of a food source to conspecifics, as suggested by Armstrong (1944; 1946) (Simmons 1972; Andersson *et al.* 1981). Götmark *et al.* (1986) suggested that this may partly be due to the fact that a school of fish is increasingly vulnerable when attacked by multiple gulls.

The following year, Götmark (1987) published a report detailing his experiments designed to test the white ventral camouflage hypothesis (initially proposed by Craik 1944a). He found that black-headed gulls (*Chroicocephalus ridibundus*) that had had their undersides dyed black showed a greater reduction in capture rate of schooling

bleak (*Alburnus alburnus*) than individuals with unmanipulated white underparts. The white control group were subjected to an identical procedure as the dying process, but without the dye. The black individuals caught fewer fish than white when hunting individually and as flocks. When hunting solitarily, black individuals actually showed a decreased attack rate, which explains the reduced rate of capture, whereas in flocks, the decreased capture rate in black gulls was attributed to reduced attack success. The conclusions of this study, when taken with those of Götmark *et al.* (1986), indicate that the white plumage in seabirds may have evolved for two non-exclusive functions – aggressive camouflage and signalling the discovery of a food source to conspecifics.

More recently, Johnsen (2002) calculated that reflectance of ventral surfaces has little to no effect on an organism's visibility in pelagic marine environments, mainly owing to the fact that downward radiances are 200 times greater than upward radiances in oceans (Denton 1990). However minimum contrast thresholds for organisms such as pelagic fish may be high (0.2) meaning white would have a slightly shorter sighting distance than black for a completely horizontal surface viewed from below. The ventral surfaces of seabirds and almost all aquatic animals are in fact curved. As the angle of the surface increases from horizontal to vertical, the benefit of white coloration increases as the surface receives more irradiance. This lends support to the notion that white ventral surfaces may be adaptive in seabirds, especially as the irradiance on the ventral surface will be much higher when the bird is still above the water, due to more reflected and scattered light.

Many seabirds are known to be kleptoparasitic, that is, they steal food from other species. The arctic skua *Stercorarius parasiticus* is kleptoparasitic towards other sea birds and shows a plumage polymorphism in that some individually are ventrally dark and others white. The frequency of these phases shows latitudinal variation, but it has been suggested that the dark phase individuals experience enhanced success rates when attacking and stealing food from other species, as their dark undersides are camouflaged against dark cliffs where they forage. Alternatively, the polymorphism may be maintained by apostatic selection due to the use of search images by potential victims of kleptoparasitism (Caldow & Furness 1991). Caldow & Furness (1991) found that the reproductive success of *S. parasiticus* in the Shetland Islands is food limited,

therefore providing the selection pressure for higher chase success during kleptoparasitic attacks. When the population of light-phase individuals declined (for reasons unknown), the remaining light-phase individuals experienced increased chase success rates relative to the more common dark-phase individuals. This supports the idea that apostatic selection, and not aggressive camouflage, is maintaining dark-light polymorphism in this species.

1.2 Refraction and Snell's Law

When electromagnetic waves (light) travel between two media with different refractive indices, the direction of the wave is altered. When light travels from one medium to another that has a higher refractive index (with a higher density), its speed is reduced and the wave bends towards the normal. The normal is the plane that is perpendicular to the boundary between the two media. Water ($n = 1.33$) has a higher refractive index than air ($n = 1.00$), meaning that when light travels from air to water, it bends towards the normal, and when it travels from water to air, it bends away from the normal. The relationship between the angle at which the light wave meets the boundary between two media relative to the normal (the angle of incidence) and the angle at which the wave propagates after the boundary relative to the normal (the angle of refraction) is defined by Snell's Law:

$$n_1 \sin \theta_1 = n_2 \sin \theta_2$$

Where n_1 and n_2 are the refractive indices of the two media, and θ_1 and θ_2 are the angle of incidence and the angle of refraction respectively. This change in the direction of light has implications for vision across a boundary between two media, for example water and air. When viewing an underwater object from the air, the light travelling from the object to the retina will bend away from the normal at the boundary, creating the illusion that the object is shallower than it really is. Similarly, when viewing an above-water object from below the water, the light travelling from the object to the retina will bend towards the normal, making the object appear further away than it really is. Refraction at the water surface also means that when looking up from below the water, the entire 180° field of view is condensed into a cone of 97° . Therefore, at angles

greater than 48.5° from the vertical, total internal reflection occurs and all that can be seen is the underwater scene reflected back from the surface. Due to its inherent association with Snell's Law, this phenomenon is called Snell's window (Lythgoe 1979; Johnsen 2012). Snell's window in reality is seldom distinct (Johnsen 2012); the above water image begins to distort with surface rippling, and completely disintegrates in rough conditions, as the wave action drastically alters the angle of incidence and hence the refraction of light entering the water. Even if the water is still, any predatory bird (a wader, or even a gull resting on the water surface) will be relatively inconspicuous when viewed through Snell's window, as only a small part of its body is above the water, and that portion is so close to the water surface that it appears compressed and obscured by the dark edge of the window where total internal reflection begins (Ward 1920). Ward (1920) also described how underwater photographs show that white plumage patches on the head of a mounted heron appear to blend in with the surrounding sky. This suggests that birds, approaching an underwater viewer, that stay close to the water, and have white plumage, may remain very inconspicuous until they have approached the viewer closely. Anecdotally, gulls do often rest on the water between catches and fly low to the water when approaching a prey item. They rarely plunge dive. This behaviour may make their approach less obvious to prey when compared with direct overhead approach if one considers the observations of Ward (1920).

But a problem still presents itself for animals that visually hunt prey through a boundary between media. They must overcome the difficulty of refraction and its effects of the apparent location of objects. There is evidence that both birds and fish are capable of making adjustments for refraction when viewing prey through the air-water interface. Katzir & Intrator (1987) studied the predatory sequence of a piscivorous wader, the western reef heron (*Egretta gularis schistacea*). This species has the ability to catch fish successfully from a range of viewing angles, which indicates its ability to correct for refraction. The capture of underwater prey by *E. gularis schistacea* included two head movement phases: a slower, more horizontal 'pre-strike' followed by a sharp change in direction and velocity – the 'strike'. Once the 'strike' phase was initiated, the path of the bill followed a straight line to the prey without passing through the apparent

prey position, indicating that the heron 'knew' the real location of the prey at the point of change between the two phases. This is supported further by the narrow gape of the bird when catching the prey, the eye being covered by the nictitating membrane during the strike, and the fact that the heron did not simply strike vertically to avoid refraction. The small variance in eye height above the water throughout the trials ($n > 200$) indicated that the heron might monitor the angle of sighting the apparent prey and the apparent position of the prey whilst moving its head forward at a constant height during the 'pre-strike', until the required combination of apparent position and angle of sighting are reached when it then strikes in a straight line.

Archerfish have also been shown to compensate for refraction when hunting insects resting on foliage above the water surface (Lüling 1963; Bekoff & Dorr 1976; Dill 1977). Lüling (1963) first described the feeding behaviour of *Toxotes jaculatrix*, a small archerfish living in coastal salt and brackish waters. He observed that they hit targets with jets of water, propelled by rapid compression of their gill covers, from a distance of about three feet. For them to feed using this method, the water surface must be calm and there must be vegetation for prey to land on, but Lüling noted that this is not their primary method of foraging. Lüling (1963) also described how their eyes being submerged was a trivial problem in his view because they generally positioned themselves vertically to reduce refraction, and that their eyes were extremely close to the water surface. This was confirmed later by Bekoff & Dorr (1976) who found that *T. jaculatrix* performed a sequence of four to six regular behaviours to catch prey. First, they orient themselves diagonally facing the prey item, then they swim to directly below the prey. Next, they rotate vertically, sometimes twice, and then either shoot a jet of water or leap towards the prey. Leaping was never successful, and shooting only had a 25.5% hit rate, which is in agreement with Lüling (1963) that this species does not rely on this method of foraging. However, Dill (1977) used video analysis to investigate spitting behaviour in a different species of archerfish *Toxotes chatareus*, which did not shoot from directly below the prey, suggesting they can set the angle of the water jet to adjust for refraction. This species showed a higher hit rate than *T. jaculatrix* and must make adjustments for both the incorrect apparent height of prey items due to refraction, and also the effect of gravity on the water droplets. Its behaviour is similar

to *T. jaculatrix* in that it orientates its body at the water surface, visually fixates the prey (presumably to orientate correctly and judge distance), then quickly rotates to a steeper angle and shoots.

1.3 Response to predator stimuli of typical sea bird prey

It is important to consider how prey respond to stimuli that simulate a predatory attack to understand which cues prey species are using to detect predators, and how they assess risk to inform escape decisions. This is relevant when considering how sea birds hunt fish and other aquatic prey. Hemmi (2005) simulated a predatory attack on fiddler crabs (*Afruca vomeris*, formerly *Uca vomeris*) by moving a model tern (one of their main predators) along a line near to their burrows. This study aimed to test the Kramer & Bonenfant (1997) model to predict flight initiation in threatening situations, in situations where the prey organism has incomplete information about predator distance and direction. Crabs did initiate evasive action (running to the burrow entrance) earlier in response to an approaching predator the further they were from their burrow, in agreement with the first prediction of the Kramer & Bonenfant (1997) model. However, the second prediction, that prey should initiate their escape response earlier when the refuge is between the predator and the prey (the prey has to run towards the predator to escape), was not fulfilled. Hemmi (2005) argued that this is because crabs do not have the necessary information required by the model. If the prey must arrive at its refuge before the predator, with a constant margin of safety, then the predator's position once the prey reaches safety should be a constant distance from the burrow, regardless of the approach direction. Crabs should assess the approach of the predator from an allocentric perspective, in other words in relation to the distance to the refuge. The results indicated that the crabs use an egocentric frame of reference, and this is probably due to the lack of distance cues available to them for aerial objects, or a lack of sufficient cognitive ability to adopt anything other than an egocentric viewpoint.

Oliva *et al.* (2007) evaluated escape behaviour in another crab *Chasmagnathus granulatus* but with a focus on the underlying neuronal responses. The stimuli presented to crabs were 5 cm black squares on computer screens which expanded to

fill the screen, which approached over a simulated distance of 70 cm at a constant speed of 20 cm s⁻¹. The crabs were positioned on a Styrofoam sphere floating on a jet of air so that they could walk or run and the sphere would rotate freely beneath them. The magnitude of the crabs' escape response varied; however, the timing of the response was consistent across individuals (approximately one second before simulated collision). The neuronal responses of the crabs were very well coordinated with both the stimulus and their behavioural response. The increasing firing rate of the looming-sensitive neurons closely matched the dynamics of the image expansion. Also, the neuronal responses to looming, receding and moving stimuli closely reflected the behavioural differences: crabs started to run when the looming-sensitive neuron firing rate increased, and the increase in their running speed followed the increment in firing rate.

Pignatelli *et al.* (2011) performed a similar experiment with fish, investigating behavioural responses to looming luminance-based and polarisation-based stimuli. Fish showed very robust startle responses to the luminance contrast looming stimulus but did not respond when the stimulus was presented in polarisation contrast. Similarly, How *et al.* (2012) found that fiddler crabs *Afruca vomeris* responded to luminance based looming stimuli in 88% of trials, but responded to polarisation based looming stimuli in only 56% of trials. Crabs also responded sooner to intensity rather than polarisation stimuli. Taken together these results indicate how aquatic and terrestrial prey respond to avian predators and offer insight into the important cues that trigger an escape response.

1.4 Conclusion and Aims

Overall, the function of countershading coloration in sea birds remains unclear. Theories of social signalling between conspecifics, and of aggressive camouflage have received the most attention historically; however, most discussions and investigations have been open-ended (Tickell 2003). Using field photography of controlled stimuli, computer-based image analysis techniques and detection experiments, I aim to quantify the cryptic effect of white ventral plumage in sea birds from an ecologically relevant viewpoint: underwater. The measure of crypticity I will

use is target-background luminance contrast. I will test for significant effects of environmental conditions on target-background contrast, including time of day and year, the light environment and the level of surface rippling. I also aim to test whether above-water white objects are detected earlier than black ones (at least to humans) when viewed from underwater using both real photographs and a realistic simulated pelagic environment, again testing for effects of environmental variables on the detectability of targets.

It is important to consider the contrast between the target and the background from the visual system of a typical receiver: a tetrachromatic or trichromatic fish. This will inevitably affect the perceived salience of an overhead, above-water object; however, the visual system of a particular typical receiver was not modelled in the following experiments. Instead, this study is composed around the human trichromatic visual system, meaning that the principles and functional significance of white plumage described hold more generally.

2 Experiments

2.1 Introduction

In order to determine under what environmental conditions white plumage is most effective as hunting camouflage for seabirds, I performed image analysis on video frames taken from an underwater perspective, of a white spherical model suspended above the water surface and floating on the surface (Experiment 1, section 2.2). Luminance contrast ratios between the target and the background were measured, and compared across videos taken under different levels of cloud cover, wind speed, rain, time of day and in a marine or freshwater environment. This field experiment was supported by a detection experiment involving human participants (Experiment 3, section 2.4), who were shown a range of video frames from the field experiment, and were required to search for the target and click on its location. In order to test for differences in detectability of different coloured targets under a range of balanced and controlled environmental conditions, I created a different detection experiment based in a realistic simulation of a natural pelagic environment (experiment 2, section 2.3). Human participants were required to search for spherical targets which moved across the computer screen. Within the simulation, the perspective of the participant was from below the water looking directly upwards, with the target moving above the water. The targets were different colours, appeared at different heights, and the environmental conditions in the simulation included a range of wave amplitudes and levels of cloud cover.

2.2 Experiment 1: Field experiment and computer image analysis

2.2.1 Methods

The first experiment involved photography of models, designed to allow quantification of the visual contrast that might be apparent in an ideally countershaded bird in the field, and subsequent image analysis. The study sites used were: Henleaze Swimming Lake, Lake Road, Bristol, UK at national grid reference ST 58048 77478; the river

Frome at Oldbury Court Estate, Oldbury Court Road, Fishponds, Bristol, UK at national grid reference ST 63382 77139; and Clevedon Marine Lake, Old Church Road, Clevedon, UK at national grid reference ST 39701 71052. The first two sites were inland and freshwater, the latter coastal and saltwater. The 'model sea-birds' used were two white polystyrene spheres measuring 150mm and 100mm in diameter. White was chosen to give the minimum luminance contrast with the sky and therefore the most effective camouflage, as opposed to any darker colour. These models were placed on the surface of water, or suspended approximately 0.5 m above the water surface using white polypropylene twine attached to a fishing rod extending over the water surface (fig. 2.1). Videos were captured of these targets from underwater with the field of view pointing directly upwards, using an Akaso Brave 4 action camera (Akaso, Frederick, MD, USA) mounted on a white plastic extendable pole (Wilko, Worksop, UK). Videos (4K resolution, 24 fps, 170° viewing angle) lasted approximately one minute, during which the camera was moved through a range of depths in the water column from 0 m to approximately 1.5 m. During each data collection session, footage was captured of each of the two targets both above and resting on the water surface. Wind speed was noted using the Beaufort scale, as well as weather conditions (overcast or clear), rain, depth and substrate of the water body. Illuminance was measured in lux using an MM-LMB01 digital lux meter (Max Measure, UK), both at eye level with the sensor pointing upwards and approximately 100 mm below the larger model (at eye level).

To ensure linearity between the incident irradiance on the target and the camera's response, it should be calibrated, as most consumer-level digital cameras do not necessarily maintain this linearity. If the camera is calibrated, then it can be ensured that if the irradiance doubles, for instance, then the sensory output from the camera also doubles. This can be achieved by checking that the camera output follows Malus' Law, or by using Bézier curves to characterise the response of the camera.

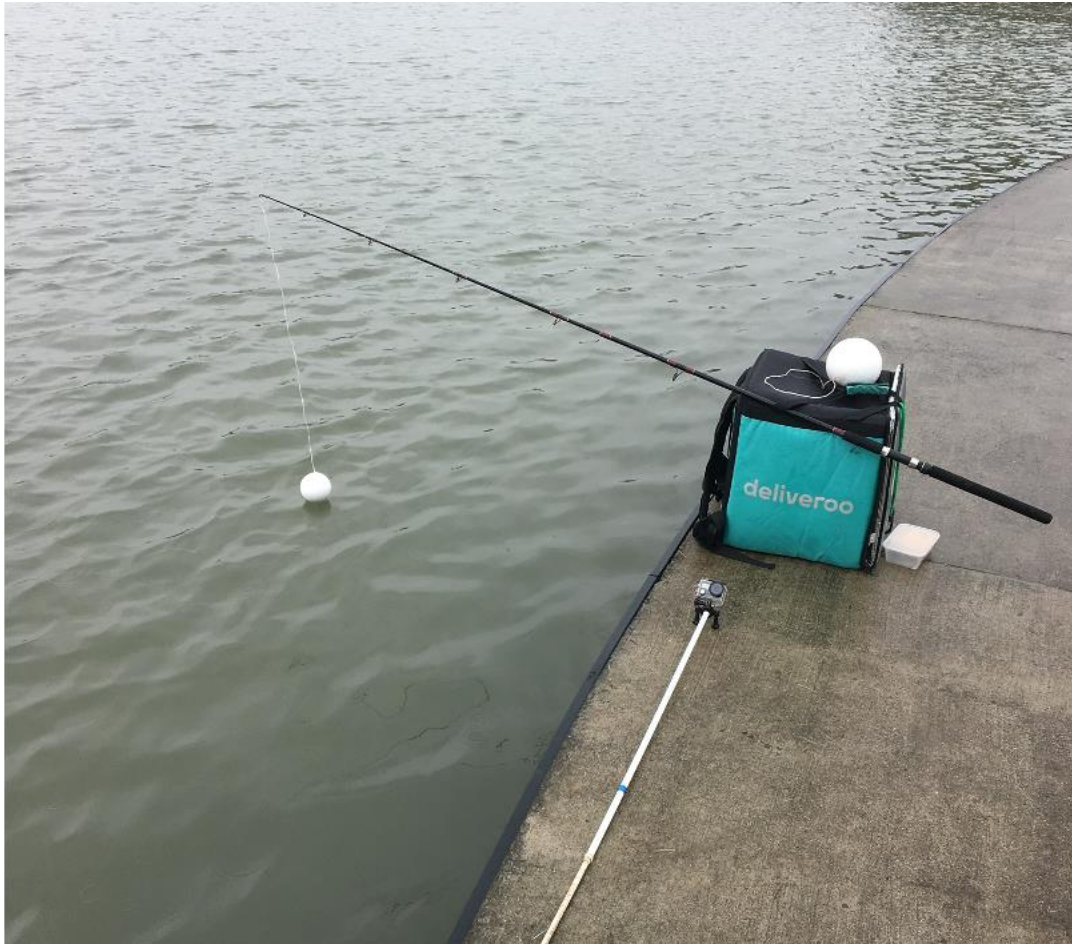


Figure 2.1. The experimental set-up for experiment 1: underwater camera and mounting pole, and white models attached to a fishing rod.

Subsequently, the videos were trimmed at either end when the target was not in view using QuickTime Player version 10.5 (Apple Inc., Cupertino, CA, USA). Still images were then extracted from the videos at a rate of one every 60 frames using custom code (written by I. Cuthill, University of Bristol) in MATLAB 9.6 R2019a (MathWorks, Natick, MA, USA). The resulting images were analysed using ImageJ version 1.52 (Rasband, NIH, Bethesda, MD, USA). First, the images were processed using the LAB stack function to produce greyscale images (the 'L' image being the achromatic luminance). For each greyscale image, the relative area of the target in square pixels was recorded, as well as the mean grey value and standard deviation of the area of the target and the mean grey value and standard deviation of a 'halo' shaped area surrounding the target with a width equal to the radius of the target. This information was tabulated in Microsoft Excel version 16.34 (Microsoft, Redmond, WA, USA).

All statistical analyses comprised univariate generalized linear mixed models (function *glmer* in the lme4 1.1-21 package, Bates *et al.* 2015) in RStudio 1.2.5019 (R Foundation for Statistical Computing, www.R-project.org). The ratio of the target's mean grey value to the background mean grey value was calculated and used as a measure of relative target-background contrast. However, the raw contrast ratios had a multimodal distribution and could not be easily modelled with any known distribution. Instead, contrast being less than 0.05 (5%) was used as a proxy measure for 'low visibility', as this could be modelled as a binomial distribution. A Weber fraction of 5% can be reasonably assumed for an achromatic visual discrimination task (used, for example, in Siddiqi *et al.*'s 2004 modification of the Vorobyev-Osorio receptor noise limited model) (Vorobyev & Osorio 1998; Siddiqi *et al.* 2004). Using a criterion equivalent to a higher discrimination ability, for example the 2% humans are capable of under ideal conditions of psychophysical testing (Wyszecki & Stiles 1982), yielded very similar results. I did not model poorer discrimination than a 5% threshold, because the goal of these experiments was to identify whether ideal countershading (a bright white underside) could provide effective camouflage, and poorer luminance discrimination will always favour that hypothesis. Picking an arbitrarily low discrimination threshold would therefore be uninformative.

Each putative predictor (target position; target size; rain; cloud cover; wind; and marine vs river environment) was the fixed effect in a different model. In each model, the response variable was the binary 'contrast less than or greater than 5%' and the random effect was video clip identity. A logit link function was applied to the data as the response variable had a binomial distribution. Likelihood ratio tests were used to compare the goodness-of-fit between models with and without each fixed effect of interest, and are quoted throughout as 'LRT_{df}', where *df* is the difference in degrees of freedom between the two models being compared (Crawley 2007). Tests were against a chi-squared distribution with *df* degrees of freedom.

The number of possible interactions for these data is large compared to the sample size, and the data are unbalanced (with respect to weather conditions, for example). Therefore, instead of attempting to fit GLMMs that included all predictors, I used the more robust approach of classification and regression trees (henceforth CARTs;

Krzywinski & Altman 2017; Lantz 2013) to investigate which factors were more or less influential and any interactions between them. CARTs are widely used in machine learning and have two main advantages over linear models with multiple predictors: first, they are effectively non-parametric and so robust, and second, they produce a simple decision tree that intuitively represents the influential predictors (including interactions). The method is recursive: first test for a relationship between the binary response and each candidate predictor, then split the data by the best predictor; then, separately for each branch at this node, test for the predictor with strongest predictive value within this subset of data, and so on until no remaining variables have predictive power for what are now the terminal branches. CARTs were implemented using the *ctree* function in the R package party 1.3-4 (Hothorn *et al.* 2006), with default values for arguments. In most implementations of CART (e.g. base R's *rpart*), trees are fitted simply to minimise classification error, and so have to be 'pruned' to avoid over-fitting. However, *ctree* does not require this step because it evaluates predictor entry at each node, using permutation tests with Bonferroni adjustment of p-values. All graphs were plotted using the functions available in ggplot2 3.2.1 (Wickham 2016). These include 'violin plots' which supplement boxplots with a depiction of the probability density of the data. This was useful in cases where distributions were multimodal, something not captured by the boxplots. Default values of the kernels for density estimation were used.

2.2.2 Results

When the target was positioned above the water surface, 18.2% of the images were 'low visibility' (the target background contrast was less than 5%). When the target was positioned on the water surface, only 0.3% of images had low visibility. For the large target, 1.2% of images had low visibility, whereas for the small target, 0.2% of images had low visibility. When it was raining, 0.1% of images had low visibility, but when it was not raining, 7.5% of images had low visibility. When it was comparatively less windy (Beaufort 2), 0.1% of images had low visibility, but when it was windy (Beaufort 5), 0.2% of images had low visibility. In the river, 0.3% of images had low visibility, whereas in a marine environment, 7.2% of images had low visibility. None of these

differences were significant (target position: $LRT_1 = 3.318$, $P = 0.069$; fig. 2.2a; target size: $LRT_1 = 0.666$, $P = 0.414$; fig. 2.2b; rain: $LRT_1 = 1.967$, $P = 0.161$; fig. 2.2c; wind: $LRT_1 = 0.035$, $P = 0.851$; fig. 2.2d; river vs marine environment: $LRT_1 = 2.325$, $P = 0.127$; fig. 2.2e). However, when it was sunny, significantly more images (78.9%) had low visibility than when it was overcast (0.3%) ($LRT_1 = 18.301$, $P < 0.001$; fig. 2.2f).

The above univariate analyses do not account for interactions. CART analysis indicated that, as in the univariate case, cloud cover was the best predictor of low visibility, but in interaction with rain: when it was overcast but not raining, none of the images had low visibility. However, when it was overcast and raining, approximately half of the images had low visibility (<5% target-background contrast) (fig. 2.3). When it was sunny, a greater proportion of the images had low visibility and there were interactions with wind speed and location (river vs marine environment). For example, when it was sunny and comparatively less windy (Beaufort ≤ 2) in the freshwater locations, approximately 70% of images had low visibility, but at the coast under the same wind and sun conditions, that dropped to under 20%. When it was sunny and windy, >90% of the images had low visibility, with location making no difference (fig. 2.3).

There were 128 images included in this analysis where the target was undetectable and could not be identified by sight or by luminance-based surface plots performed in ImageJ. The conditions under which such images occurred was analysed with CART. Wind explained the most variance in undetectability, followed by cloud cover being the second-best predictor of detectability (fig. 2.4). When the wind speed was comparatively low (Beaufort ≤ 2), the target was always detectable regardless of other factors. On the other hand, when the wind speed was higher than 2, there were interactions with presence of rain and where the target was placed relative to the water surface. When it was windy, sunny, and the target was positioned on the water surface, almost all (97%) of the images had undetectable targets, but when the target was above the surface that dropped to 67% (fig 2.4). When it was windy and overcast, failed detection was less likely, with no targets undetectable when it wasn't raining, but 40% undetectable when it was raining (fig 2.4).

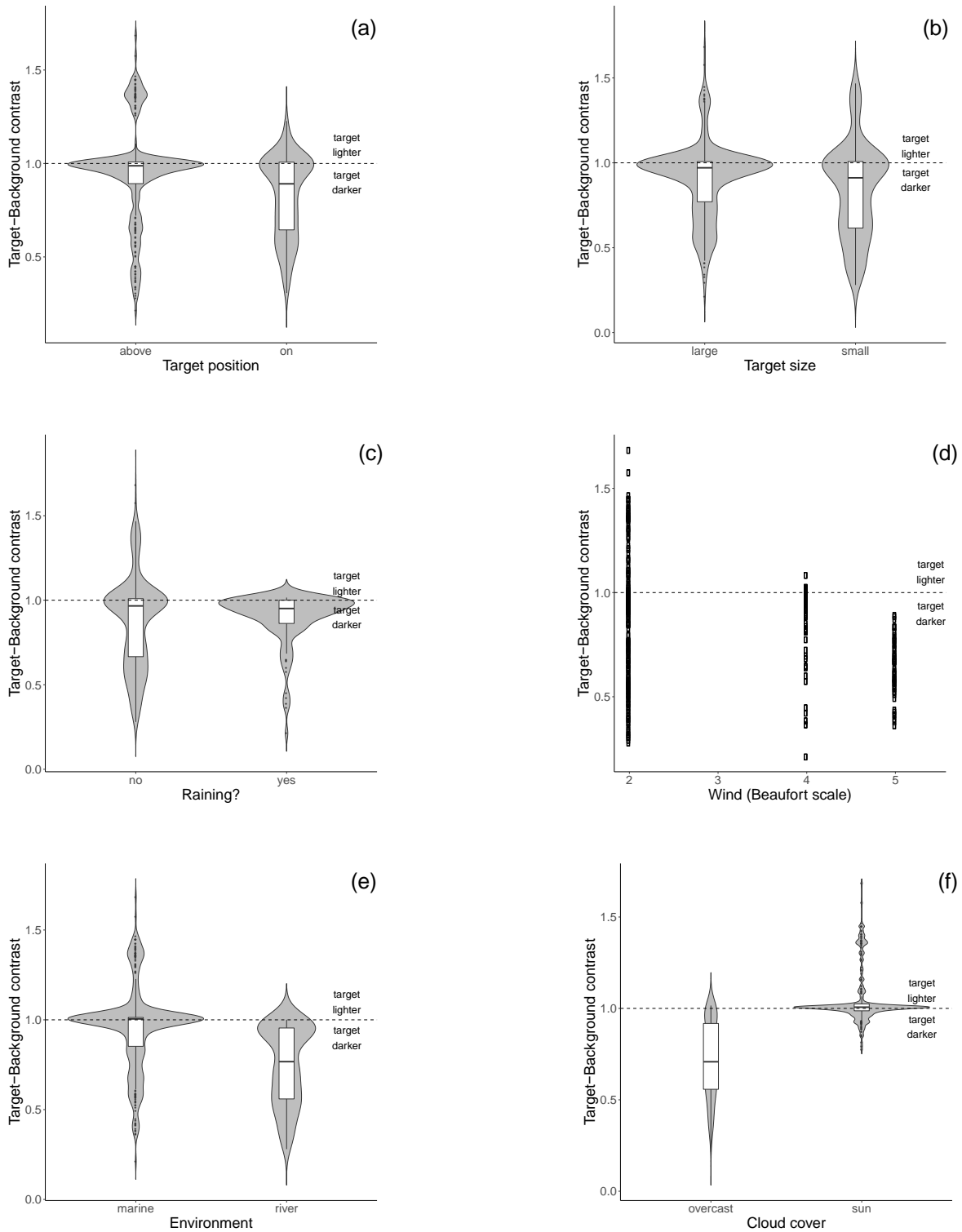


Figure 2.2. Violin plots for binary factors (a, b, c, e, f). Boxes show median and quartiles for response variable (target-background contrast). Each violin shows the probability density of the data across the range of the target-background contrast. Scatter plot for relationship between wind speed and target-background contrast (d). Figures produced using the ggplot package (Wickham 2016) in RStudio.

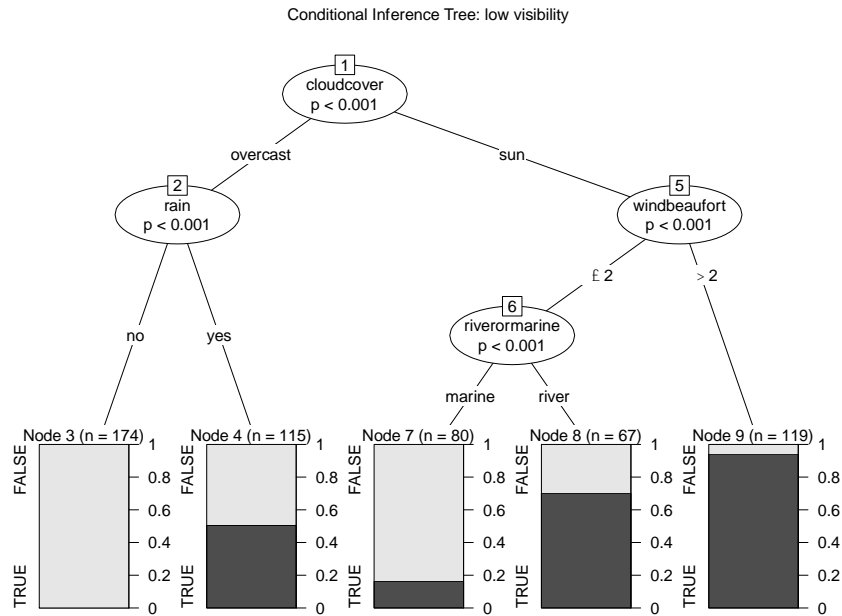


Figure 2.3. Decision tree showing proportions of images with low visibility targets under different conditions. Factors that appear higher in the tree explain more variance in low visibility of targets. True: the proportion of images with low visibility targets (dark bars). False: the proportion of images without low visibility targets (light bars).

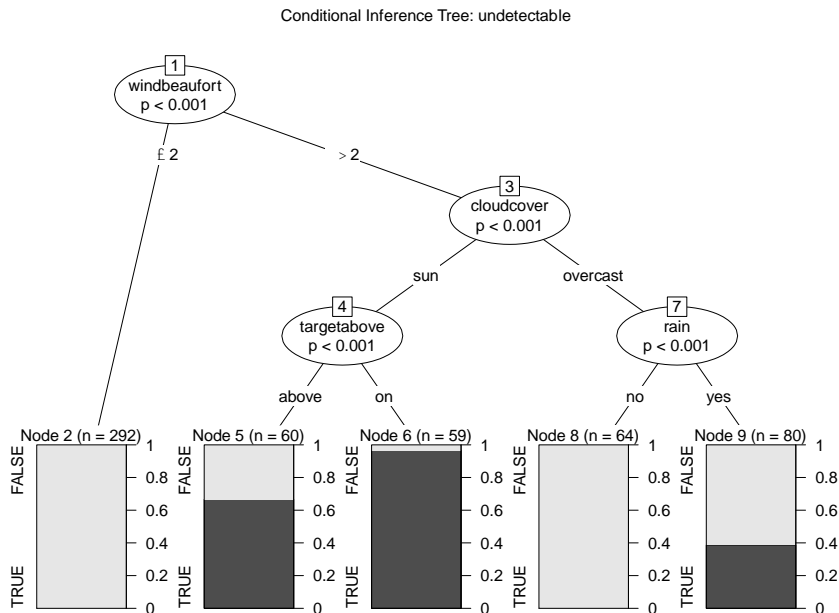


Figure 2.4. Decision tree showing proportions of images with undetectable targets under different conditions. Factors that appear higher in the tree explain more variance in undetectability of targets. True: the proportion of images with undetectable targets (dark bars). False: the proportion of images without undetectable targets (light bars).

2.3 Experiment 2: Detection experiments in a simulated pelagic environment

2.3.1 Methods

The simulated pelagic environment and associated experimental task was created and executed in Unreal Engine 4 (Epic Games, Cary, NC, USA). Stimuli were viewed by human participants on a gamma-corrected computer screen (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 268.11 mm by 476.64 mm, and a mean luminance of 64 cd m⁻²) at a distance of 40-50 cm. The simulated pelagic environment was based on the open-source Unreal Engine project 'OceanProject' (www.github.com/UE4-OceanProject/OceanProject). OceanProject allows for control of a number of environmental variables within the simulation, including wave amplitude, wind speed, cloud cover, time and date.

On each trial participants were presented with one moving target (the predator) within a simulated pelagic environment. The target moved above the water, and the point of view of the participant was from below the water facing directly up. The simulated depth of the participant was equivalent to five metres. Participants detected the moving target and clicked on it using the computer mouse; they had five seconds and one chance to click on the target for each trial. There were four levels of cloud cover and wave amplitude (0-3), with 0 being no cloud or zero wave amplitude and 3 being 100% cloud or 5 metre wave amplitude. Cloud cover and wave amplitude formed a four-by-four factorial design, such that each participant was exposed to 12 repeats of each of the 16 treatment combinations, totalling 192 trials delivered in a randomized order. For each of these 12 repeats, the target was presented randomly at one of three different simulated heights above the water surface (equivalent to 5, 25 and 50 m) and clad in one of four different 'materials' or coloration types. These coloration types were matte black, white, grey (80% of the white luminance value) and a light grey-brown mottled feather pattern. This meant that the treatments were balanced with respect to cloud cover and wave amplitude, but not with respect to target height and material, although this averaged out to approximately balanced over the 25 participants. The target was

a three-dimensional spherical object with a simulated diameter equivalent to one metre, and its appearance and destination locations around the circular field of view were random, picked from discrete uniform distributions using Unreal Engine's random integer generator. The location was constrained so that during each 5 s trial, the target was always within the circular field of view. Two primary response variables were recorded for each trial: outcome (hit, miss or time out) and response time to the nearest 10 ms. The start and end coordinates of the target were also recorded.

A total of 25 participants (10 male, 15 female, 18 – 35 years) were recruited opportunistically from the School of Biological Sciences of the University of Bristol. Each participant was naïve to the experimental procedure, had normal/corrected-to-normal vision and had provided written consent for participation and inclusion of their results. The experiment was approved by the Research Ethics Committee of the Faculty of Science, University of Bristol. There were 192 trials per participant, the delivery of which was independently randomised for each. Prior to starting the experiment, participants were given a detailed information sheet with instructions for completing the trials and a screenshot of an example trial to ensure participants understood the task. They were also given the opportunity to ask any questions and discuss the experiment before it commenced. Each trial was separated by a break screen with instructions for continuing and a central cross for fixation. The cursor location reset to the centre of the screen at the start of each trial. Each trial was completed with the room lights off and window screened to remove screen glare and aid the focus of participants during the trials.

All statistical analyses were performed in RStudio 1.2.5019 and comprised of generalized linear mixed models (function *glmer* in the lme4 package, Bates *et al.* 2015; using the *multcomp* package for pair-wise comparisons, Hothorn *et al.* 2008). Participant was included as a random effect as 192 repeated measurements were taken from each subject. The response variable was response time. Normality of residuals was checked by visual inspection of histograms; an inverse transform achieved the best normalisation of residuals for response time (better than log-transformation). For plotting, bootstrapped parameter estimates and 95% confidence

intervals were obtained from 5000 simulations using the merTools package (Knowles & Frederick 2019).

2.3.2 Results

After initially testing a full model with all terms and interactions, the final minimum adequate model for (inverse-transformed) response time included the three-way interaction of cloud cover, wave amplitude and simulated target height ($LRT_{18} = 30.0$, $P = 0.037$) and all component two-way interactions and main effects. The test statistic, degrees of freedom and p-value for each sequentially removed term are presented in table 2.1. To examine the source of this interaction, separate models were then fitted for each target height.

Table 2.1. Test statistic, degrees of freedom and P-value for each term sequentially dropped from the model for response time in the simulated detection experiment.

Term	χ^2	D.f.	P
Material:cloud:wave:height	51.1	54	0.586
Material:cloud:height	20.8	18	0.291
Material:cloud:wave	30.5	27	0.290
Material:cloud	3.0	9	0.966
Material:wave:height	27.0	18	0.079
Material:wave	8.6	9	0.476
Material:height	11.0	6	0.088
Material	0.9	3	0.819

When the target was at the lowest simulated height (near), there was a significant effect of cloud cover, but not wave amplitude on participant response time ($LRT_3 = 68.2$, $P < 0.001$). Response time was significantly faster for cloud categories 2 and 3 compared to 0 and 1 (2-0: $z = 6.1$, $P < 0.001$; 3-0: $z = 6.4$, $P < 0.001$; 2-1: $z = 5.4$, $P < 0.001$; 3-1: $z = 5.6$, $P < 0.001$; but 1-0: $z = 0.7$, $p = 0.906$; and 3-2, $z = 0.2$, $p = 0.995$; fig. 2.5).

When the target was at the middle height distance, there was a significant interaction of cloud cover and wave amplitude ($\chi^2_9 = 17.7$, $P = 0.038$). When wave amplitude was level 0, response time decreased significantly from cloud level 0-1 but remained similar with further increases in cloud cover ($\chi^2_3 = 49.8$, $P < 0.001$; pairwise 0-1: $z = 4.0$, $P < 0.001$; 0-2: $z = 6.1$, $P < 0.001$; 0-3: $z = 6.6$, $P < 0.001$; but 2-1: $z = 2.1$, $P = 0.148$; 3-1: $z = 2.5$, $P = 0.063$; 3-2: $z = 0.3$, $P = 0.990$; fig 2.5). When wave amplitude was level 1, response time decreased with greater cloud cover, but only the differences between 0-3 and 1-3 were significant ($\chi^2_3 = 12.6$, $P = 0.006$; pairwise 0-1, $z = 0.4$, $P = 0.973$; 0-2, $z = 2.3$, $P = 0.104$; 0-3: $z = 3.0$, $P = 0.013$; 1-2, $z = 1.9$, $P = 0.228$; 1-3: $z = 2.7$, $P = 0.036$; 2-3, $z = 0.8$, $P = 0.854$; fig 2.5). When wave amplitude was level 2, response time was faster for cloud levels 2 and 3 than 0 and 1 ($\chi^2_3 = 37.1$, $P < 0.001$; pairwise 0-1, $z = 1.9$, $P = 0.243$; 0-2, $z = 5.2$, $P < 0.001$; 0-3, $z = 5.0$, $P < 0.001$; 1-2: $z = 3.3$, $P = 0.005$; 1-3, $z = 3.2$, $P = 0.008$; 2-3, $z = 0.1$, $P = 0.999$; fig 2.5). When wave amplitude was level 3, response time decreased between cloud levels 1 and 2, but remained similar between cloud levels 0-1 and between 2-3 ($\chi^2_3 = 42.9$, $P < 0.001$; pairwise 0-1, $z = 0.1$, $P = 0.999$; 0-2, $z = 5.0$, $P < 0.001$; 0-3, $z = 4.4$, $P < 0.001$; 1-2: $z = 5.0$, $P < 0.0001$; 1-3, $z = 4.4$, $P < 0.001$; 2-3, $z = 0.7$, $P = 0.887$; fig 2.5).

When the target was at the far distance, there were significant effects of both cloud cover and wave amplitude but no interaction (cloud: $LRT_3 = 372.3$, $P < 0.001$; wave: $LRT_3 = 9.2$, $P = 0.027$; interaction: $LRT_9 = 13.7$, $P = 0.133$). Response time decreased between cloud levels 0 to 1 to 2, but remained similar between cloud levels 2-3 (0-1: $z = 4.7$, $P < 0.0001$; 0-2, $z = 16.3$, $P < 0.001$; 0-3, $z = 16.7$, $P < 0.001$; 1-2: $z = 11.3$, $P < 0.001$; 1-3, $z = 11.8$, $P < 0.001$; 2-3, $z = 0.6$, $P = 0.919$; fig 2.5). Response time tended to decrease at higher wave amplitudes, but the only significant difference was between levels 0 and 3 (0-1: $z = 1.8$, $P = 0.250$; 0-2: $z = 2.5$, $P = 0.056$; 0-3: $z = 2.7$, $P = 0.037$; 1-2: $z = 0.7$, $P = 0.898$; 1-3: $z = 0.8$, $P = 0.840$; 2-3: $z = 0.1$, $P = 0.999$; fig 2.5).

In summary, apart from the unsurprising slower detection at greater distances, the main effect was that detection was faster with greater cloud cover and, to a lesser extent, more wave disturbance. Although the interaction was not significant at all

distances, the general pattern was for detection to be most difficult with a combination of no clouds and no waves (fig. 2.5).

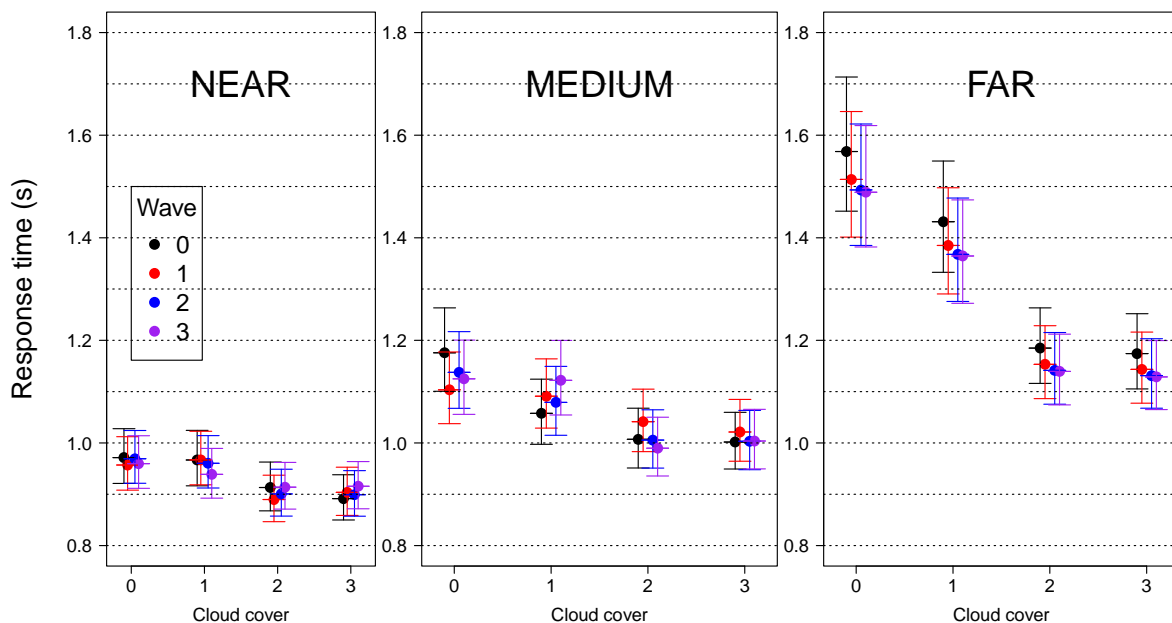


Figure 2.5. Mean participant response times with 95% confidence intervals for different levels of cloud cover, wave amplitude and simulated target height (see text for explanation of the coding of wave height and cloud cover). Means and confidence intervals are based on the fitted models.

2.4 Experiment 3: Detection experiments with real video frames

2.4.1 Methods

Participants were exposed to stimuli consisting of colour photographs of real spherical targets in the field (the same video frames used in the contrast analysis experiment (section 2.2)). Photographs of the targets were subjectively classified into three categories: ‘easy’ (target is clearly visible); ‘hard’ (target is difficult to detect but still visible) and ‘no signal’ (target is not visible). From the complete video database, 144 frames were selected so that ‘difficulty’ (target visibility as described previously), cloud cover (clear or overcast) and target location (on or above the water surface) formed a three-by-two-by-two factorial design. Twelve images were selected for each of the 12 treatment combinations. Each trial consisted of participants being presented with one

of the selected photographs on a computer screen, and the experimental task was simply for participants to click on the target as soon as they detected it. Participants were instructed to click in a (digitally inserted) red square in the top left corner of each stimulus image if they could not detect a target in the photograph. The delivery of these 144 stimuli to each participant was randomised and executed in MATLAB 9.6 R2019a, using custom code (written by I. Cuthill, University of Bristol). Participants had one opportunity to detect the target per photograph and were not made aware if they had been successful. There was a grey screen with a central fixation cross between each trial. Participants completed five practice trials prior to commencement of the experimental trials so that they were familiar and comfortable with the task. During the experimental trials, stimuli were delivered in blocks of 24, with the opportunity to take a break after each block; in practice, participants only paused briefly. The cursor location reset to the centre of the screen between each trial. All trials were delivered with the room lights off and window screened to reduce screen glare and aid participant concentration.

Participants were the same 25 individuals who completed the simulated detection experiment (section 2.3). They completed both experiments in the same session, with 12 doing this experiment first and the other 13 the reverse order. Each participant was naïve to the experimental procedure, had normal/corrected-to-normal vision and had provided written consent for participation and inclusion of their results. The experiment was approved by the Research Ethics Committee of the Faculty of Science, University of Bristol. Prior to starting the experiment, participants were given a detailed information sheet with instructions for completing the trials.

All statistical analyses were performed in RStudio 1.2.5019 and comprised generalized linear mixed models as for the previous experiment. Package `bmp` was used to read Windows Bitmap images (Jefferis 2017). Participant and image were included as random effects. The response variables were response time (which included all data, regardless of whether the participant hit or missed the target) and proportion of trials where the target was missed.

2.4.2 Results

After initially testing a full model with all terms and interactions, the final minimum adequate model for proportion of misses only included the fixed effects of cloud cover and detection difficulty (cloud: $LRT_1 = 4.6$, $P = 0.032$; difficulty: $LRT_2 = 79.1$, $P < 0.001$). The test statistic, degrees of freedom and p-value for each sequentially removed term are presented in table 2.2.

Table 2.2. Test statistic, degrees of freedom and P-value for each term sequentially dropped from the model for the proportion of misses in the detection experiment with real video frames.

Term	χ^2	D.f.	P
Cloud:position:difficulty	5.7	2	0.059
Cloud:position	-0.0078	1	1.000
Cloud:difficulty	0.42	2	0.809
Position:difficulty	2.7	2	0.258
Position	1.5	1	0.221

The proportion of misses increased significantly when the target was hard to detect or not visible, compared to targets that were easy to detect (note that a miss is classed as not clicking in the red square for an image where the target was not visible) (easy-hard: $z = 5.0$, $P < 0.001$; easy-not visible: $z = 6.6$, $P < 0.001$; hard-not visible: $z = 3.0$, $P = 0.007$; fig. 2.6). The proportion of misses was greater when it was sunny compared to when it was cloudy ($z = 2.2$, $P = 0.031$; fig. 2.6).

After initially testing a full model with all terms and interactions, the final minimum adequate model for response time included the fixed effects cloud cover, target position, and the two-way interactions of cloud cover and difficulty, and target position and difficulty (cloud:difficulty: $LRT_2 = 6.0$, $P = 0.050$; position:difficulty: $LRT_2 = 7.6$, $P = 0.023$). The test statistic, degrees of freedom and p-value for each sequentially removed term are presented in table 2.3.

Table 2.3. Test statistic, degrees of freedom and P-value for each term sequentially dropped from the model for response time in the detection experiment with real video frames.

Term	χ^2	D.f.	P
Cloud:position:difficulty	0.4	2	0.801
Cloud:position	0.5	1	0.494

There were no significant effects of cloud cover or target position on participant response time for images where the target detection difficulty was classed as easy or hard. When the target was not visible, participant response time was longer when it was cloudy compared with sunny ($LRT_1 = 8.9$, $P = 0.003$; fig. 2.7).

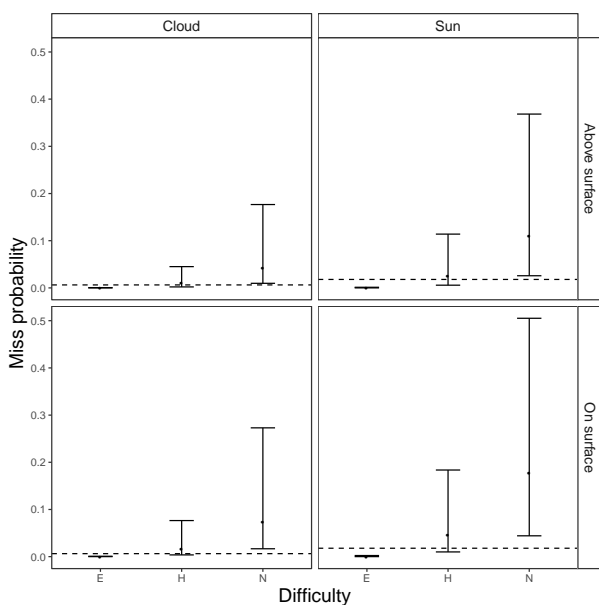


Figure 2.7. Mean miss probability and 95% confidence intervals across different levels of cloud cover, target position and detection difficulty (E: easy, H: hard, N: not visible). Dotted lines show mean miss probability across the three target detection difficulty categories. Means and confidence intervals are based on the fitted models.

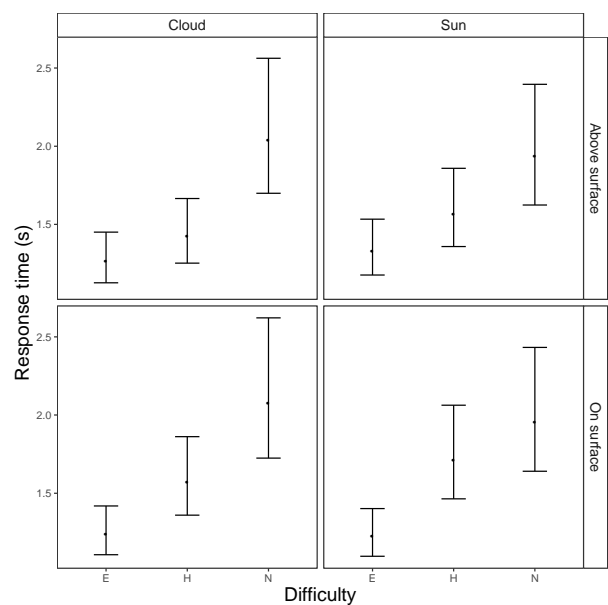


Figure 2.6. Mean response time and 95% confidence intervals across different levels of cloud cover, target position and detection difficulty (E: easy, H: hard, N: not visible). Means and confidence intervals are based on the fitted models.

3 Discussion

Analysis of the videos taken in the field, whether using the criterion of a target-sky contrast below 5% or of complete undetectability, showed that targets were hardest to detect when it was windy and sunny. Both wind speed and whether the illumination was direct or diffuse were expected to have an effect on the detectability of targets to some extent. It was not surprising that in windy conditions the target was generally harder to detect, because the above water image is distorted with increased surface rippling, in accordance with Snell's Law (Johnsen 2012). However, it was not wholly expected that under direct illumination resulting from cloudless skies, the target would be more difficult to detect. One might have intuitively assumed that a white target would be less conspicuous against cloudy skies, given both would appear white or grey from below. Given that no back-lit object can be as bright as its background (Penacchio *et al.* 2015b), it was also surprising that in 23% of the frames included in the analysis, the target was undetectable, both by using luminance-based surface plots in ImageJ software, and through human observation. Of the 128 frames where the target was undetectable, 97 frames (76%) were from videos recorded under sunny conditions. When it was sunny and windy, >90% of frames had targets with <5% visibility, regardless of whether the video was recorded in a freshwater or marine environment. Furthermore, in the detection experiment with real video frames, participants were less accurate at detecting targets when it was sunny compared with cloudy.

The results of Experiment 2 (detection in a simulated pelagic environment, section 2.3) echo the conclusions drawn from the other experiments. When the target was at its lowest simulated height, participants took longer to respond to cloud categories 0 (clear) and 1 (less cloud) compared with 2 and 3 (more cloud). Similarly, when the target was at its middle simulated distance, cloud cover interacted with wave amplitude, with participants tending to take longer to detect targets under reduced cloud cover. When the target was at its highest simulated distance, participants' response time decreased significantly between cloud levels 0 and 1 and 1 and 2. The effect of wave amplitude on participant response time was less clear. When the target

was at its highest simulated distance, response time was actually significantly faster for high wave amplitude compared with a still water surface, although the effect size for this factor was small.

These results appear to contradict the findings of Penacchio *et al.* (2015b), who used computational modelling to elucidate the distinction between countershading for background matching and for obliteration of three-dimensional shape (SSC), and to determine the optimal pattern of countershading for SSC. They argued that, since the reflectance of a surface cannot exceed 1, background matching cannot be fulfilled for downward facing surfaces, such as the ventral surfaces of birds or fish, because these regions of the body are unlikely to receive much light when the animal is orientated naturally. Even in cases where a large amount of reflected or scattered light is incident on an animal's ventral surface, the radiance of the background (sky) will still be orders of magnitude greater than the outgoing radiance of the shaded ventral surfaces of the animal's body. Penacchio *et al.* (2015b) presented this as a logical counterargument to the theory, largely accepted without much in the way of rigorous testing, that pelagic fish and seabirds are countershaded to match the background from different viewing angles (Craik 1944a). However, the assertion that a white, maximally reflective object viewed against the sky cannot ever be completely undetectable does not take into account the potential effects of environmental conditions on the visibility of objects through the air-water boundary. Direct sunlight causes glare, making it difficult to see objects in the same field of view due to a large ratio of luminance between the object and the glare source. Furthermore, the agitating effect of wind on the water surface creates additional visual noise in the background which would be predicted to make the target harder to detect. Snell's window is known to distort and eventually completely disintegrate with increased wave amplitude. Waves cause the angle of the water surface to deviate from horizontal, thereby altering the angle of incidence and hence the angle of refraction of light passing through the media boundary (Johnsen 2012).

That under sunny and windy conditions, white objects above and resting on the water surface may be completely undetectable from below raises a number of key questions that warrant further investigation. Firstly, do prey recognise these conditions as

circumstances where the risk of predation is significantly increased? Oliva *et al.* (2007) showed that evasive responses to predatory cues (looming stimuli) in the crab *Chasmagnathus granulatus* are controlled by looming-sensitive neurons, and that the increase of the crabs' running speed followed the increment in neuronal firing rate, which in turn closely corresponded to the dynamics of the expanding predatory stimulus. If the escape response in crabs is innate, then one might hypothesise that they do not recognise increased risk resulting from sunny conditions in the absence of a predatory cue. This poses an additional question of whether avian predators exploit these conditions to increase foraging success when hunting aquatic prey.

On the other hand, avian prey have been shown to both recognise conditions of increased predation risk and respond by increasing anti-predator behaviour. Beauchamp (2017) studied semipalmated sandpipers *Calidris pusilla*, which are preyed upon by peregrine falcons, *Falco peregrinus*. He observed sandpipers foraging on mudflats as the tide receded at different times during the day, noting the density of individuals in 6 m² plots, the number of pecks to the substrate, the occurrence of successful capture and the time taken to cross the plot during a focal observation. He found that sandpiper density decreased to a greater extent as the sun lowered in the sky on sunny days when the sun glared compared to when the sun was obscured by clouds. The rate of pecking decreased with time of day, and this pattern was more pronounced when it was sunny compared to cloudy. Furthermore, the proportion of successful pecks decreased with time of day when it was sunny, but not when it was cloudy. Overall, vigilance and antipredator behaviours were more pronounced in sandpipers when the sun glared.

Returning to aquatic prey, another question which presents itself is: in the absence of luminance-based cues to predator approach, do prey rely on other sources of information such as polarisation cues? We know that four fish species (*Carassius auratus*, *Danio rerio*, *Chromis viridis*, *Pomacentrus amboinensis*) do not respond to looming predator stimuli presented in polarisation contrast, whereas three cephalopod species (*Sepia plangon*, *Sepioloidea lineolata*, *Sepioteuthis lessoniana*) consistently responded to the same polarisation stimulus with a change in body pattern and texture, and in some cases a sudden body movement (Pignatelli *et al.* 2011). How *et al.* (2012)

found that fiddler crabs *Afruca vomeris* only responded to polarisation-based looming stimuli in 56% of trials and responded to polarisation stimuli later than they did to luminance-based stimuli. Later work on polarisation vision in fiddler crabs revealed that *Afruca tangeri* process polarisation and intensity information independently and in parallel when presented with looming predatory stimuli (Smithers *et al.* 2019). Fiddler crabs responded strongly to both intensity and polarisation stimuli, with the response probability being greater both when the target was darker than, and less polarised than, the background. When polarisation and intensity information were combined into the same stimulus, the crabs were only as likely to respond as they were to the most contrasting channel alone. That these fiddler crabs utilise two alternative non-conflicting sources of visual information means that the chance of a predatory threat being detected is both higher and more consistent across environmental conditions (Smithers *et al.* 2019). Smithers *et al.* (2019) pointed out that polarisation information is not available against a cloudy sky, whereas my experiments highlight that intensity information is not always available when it is sunny. Therefore *A. tangeri* could use different visual information for detection of predatory threats depending on the prevailing conditions and the information that is consequentially available. Different groups of aquatic prey respond to polarisation-based predator cues to varying degrees. A question that arises from this is whether seabirds experience increased capture success of prey which do not respond to polarisation stimuli, compared to those that do, when the luminance cue is obscured by the sun's glare.

Another aspect of vision which would be beneficial to investigate in future is how the visual acuity of prey affects detection of avian predators. The focus of the detection experiments (sections 2.2 and 2.3) was aimed towards investigating the effects of environmental conditions and verifying the results of the field experiment. However, it would be interesting to perform a similar detection experiment to the ones herein, but with stimuli adjusted to match the visual acuity of typical prey species. This would be best achieved with real video clips of moving targets, or even clips of real foraging seabirds, taken from an underwater perspective. The frames could then be blurred and used in a detection experiment. It seems obvious that blurring stimuli to match the

visual acuity of prey species would simply make targets harder to detect at greater distances. However, testing the effects of environmental conditions on target detectability when the image is adjusted to the appropriate acuity would nonetheless be a useful addition to the results presented here. One issue that arises in modelling the visual acuity of seabird prey is the sheer variety of prey that gulls and many other seabirds take. Gulls are opportunistic scavengers, and exploit a variety of food sources including terrestrial, marine and freshwater invertebrates, fish, and small terrestrial vertebrates such as frogs, reptiles and rodents, all of which have different visual systems.

Epipelagic fish tend to congregate around floating objects, including flotsam, rafts, floating seaweed, jellyfishes, whale corpses and parts of trees (Castro *et al.* 2001). This could be for a number of reasons, including protection from predators, enhanced food availability or as a meeting point with conspecifics (Castro *et al.* 2001). Being so close to the surface when aggregating around floating objects leaves epipelagic fish at risk of predation by seabirds. The results contained in this thesis are applicable to situations where prey are within a few metres of the water surface and are therefore more vulnerable to predation by seabirds. It would be interesting to investigate if pelagic fish are still attracted to floating objects to the same extent under conditions of increased predation risk, such as under direct sunlight. A trade-off might occur for epipelagic fish between increased predation risk from avian predators, but potentially increased food availability and protection from aquatic predators when aggregating around floating objects, compared with reduced predation from avian predators but increased predations risk from aquatic predators and other costs associated with open ocean.

Burger (1988) found that, except for picking up items from the ground on land, the most common feeding method used by gulls was surface dipping (dipping the head below the water to catch food), followed by 'jump plunge', where an individual flies less than 1 m into the air, from a starting position floating on the surface, before plunging into the water to catch prey. Gulls tend to forage in this way when I have observed them, predominantly swimming on the water surface and occasionally plunging to catch more agile prey. This close proximity between predator and prey suggests that

after the initial approach, the presence of the predator is obvious to the prey through auditory and vibrational cues if not visual, and that concealment is therefore less important. This could be because when feeding in groups, individual gulls consume more fish than when foraging alone, perhaps owing to the aggregation of prey being attacked from all sides (Götmark *et al.* 1986). One might even argue that visual concealment is not even important for sea birds during the initial approach to the prey, since the prey's visual acuity is likely to be so poor that whatever the predator's coloration, it would not be detected until it was on, or just above the water surface. Still, incremental decreases in the time the prey has to take evasive action after detecting the approaching predator might be the difference between successful or failed capture for the predator. Furthermore, white seabirds attacking an aggregation of epipelagic fish may be harder to detect than black ones in terms of trajectory, speed of approach, and other information needed by the prey to evade capture, especially when combined with the confusing effect of being attacked from many angles by many individuals.

One factor that was not directly investigated, but which is likely to be important for visibility between avian predators and aquatic prey, is water turbidity. One of the main differences between the two types of data collection sites (freshwater or marine) was the turbidity of the water. The depth of the water, substrate, vegetation and associated shade also varied between the marine and freshwater sites. Overall, the turbidity of the water was greater at the marine site, however there was also lots of variation in turbidity within this site. This is likely to be affected by recent storms or heavy rain. Furthermore, the marine site was dredged between different data collection visits, and I noticed a decrease in water turbidity after this occurred. It is possible that turbidity of the water is recognised by predators and prey, and could affect their behaviour. For example, prey may venture closer to the water surface in turbid conditions. Fathead minnows (*Pimephales promelas*) have been shown to relax anti-predator behaviour in turbid water compared to clear, presumably because the lack of visual cues to the presence of predators reduces the perceived predation risk (Abrahams & Kattenfeld 1997). Turbidity of the water might also affect choice of foraging method or site in seabirds, as it may be energetically costly to forage in waters where the location of

prey is masked by turbidity. On the other hand, if turbidity is the result of planktonic aggregations which in turn can support large populations of fish, then some seabirds may exploit turbid waters as profitable foraging grounds (Henkel 2006; Urbanski *et al.* 2017). Whether and how avian predators respond to frequent local temporal changes in water turbidity, resulting from storms for example, would be a good line of further investigation.

Different coloured models were not tested in the field experiment, as basic reasoning and previous work (e.g. Phillips 1962; Cowan 1972; Götmark 1987) dictate that white is the most cryptic coloration for ventral surfaces of seabirds. The results of the detection experiments in a simulated pelagic environment (section 2.3) indicate that, at least for human participants, and within the simulation, the coloration of the target has no effect on detection. In nature, this may not be the case; however, these results suggest that coloration may not be as important for camouflage as one might assume in a pelagic predator–prey interaction. As previously discussed, white ventral coloration in seabirds may have resulted from multiple non-exclusive selection pressures. The most likely explanation to my mind is that although white coloration is optimal for aggressive camouflage, it also functions to signal the discovery of ephemeral food sources to conspecifics (Armstrong 1946; 1971; Simmons 1972; Andersson *et al.* 1981; Götmark 1987), as it has been shown that *C. ridibundus* have increased foraging success when feeding in flocks, including the individual who first finds the food source (Götmark *et al.* 1986). The social signalling hypothesis for white plumage requires more robust testing using modern methodologies. Firstly, it must be established whether white is better than black, or any other coloration, for visibility across long distances in pelagic environments (Phillips 1962; Simmons 1972). The opposite was proposed by Abbott Thayer for naval camouflage at the start of the 20th century (Thayer 1909) but, apart from the ‘dazzle’ painting used to misdirect U-boat attacks in WWI, ‘battleship grey’ has always been the preferred marine camouflage colour (Williams 2001). The visibility of different colours could involve analysis of images of different coloured models in a pelagic environment, similar to the present study, but images would have to be taken above water, and at a range of distances. Luminance measurements of these images could then be taken to establish if white

coloration maximises luminance contrast against an ocean background. If white models have the greatest contrast against an ocean background, then this raises the possibility that predominantly white plumage in seabirds functions to both maximise and minimise conspicuousness from different viewing angles, and to different viewers.

This thesis has, for the most part, concerned the white undersides of gulls, but what about their dorsal sides? The classic explanation is that the grey or black mantle and upper wings of many gulls could be construed to provide background matching camouflage against the ocean, as originally described by Thayer (1909). However, Thayer (1909) also points out that adult gulls suffer little to no predation from other birds. Skuas might take juvenile gulls that are vulnerable, but they are coloured a mottled brown-grey all over in most of the Laridae, presumably to enhance crypsis against the coastal backgrounds where they are most commonly encountered. So why, then, are adults coloured grey or black on their dorsal surfaces? Perhaps their coloration does provide background matching camouflage, but against cliffs where many seabirds nest, rather than the ocean. Nesting and rearing chicks presumably increases vulnerability of seabirds to predators, and there are likely to be many more potential terrestrial predators of gulls and their eggs or chicks, than species which pose a threat to gulls when airborne. This is another area with large scope for data collection. To my knowledge, there has been no formal investigation into how well countershaded seabirds are concealed against the ocean from above, or against cliffs and other coastal nesting sites. Alternatively, there is also the possibility that countershading in seabirds is simply an adaptation that affords protection from UV-radiation-induced tissue damage, since the dorsum is the part of the body which receives the most UV radiation. In this scenario, the white undersides could still be for camouflage with respect to prey, but could also be simply so because pigmentation is energetically costly and is unnecessary for parts of the animal's body that receive little sunlight. Countershading has been shown to function as UV protection in another pelagic organism, the hammerhead shark *Sphyrna lewini* (Lowe & Goodman-Lowe 1996). Finally, there is also evidence to suggest that countershading coloration could increase the endurance of migratory seabirds. Black top sides and white undersides of wings generated less skin friction drag than other black-white wing coloration

configurations when the thermal properties of different wing colour configurations were modelled for migratory seabirds in flight over water (Hassanalian *et al.* 2018).

Having discussed detection of above-water targets from below, I will now turn to recognition of the target. Most of the literature regarding white plumage as camouflage in seabirds focusses on detection and not identification of the object. A clear problem for aquatic prey that are able to detect avian predators moving overhead is the cost of diving for safety if the object in fact poses no predatory threat. Non-threatening objects might include boats, aircraft, debris, floating seaweed, and non-predatory birds. How do epipelagic fish recognise predators and react according to the level of risk? An obvious answer which would rule out a number of overhead objects is size, and another might be speed of movement. Some objects such as plastic debris could be misidentified by prey as a predator, especially in conditions where the waves are high and frequent, as the shape of objects above and resting on the water surface is heavily distorted due to refraction (Johnsen 2012). I found that in many of the video clips collected, the image of the spherical target was heavily distorted when the water was not still. One might expect that marine prey species experience a high frequency of false positives (i.e. diving to safety in response to a non-threatening object), as the costs of doing so are heavily outweighed by the cost of misidentifying a real predator. Therefore, a future extension of my work could include tests of the ability to recognise different objects through the air-water interface under different weather conditions.

There were a number of limitations associated with the methodology of my experiments. Improvements include collecting more video clip data from a wider range of sites, under a wider range of environmental conditions and at different times of day. The times of day I collected data tended to be very similar, either around 10-11 am, or just after noon. I occasionally managed to collect data in the late afternoon, but not with enough replicates under different weather conditions to permit rigorous analysis. It would have been interesting to investigate the effect of time of day, not least because of how it might affect the visibility of targets, and also because of how it might increase glare on sunny days, as reported by Beauchamp (2017). One way to capture a greater quantity of data, under a wider and balanced range of sites, conditions and times of day would be to use permanently mounted underwater cameras where seabirds

forage, positioned for long periods of time collecting continuous data. Since seabirds feed on transient food sources, it would probably be advisable to 'bait' these data collection sites to attract foraging gulls to the underwater camera. This could possibly be achieved manually whereby food is released into the water around the camera by experimenters. Similarly, my data collection was limited to sites where I could extend the camera and its mounting pole into the water safely from the shore, and this prevented me from collecting data at some of the locations I visited. Furthermore, some video clips were taken too close to the edge of the water body, so that above-water objects, such as the bank or concrete landing, were in the background behind the target. These clips had to be discarded.

Overall, the results of these experiments highlight that, under certain environmental conditions, above-water white objects are completely undetectable, not just less conspicuous than darker ones when viewed from underwater. The glare from direct sunlight appears to cause undetectability of above water objects from below the surface. Increased wind speed also contributes to low visibility of above-water objects, likely due to increased wave amplitude and frequency and the implications for refraction at the water surface. But can these results be applied more broadly to other countershaded pelagic species, for example cetaceans and elasmobranchs? The way in which Snell's window is distorted by wave action does not apply to concealment of these animals, as it does to an aerial predator; however increased visual noise in the background could have an effect on the salience of these organisms viewed from below. Do the same conditions as those reported herein, such as direct sunlight, reduce detectability of pelagic predators like cetaceans and sharks when viewed from below? These results suggest they do; however, this question certainly warrants further data collection of targets, such as the ones used in this study, submerged below the water surface.

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