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Camouflage in a dynamic world

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Abstract

This thesis concerns the effects of variable illumination on prey detection by predators. The environment plays a significant role in shaping the visibility of signals both to and from an organism. For example, against a static background movement is highly conspicuous, which favours staying still to optimise camouflage. However, backgrounds can also be highly dynamic, such as areas with wind-blown foliage or frequent changes in illumination. These dynamic features introduce visual noise which could serve to mask motion signals. Two forms of illumination change – the net-like underwater patterns known as caustics, and dappled forest light - are of particular interest because of their prevalence in the natural world. An experimental approach was taken: the gaming software, Unreal Engine 4, was used to simulate scenes containing each illuminant, and used to create interactive foraging tasks. Using model organisms from different taxa and environments – humans, birds and fish – I investigated the extent to which dynamic lighting influenced prey detection. When asked to capture moving prey items within the simulated terrestrial and aquatic scenes, human participants were significantly slower and more error-prone when viewing scenes with dynamic illumination. The presence of dynamic water caustics also significantly increased response times when searching for patterned prey items, particularly those with low contrast. In behavioural experiments with newly hatched domestic fowl chicks (*Gallus gallus domesticus*) and a wild-caught reef fish, the Picasso triggerfish (*Rhinecanthus aculeatus*, family: Balistidae), similar conclusions were drawn. Dynamic dapple, however produced, increased a chick's latency to both fixate and peck the prey, while the presence of dynamic water caustics was shown to negatively affect prey detection and attack latency by triggerfish, an effect that should be most prominent in shallow water. Overall, I have identified a widespread factor lessening the saliency of motion, a finding that is likely to shape many aspects of predator-prey interactions.

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Author's declaration

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

SIGNED:  DATE: 21/11/2019

Published work and collaborations

Three of the chapters contained in this thesis appear in published form elsewhere, and one is submitted for publication. In all cases, these papers/chapters were authored by me, with no more input from supervisors than would have been provided in any normal Ph.D. For the work on triggerfish in Chapter 7, Prof. Justin Marshall and Dr. Karen Cheney of the University of Queensland provided research facilities on Lizard Island (Great Barrier Reef) and invaluable advice on working with triggerfish.

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Chapter 7: Matchette, S. R., Cuthill, I. C., Cheney, K. L., Marshall, N. J., Scott-Samuel, N. E. Underwater caustics disrupts prey detection by a reef fish. (under review at Proceedings of the Royal Society B: Biological Sciences)

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Chapter 1.

1.1 Camouflage, signal and noise

Concealing colouration (Thayer, 1896; 1909), later termed camouflage, serves as a very effective and widely deployed, anti-predation adaptation (Cott, 1940; Ruxton, Allen, Sherratt, & Speed, 2018; Stevens & Merilaita, 2009). Camouflage can be attained through multiple mechanisms relating, variously, to the physical pattern, the stage in the attack sequence a defence operates, or the perceptual/cognitive mechanism the camouflage interferes with (Cuthill, 2019; Endler, 1981; Ruxton et al., 2018; Skelhorn & Rowe, 2016; Stevens & Merilaita, 2009). A particularly useful framework for my thesis, however, characterises camouflage in terms of minimisation of the signal-to-noise ratio (henceforth, 'SNR'; Merilaita, Scott-Samuel, & Cuthill, 2017). Here, 'signal' may refer to the organism and its characteristics (i.e. identity, edibility, likelihood of capture .etc.) or lower-level features (i.e. surface luminance, texture, edges) that aid in detection and subsequent identification (Merilaita et al., 2017). Noise constitutes all factors that interfere with the extraction and identification of a given signal (Merilaita et al., 2017).

The emphasis for most camouflage strategies is on the use of colour-based visual elements to address signal or noise. There are two broad methods by which the SNR can be reduced and, in doing so, increase the likelihood of concealment: minimise the signal in question, and/or increase the surrounding noise (Merilaita et al., 2017). For example, background matching minimises the disparity between an object's surface and that of the background in terms of luminance, colour or texture (Endler, 1984; Merilaita & Stevens, 2011), while self-shadow concealment, through countershading, minimises the cues associated with depth and shape (Allen, Baddeley, Cuthill, & Scott-Samuel, 2012; Cuthill et al., 2016; Penacchio, Harris, & Lovell, 2017; Penacchio, Lovell, Cuthill, Ruxton, & Harris, 2015; Rowland, 2009). Conversely, disruptive colouration both minimises edge signals from the body outline (Cuthill et al., 2005; Troscianko, Skelhorn, & Stevens, 2017) and increases noise by generating false edges away from the true outline (Egan, Sharman, Scott-Brown, & Lovell, 2016; Stevens & Cuthill, 2006; Stevens, Winney, Cantor, & Graham, 2009), a combination which disrupts feature binding (Espinosa & Cuthill, 2014). Similarly, mimicry and masquerade minimise recognition of true identity by promoting noisy false identity cues that are associated with irrelevance (e.g. a dead twig; Skelhorn, Rowland, & Ruxton, 2010; Skelhorn, Rowland, Speed, & Ruxton, 2010) or unprofitability (e.g. a toxic species; Mappes, Marples, & Endler, 2005; Skelhorn, Halpin, & Rowe, 2016).

Crucially, the principal components of the SNR framework (signal and noise) remain unchanged for motion-based signals (e.g. predator or prey movement): provided a motion signal falls within the distribution of background motion noise, concealment to some extent would be achieved. This is pertinent because motion has long been considered the enemy of camouflage: moving features pop-out of from the scene (Brunyé, Martis, Kirejczyk, & Rock, 2019; Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Ioannou & Krause, 2009) and can aid in object identification (Mély, Kim, McGill, Guo, & Serre, 2016). Indeed, as a result, 'freezing' behaviour is a common trait among cryptic prey when danger is sensed (Caro, 2005). In the context of motion, the SNR can be similarly reduced as in other camouflage strategies (i.e. minimise signal or increase noise), but with the immediate environment playing a pivotal role.

1.2 A dynamic world

Motion is ubiquitous in natural environments, varying in source, form and relevance. Animals engage in a number of tasks in which using motion cues is pertinent and thus have a series of neural mechanisms to facilitate this. These range from simple object tracking to the rapid detection of a looming stimulus (that might represent approaching threat or the risk of a collision), as well as flow-field analysis from self-motion to guide movement (Frost, 2010). Animals can also use motion parallax to judge depths (Frost, 2010). The dynamism of features in an environment can loosely be classified by their unpredictability at a given spatial scale; some features, typically in far sight, will be considered to be moving randomly, while others consist of coherent and directed motion. The detection of relevant moving objects therefore involves more than the detection of non-random motion of features and the subsequent perceptual binding into 'a potential target of interest' (dynamic signal), but also the discrimination of that target from irrelevant and non-random motion of surrounding objects (dynamic noise).

Non-random dynamic noise most commonly arises from abiotic sources, namely the motion of physical objects within an environment: for example, the motion of vegetation, debris, substrate or the water's surface by wind, rainfall, water currents or tidally. Windblown vegetation is common and highly variable, governed by several environmental conditions and the vegetative composition (Peters, 2013), and is known to influence motion-based visual signalling (Ord, Peters, Clucas, & Stamps, 2007; Ord & Stamps, 2008; Peters, Hemmi, & Zeil, 2007) and motion masquerade (Bian, Elgar, & Peters, 2016; Fleishman,

1985, 1986). Water surface disruption also affects vision and detection, particularly predator-prey interactions that occur across two media (i.e. terrestrial predator and aquatic prey, or vice versa). For example, aquatic organisms that look through a wavy water body from below will see a complex Snell's window [1] (Johnsen, 2012; Molkov & Dolin, 2019) with poorly defined edges, that becomes more visually noisy with further wave motion (Lynch, 2015). Similarly, looking through a water surface from above can be made difficult by sunlight: the reflection of sun and sky from a water surface is fragmented into glitter points (glare) by the facets of waves (Lythgoe, 1979), an effect that is accentuated when the sun is lower in the sky ('disability glare'; Koch, 1989; Martin & Katzir, 2000). Indeed, white sharks, *Carcharodon carcharias*, may utilise the impact of disability glare to remain undetected when approaching prey at the surface (Huveneers et al., 2015). Moreover, the dynamism of the glare and reflectance is directly correlated with the motion of the water surface (Lythgoe, 1979). Rainfall can also introduce dynamic noise, either via buffeting physical structures (e.g. water surface or vegetation) or multidirectional splash during heavy rainfall. That said, rainfall also has consequences for other aspects of vision, as well as olfactory and tactile cues by predators, making conventional foraging during these periods less likely (Czaja, Kanonik, & Burke, 2018).

Figure 1.1 Examples of water caustics (left) and dappled light (right). The visual features of water caustics comprise high-intensity circular light boundaries ('caustic boundaries') that enclose regions of low-intensity light ('caustic shade'). Photos © S. Matchette.

[1] Snell's window is the phenomenon whereby, for organisms looking up through the water surface, the entire hemisphere of sky is compressed into a cone of about 96° across due to the refraction light by the water surface. Beyond this angle from the zenith, viewers lose the ability to see what's above the water surface, instead seeing a mirrorlike internal reflection.

In bright conditions, a common biproduct of dynamic physical features within the light-path is a variation in local illumination (Endler, 1993; Endler & Théry, 1996). Varying illumination also introduces dynamic noise, which varies in time and space, and is prevalent in both the terrestrial (e.g. dappled light) and aquatic (e.g. water caustics) domain (Figure 1.1). Light becomes dappled by passing through a latticework of vegetation, creating a mosaic pattern upon the substrate (Bian, Chandler, Pinilla, & Peters, 2019). Water caustics are now understood, using catastrophe theory, as physical realisations of Lagrangian singularities (Joets, 2012) triggered in sequence (Berry & Upstill, 1980; Nye, 2018). They form when descending light rays are refracted and converged by the curvature of a water surface (Lythgoe, 1979; McFarland & Loew, 1983; Schenck, 1957; Swirski, Schechner, Herzberg, & Negahdaripour, 2009). In this way, water surface waves act as dynamic lenses (Loew & McFarland, 1990), focusing and defocusing light that penetrates the water (Figure 1.2). The depth at which the converged light focuses (focal depth) is dependent upon the complexity of the surface wave (both in amplitude and wavelength) and, because the curvature of water is not even, will occur over a local depth range rather than a single focal point (Loew & McFarland, 1990).

Water caustics and dappled light are visible only when projected upon a reflective surface, such as objects, a suspension of fine particles or the substrate (McFarland & Loew, 1983). When projected upon a three-dimensional object of an appropriate size, the object's orientation determines the form of water caustics: projections onto surfaces parallel to the water surface comprise a mosaic of high-intensity light rings (hereafter, 'caustic boundaries') that enclose regions of low-intensity light (hereafter, 'caustic shade'; Figure 1.1), while perpendicular surfaces elongate the reticulate mosaic into linear bands (McFarland & Loew, 1983; Partridge, 1990; Figure 1.3). Water caustics projected upon smaller objects will lose apparent form and instead simply appear as a luminance flash (McFarland & Loew, 1983). A similar outcome will occur for dappled light; while there is no strict template for patch shape when projected upon parallel surfaces, elongation of light will occur when projected upon vertical objects, such as tree trunks.

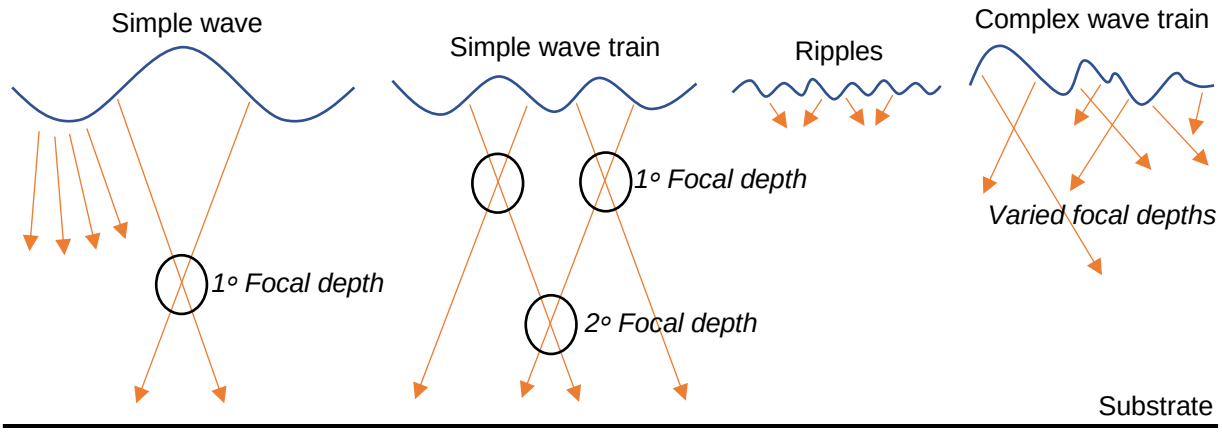

Figure 1.2 An illustration adapted from Loew and McFarland (1990) *displaying how surface waves (blue lines) act as lenses in the creation of water caustic networks. The depth at which refracted light rays (orange arrows) are re-focussed (focal depth) depends on the type of surface wave through which they pass; for example, simple wave trains have longer wavelengths and therefore focus light at broad depths, while the focal depths of ripples are comparably short. Because surface waves are not of even curvature, focal depths will tend to occur over a local range of depths (represented by the black ellipses) rather than single focal points. Within the region of focus, the intensity of light (a product of all contributing light rays) is greater than the average light intensity of single rays, which provides the basis to regions of caustic boundary and caustics shade. Multiple focal depths will occur in conjunction with the number of neighbouring waves (with primary focal depths, secondary focal depths etc.), while the complexity of such will be governed by the complexity of the surface waves (e.g. complex wave train). In terms of visual form and structure, there is an intimate relationship between surface wave complexity, the subsequent focal depths and the substrate depth, at which point the light rays become visible.*

Further diversity in form is a function of the forces acting on the given physical feature (vegetation or water surface). Water depth and canopy height play a major role in the diversity and form of water caustics (McFarland & Loew, 1983) and dappled light (Endler, 1993) respectively, with both typically exhibiting a loss in contrast with increasing depth and height. However, in terms of visual form and structure of water caustics, there is an intimate relationship between surface wave complexity and the relative disparity between the subsequent focal depths and the substrate depth (Loew & McFarland, 1990; Figure 1.3). For example, caustic boundaries will appear bright and concentrated if the substrate depth falls within the focal depth range, while a disparity here leads to caustic boundaries appearing

divided and diffuse. However, this will change temporally as the structure and complexity of the surface wave changes, chiefly due to the strength and direction of wind or current (McFarland & Loew, 1983). The intensity of flicker is most acute in shallow depths, typically within 5m (Lythgoe, 1979), but if conditions are appropriate can be present up to 10m and beyond, though the spatial and temporal frequency will be far lower (Loew & McFarland, 1990). The form of dappled light is similarly governed by the strength and direction of wind (in turn governed by topography and location; Hannah, Paluikof, & Quine, 1995), but also by the composition and geometry of vegetation present, with different plant species or polymorphs of the same species moving differently in response to wind (Peters, 2013; Peters, Hemmi, & Zeil, 2008). In this way, microhabitats within both domains represent distinct 'image motion environments' (Peters, 2013; Peters et al., 2008). Both water caustics and dappled light are also dependent upon the altitude and angle of the sun (McFarland & Loew, 1983; Théry, 2001).Though both forms of illumination are common in their given domains, they differ in their scope: water caustics are more global than dappled light, which is often localised at the margins of shade (Théry, 2001).

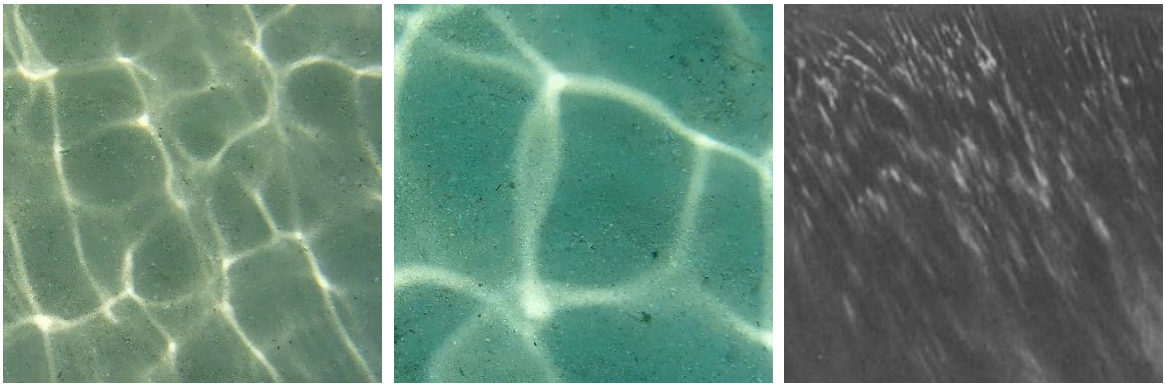

Figure 1.3 The form of water caustics is very diverse, and dependent on several factors. For example, the orientation of the substrate governs whether the projections represent a traditional mosaic (if the substrate is parallel; left and centre; Photos © S. Matchette) or elongated bands (if the substrate is perpendicular; right, reproduced from McFarland & Loew (1983)). Water depth also typically governs the scale and contrast of the caustic boundaries; for example, water caustics projected at 0.5 m depth (left) are finer scale than those at 2 m (centre), while a loss of contrast is likely if there is major disparity between water depth and focal depth.

1.3 Organisms and their dynamic world

The presence of this dynamic illumination (or 'illuminants') within habitats has been closely linked to some aspects of concealment; for example, certain markings of pelagic fish, such as vertical barring,

seem to match the elongate form of water caustics for camouflage (McFarland & Loew, 1983), while some felid coats appear to match the patchiness of dappled light in vegetative habitats (Allen et al., 2012; Caro, 2013; Ortolani & Caro, 1996). The very existence of water caustic flicker could also have played a significant role in the initial evolution of colour vision with, in the presence of caustics, the ratio of different wavelengths being a more stable cue to an object's boundary than luminance (Maximov, 2000). Furthermore, many aquatic organisms have a peak contrast sensitivity that could have arisen from spatial and temporal frequency responses that fall within the typical range of water caustic flicker (Loew & McFarland, 1990; McFarland & Loew, 1983; Sabbah, Gray, & Hawryshyn, 2012). This is an adaptation allowing the visual system to function in a time-frame set by caustic flicker, facilitating the detection of reflective objects that are subsequently illuminated in midwater, particularly near the surface where flicker is most acute (Loew & McFarland, 1990; McFarland & Loew, 1983; Sabbah et al., 2012).

Dynamic information within an environment can also arise from biotic sources, such as from the movement of other organisms, particularly those that move collectively within a habitat. Here, the social ecology of such organisms governs the distribution of velocities presented; for example, European starlings, *Sturnis vulgaris,* form highly coordinated flocks (Ballerini et al., 2008; Hogan, Hildenbrandt, Scott-Samuel, Cuthill, & Hemelrijk, 2017), while a swarm of *Daphnia* would exhibit motion that appears more random (Krasky & Takagi, 2018; Ordemann, Balazsi, & Moss, 2003). When living in groups, the conspecifics that surround an animal constitute a major part of the visual canvas for an onlooker and therefore, in the case of predatory threat, it is important for an individual to fall in step and minimise cues that allow individuation (Hall, Baddeley, Scott-Samuel, Shohet, & Cuthill, 2017; Ioannou, Guttal, & Couzin, 2012; Rodgers, Kimbell, & Morrell, 2013). In this regard, there is also pressure to maintain relative position and distance to others while moving, to minimise individual threat during predatory attacks (Ioannou, Rocque, Herbert-Read, Duffield, & Firth, 2019).

Dynamic noise can also be self-induced: many organisms do not always view natural scenes from a fixed position, rather doing so on the move. When an organism moves, objects within the viewed scene (irrespective of their relevance and motion) will elicit apparent motion across the organism's retina in conjunction with its own motion, termed optic flow (Gibson, 1950). Inconsistencies in optic flow between stationary and moving objects (Gibson, 1950), as well as the continued perception of motion after motion has stopped, provide an extra source of optical information which can be used to break

camouflage, with or without stereopsis (Pan, Bingham, Chen, & Bingham, 2017). Indeed, the success of the active motion camouflage techniques used in hoverfly (Srinivasan & Davey, 1995) and dragonfly flightpaths (Mizutani, Chahl, & Srinivasan, 2003) are due to the ability to mimic the optic flow of the background.

Collectively, this motion – that of background objects, light or other organisms - provides the context within which an animal must conceal itself, whether to avoid detection or recognition by predators, or to capture its own prey.

1.4 Minimising the signal

Background matching in the temporal domain includes the self-motion (either components or as a whole) that falls within the energy distribution of the dynamic background. The swaying of an organism (or 'oscillation') is the most commonly proposed example, exhibited by stick insects (Phasmidae) and lizards of the *Chamaeleo* genus (Gans, 1967) in conjunction with the movement of plants in a light breeze (Bian et al., 2016); though it must be noted that this behaviour also mirrors an individual's need to maintain both contact with the substrate and balance (Kelty-Stephen, 2018; Stevens & Ruxton, 2019). Fleishman (1985) highlighted that the neotropical vine snake *Oxybelis aeneus*, when stalking prey, shows sinusoidal oscillations at the same frequency as the surrounding wind-blown foliage, and consistently initiated such behaviour in response to visual cues of wind-blown vegetation and, on some occasions, to the tactile presence of wind alone. Moreover, Ryerson (2017) identifies three species of colubrid snake that pair head oscillations with a dorsal pattern to achieve the same result. Overall, unequivocal evidence for background motion matching is sparse, with many 'examples' representing something closer to motion masquerade, whereby camouflage is achieved by mimicry of an irrelevant moving object (thus increasing noise by introducing false identity signals) rather than matching the generic background (Endler, 1981; Hall et al., 2017; Ruxton et al., 2018; Skelhorn, Rowland, Speed, et al., 2010). In fact, the reverse problem has attracted more empirical research: how dynamic signals are designed to stand out from generic background motion (Fleishman, 1986; Peters, Clifford, & Evans, 2002; Peters et al., 2007; Peters & Evans, 2003; Ramos & Peters, 2017a, 2017b). That said, the analysis of motion camouflage itself will be made more achievable with the attention received by the latter, both theoretically and computationally (Bian, Chandler, Laird, Pinilla, & Peters, 2018; Bian et al., 2019; Ramos & Peters, 2017c; Woo, Rieucau, & Burke, 2017).

Background matching also encompasses motion that is undetectable against a relatively static background, such as moving slowly or in a saltatory fashion that eliminates a consistent velocity signal. This is pertinent as many organisms, such as primates (Watson & Robson, 1981; Yin et al., 2015), are acutely sensitive to both the presence and direction of motion of even low contrast targets, while the presence of even a small number of features exhibiting coherent motion can be used in identification by humans and other animals (Atsumi, Ide, & Wada, 2018; Sokolov et al., 2018). A commonly considered example is the stalking behaviour of predators such as cats, but this is yet to be quantitatively connected to the motion detection thresholds of the relevant prey, despite interest from the reverse perspective i.e. the visual sensitivity of grazing herbivores to lions at a given distance (Melin, Kline, Hiramatsu, & Caro, 2016). The switch by cuttlefish, famous for rapid colour change (Hanlon & Messenger, 2018), to low contrast patterns when moving (Zylinski, Osorio, & Shohet, 2009) is also consistent with motion signal minimisation: there is a lack of internal contrast that would otherwise trigger a viewer's motion detectors (Umeton, Tarawneh, Fezza, Read, & Rowe, 2019).

As mentioned previously, the tracking flights of hoverflies (Srinivasan & Davey, 1995) and dragonflies (Mizutani et al., 2003) mimic the optical information of the background and, in doing so, represent the best known example of motion signal reduction. When tracking potential mates or chasing off conspecifics, the pursuing insect matches its relative position and speed to that of the target individual such that its projected image on the target's retina is relatively invariant, thus achieving an optic flow that is similar to that created by the background (Mizutani et al., 2003; Srinivasan & Davey, 1995). So effective is this strategy that the possible algorithms at play have, more recently, been applied to the systems controlling missile and ship movement (Colonnier, Ramirez-Martinez, Viollet, & Ruffier, 2019; Gao, Li, & Jing, 2016; Kim, 2019).

When viewing group living organisms, the strongest background motion signals generally come from conspecific organism motion. If these conspecifics have a similar form and motion to the target of interest, such as in fish shoals or bird flocks, then they will act as "distractors". Crucially, both similarity in appearance between target and distractor (Hall et al., 2017, 2013; Hogan, Cuthill, & Scott-Samuel, 2016) and similarity of motion (Hogan, Cuthill, & Scott-Samuel, 2017) impedes individuation and target tracking.

1.5 Increasing the noise

If it is not possible to minimise a motion signal, the alternative for reducing SNR is to introduce visual noise (Merilaita et al., 2017). One solution would be for mobile organisms to seek out environments with high motion noise, such as habitats with dynamic vegetation or illumination, within which to mask their motion signal. Whether motion noise disrupts prey detection at any level, and indeed if this effect would hold for wild animals, is yet to be tested and should become a key area of focus. If true, one would also predict some level of habitat selection: mobile prey should seek safety in environments with moving background elements and/or illumination, while visually oriented predators should hunt preferentially in low-dynamic-noise environments or where the dynamic noise provides only the predator with a sensory advantage (e.g. white sharks and disability glare; Huveneers et al., 2015). Indeed, water caustics could be a vital source of dynamic noise within coral reef 'visual complexity', which Alonso (2015) proposes to explain the prevalence of highly conspicuous and colourful patterning in reef fish. Here, in a 'hyper-visible world', the traditional selection for colour-based camouflage is relaxed; instead, the visual complexity of the reef itself allegedly allows fish colouration to be driven more by sexual selection and aposematism (Alonso, 2015). Furthermore, high-dynamic-noise environments already pose problems to other visually guided behavioural tasks: for example, many lizards can adjust motion-based visual signals, aimed at conspecifics, in the face of noisy conditions (Ord et al., 2007; Ord & Stamps, 2008; Peters et al., 2007).

The motion of animals is typically coherent and directed, and consequently predictable. While irrelevant motion of the environment may provide a temporary blanket of visual noise, there are means by which an organism itself can lessen the coherence and predictability of a motion signal. A long-proposed solution is protean motion: movement that is sufficiently unpredictable so to minimise a predator's ability to anticipate future position or action (Humphries & Driver, 1970; Richardson, Dickinson, Burman, & Pike, 2018; Scott-Samuel, Holmes, Baddeley, & Cuthill, 2015). Although untested, protean movement could even act as a moving equivalent of disruptive colouration, by reducing the viewer's ability to bind features into a single percept (Espinosa & Cuthill, 2014), in this case by coherent motion of the salient visual elements of the target. The coherence of motion can also be broken by punctuated motion, achieved by bouts of movement (regular or irregular) or movement obscured via occlusion by the habitat. In both cases, the viewer is forced to estimate the direction and speed in order to extrapolate

the next position. While extrapolation is achievable, there is systematic error introduced (termed representational momentum) which diminishes the efficacy of final detection (Freyd & Finke, 1984). This error can be exploited further by introducing false cues of direction or speed, via so-called dazzle coloration (Behrens, 1999, 2012; Hogan, Cuthill, et al., 2016, 2017; Hogan, Scott-Samuel, & Cuthill, 2016; Hughes, Magor-Elliott, & Stevens, 2015; Hughes, Troscianko, & Stevens, 2014; Murali & Kodandaramaiah, 2018; Murali, Merilaita, & Kodandaramaiah, 2018; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011; Stevens, Searle, Seymour, Marshall, & Ruxton, 2011; Stevens, Yule, & Ruxton, 2008). Here, the use of typically high contrast, repetitive patterns induces illusory effects which make estimations of speed (Hall et al., 2016; Scott-Samuel et al., 2011) and/or direction (Hughes, Jones, Joshi, & Tolhurst, 2017) difficult. This effect can be accentuated by internal pattern motion in addition to whole-body motion (Hall et al., 2016; Murali, Kumari, & Kodandaramaiah, 2019), much like the 'passing cloud' display of cuttlefish (Hanlon & Messenger, 2018).

As alluded to previously, some organisms can use motion masquerade, whereby irrelevant moving objects are mimicked, to introduce false identity signals (Endler, 1981; Hall et al., 2017; Ruxton et al., 2018; Skelhorn, Rowland, Speed, et al., 2010). For example, the catfish, *Tetranematichthys quadrifilis*, which resembles a dead leaf when static but, when disturbed, drifts "like a waterlogged leaf moving slowly in the water flow, with no apparent movements of its fins (pp. 120)" (Sazima, Nobre Carvalho, Pereira Mendonça, & Zuanon, 2006). Huffard et al. (2005) also identify two species of octopus, *Octopus marginatus* and *Octopus aculeatus,* that adopt a bipedal walk to move quickly along the seafloor while simultaneously mimicking the roll of specific vegetative debris with their other six tentacles. Moreover, there are a few examples documenting the use of dynamic elements to reinforce Batesian mimicry, whereby a palatable organism mimics the aposematic colouration of an unpalatable organism. For example, nestlings of the tropical lowland bird, *Laniocera hypopyrra*, pair specific head movements with their bright orange, hair-like plumage to mimic a local toxic caterpillar (family Megalopygidae; Londoño, García, & Sánchez Martínez, 2015), while some theorise that juvenile zebra sharks, *Stegostoma fasciatum*, use high contrast banding and undulatory swimming movements to mimic highly venomous banded sea snakes (family Elapidae; Dudgeon & White, 2012).

Some organisms also benefit from an ability to change colour, via active and passive means (Duarte, Flores, & Stevens, 2017; Umbers, Fabricant, Gawryszewski, Seago, & Herberstein, 2014). In the case of rapid colour change, the signal will be inconsistent across space and/or time and would therefore

interfere with the detection and binding of relevant features (Duarte et al., 2017; Espinosa & Cuthill, 2014; Murali & Kodandaramaiah, 2018; Murali et al., 2018). For example, dynamic colour change has been shown to reduce the capture success and capture accuracy of isolated moving targets (Murali et al., 2018; Pike, 2015), as well as the detection of targets moving as a group, presumably a consequence of confusion effect enhancement (Murali et al., 2019). Similarly, Kjernsmo *et al.* (2018) demonstrate that iridescence (both diffraction grating and multilayer) can act as an effective means of camouflage by impairing shape recognition by insects. The hue and intensity of the reflected light from an iridescent feature varies with the angle of view and illumination (Barrows & Bartl, 2014; Doucet & Meadows, 2009; Seago, Brady, Vigneron, & Schultz, 2009), hence iridescence should hinder feature binding of motion signals too, though this is yet to be explored further than Pike (2015). Indeed, the inconsistency in illumination that characterises, for example, water caustics and dappled light also introduces inconsistencies to the perceived prey signal while it moves (in time, space, angle of view and perceived hue), and would similarly impair feature binding and detection efficacy.

1.6 The role of attention

As outlined, the detectability of movement within a habitat is underpinned by the relative levels of motion signal and motion noise (Merilaita et al., 2017). As a receiver, it is therefore necessary to filter incoming visual information and selectively focus upon what is relevant (i.e. increase the motion signal), while disregarding what is not (i.e. decrease the motion noise), a process governed by the receiver's attention (Carrasco, 2011). Selective attention to a movement event is a function of several factors: an observer's sensory capacity, the specific context of motion, the pay-offs for responding in that instance, past learning ability and the presence of other visual distractions (Bian et al., 2019). However, attention is a limited resource (Dukas & Kamil, 2001; Simons & Chabris, 1999), and this has important implications for the detection and identification of moving targets. Indeed, target complexity greatly increases the attentional load for foraging tasks, which governs the foraging strategy (Dukas & Kamil, 2001; Kristjánsson, Thornton, Chetverikov, & Kristjánsson, 2020). In this regard, attention has a critical role, allowing what might otherwise remain undetected (or unidentified) to be revealed, while an inability to attend to a specific target confers potential protection. Crucially, attention is therefore susceptible to exploitation by prey. One means of exploitation is via the confusion effect: the reduced predation success caused by difficulty in individuating prey items in a group (Krause & Ruxton, 2002). This inability

to pick out a single item can be attributed to an attentional bottleneck in the cognitive system of a predator, whereby increasing numbers of potential prey items make the targeting of a specific individual more difficult because of the expanding attentional resources required to achieve this (Krakauer, 1995). Coloration (Hogan, Cuthill, et al., 2016; Hogan, Scott-Samuel, et al., 2016), density (Hogan, Hildenbrandt, et al., 2017; Scott-Samuel, Holmes, Baddeley, & Cuthill, 2012) and behaviour (Hogan, Cuthill, et al., 2017) influence the magnitude of the effect.

1.7 Thesis structure

Following the insight of previous literature regarding motion and concealment, and considering such work within the framework of signal and noise, I wished to investigate an otherwise untested perspective: does the presence of dynamic illumination significantly impede the detection of moving objects? This question is the focus of my thesis and is addressed using an array of methods and model organisms. I first outline the initial pilot experimentation (Chapter 2) and then highlight the subsequent methodological changes necessary for further investigation (Chapter 3). Within the following chapters, I then address the question in turn using human (Chapter 4 and 5), bird (Chapter 6) and fish (Chapter 7) observers. Finally, I summarise my findings and discuss possible directions of future investigation (Chapter 8).

Chapter 2. Pilot experimentation.

2.2 Introduction

A pilot experiment was necessary to confirm whether (1) dynamic illumination could be successfully simulated using computer software and (2) test the assumption that the presence of simulated dynamic illumination can influence prey item detection. One would expect the effect of dynamic illumination to mirror that of dynamic visual noise caused by the movement of background objects (New & Peters, 2010; Peters et al., 2007), reducing the SNR (Merilaita et al., 2017) and masking motion signals. This is particularly pertinent as motion has long been considered the enemy of camouflage (Cott, 1940; Hailman, 1977; Hall et al., 2013; Rushton et al., 2007; Stevens et al., 2008; Zylinski et al., 2009).

The context chosen for this experiment was an underwater scene, with computer-simulated water caustics being the dynamic illuminant in question. Human participants acted as visually guided predators, tasked with detecting and "capturing" a single prey item (stationary or moving) within scenes where the illuminant was present and moving or absent. Though water caustic flicker, as it hits a prey, has been proposed as a means by which organisms can detect objects in the midwater (Loew & McFarland, 1990; McFarland & Loew, 1983), the perspective for the simulated scenes was as if the participant were looking down upon the substrate, therefore viewing the full mosaic of water caustics.

2.3 Methods

Scene generation

The simulated underwater scene was created using the graphics software, 3D Studio Max v.2017 (Autodesk, San Rafael, CA, USA; www.autodesk.co.uk/products/3ds-max/overview). There were five major components of the scene to create within 3D Studio Max (from bottom up): a floor plane, the prey item, a target camera, a water surface plane and a light source. The floor plane was a 'flattened box primitive' (200 x 200 x 10 pixels; see Table 2.1 for a glossary of terms) that acted as the backdrop for the trials: a series of rock textures were added to the upper surface of this box using the Material Editor, giving the impression of a rocky seafloor. The rock textures, of which there were four, were bitmap images of rock faces retrieved from Google Images (Google, Mountain View, CA, USA; images.google.com). Above the floor plane was the prey item: a sphere mesh that, when viewed from

above, appeared circular (9.1 pixels radius; 0.9° visual angle) and was realistically shaded (Figure 2.1). As with the floor plane, textures could be applied to the prey item using the Material Editor, wrapped over its viewed surface. The prey item could either remain stationary or begin moving, constrained to an arced motion pathway for the duration of the clip. Prey item movement was fixed (30 mm/s; 3.4 degrees/s at the viewing distance of participants) and could occur in a clockwise or anticlockwise direction. The arc was such that the distance between the moving prey item and the centre of the scene was always equal. The prey item's starting position (whether moving or stationary) was one of eight fixed positions (north, south, east, west; north-east, north-west, south-east, south-west) located around a central ring (590 pixels diameter; Figure 2.2). Above the prey item and floor plane was a second plane of equal dimensions, which acted as the water surface, together with a light source ("mental ray omni light") positioned centrally and perpendicularly above the scene. These two components were essential for rendering the water caustic effect. The light source settings were defined by adjustments made to the caustic and photon mapping settings, such that the light could generate caustic effects, while the scene settings required the activation of 'mental ray photographic exposure control'. The caustics feature within Render Setup needed also to be enabled. Using the Material Editor, the noise modifier of the water surface plane was adjusted to create a watery texture with waves that could vary in strength and frequency. The last component of the scene was a target camera, positioned centrally below the water surface plane and perpendicular to the scene, which provided a birds-eye-view perspective of the scene below. The camera positioning was such that the view was never obscured by the ebb and flow of the water surface plane's noise parameter. A filter was applied to the target camera to render viewed scenes monochromatic.

The subsequent scene covered an area of 730 x 730 pixels, and had a mean luminance of 108 cd/m^2 (measured directly from the screen with a Konica Minolta CS-100A photometer; Konica Minolta Sensing America, Inc., Ramsey, NJ, USA; www.sensing.konicaminolta.us). Each scene was then rendered (utilising the 'mental ray' renderer) for 200 consecutive frames, forming a short video clip (30 fps, ~6 s; hereafter 'stimulus clips'). While rendering each stimulus clip, a second clip could be simultaneously rendered: clips had an activated alpha channel, where all but the corresponding prey item (pixelated white) was inert (hereafter, 'alpha clips'). Every alpha clip was unique to the stimulus clip that it was

rendered alongside. In addition to the stimulus clips, a small set of practice clips was created, which displayed the prey item upon a white background in the absence of water caustics.

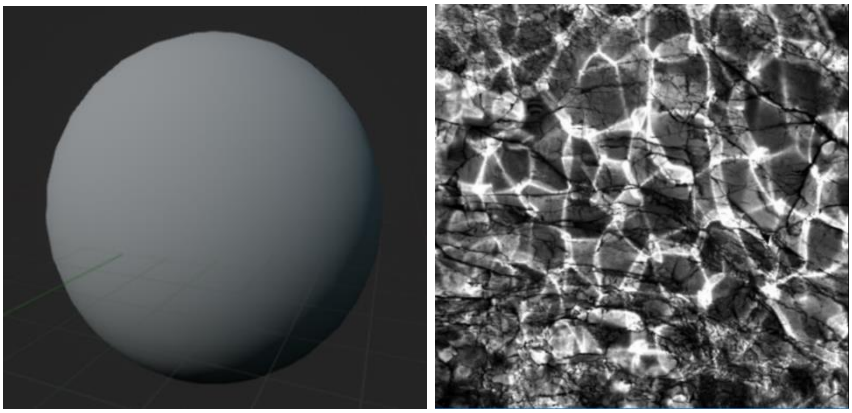

Figure 2.1 A close-up of the prey item outside of the experimental context (left) and the experimental scene showing simulated water caustics overlaying a rock background (right).

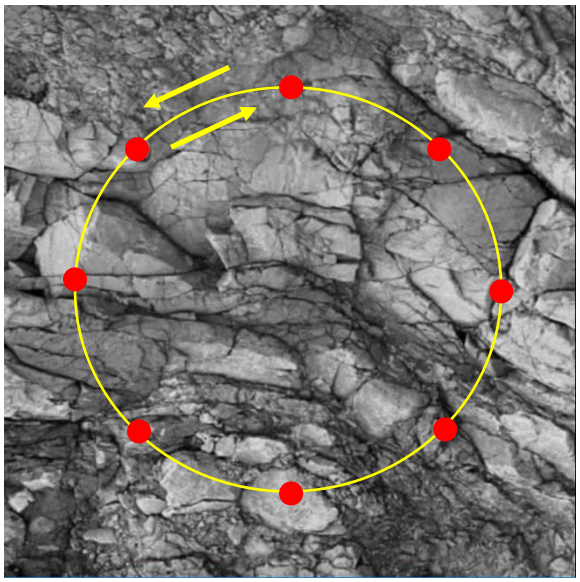

Figure 2.2 Experimental scene with an example rock background (no caustics treatment), together with the fixed prey item start locations (not visible during the experiment). Prey items could 'spawn' at any one of the spawn starts (red points), then remain stationary or move in either an anticlockwise or clockwise direction (yellow arrows) following the spawn ring (yellow circle) for a quarter of its circumference.

Table 2.1. Glossary of terms derived from 3D Studio Max.

Term	Description	Chosen settings
Standard primitive	*Standard primitives are one of the foundational types of renderable geometry. Several shapes are available, including planes, boxes and cylinders.*	n/a
mental ray	*mental ray (mr) refers to the general -purpose renderer (a product of NVIDIA, Santa Clara, CA, USA; www.nvidia.com/en-gb/) that can generate physically correct simulations of lighting effects, including refractions and caustics.*	n/a
Omni light	*An omni light casts rays in all directions from a single source.*	n/a
Caustic and photon mapping	*When this feature is enabled, the mental ray renderer calculates caustics effects. There are several accompanying settings: the multiplier controls the intensity of the indirect light accumulated by caustics; the emission refers to the number of photons emitted by each light for use in caustics; decay specifies how photon energy decays as it moves away from each light source.*	Enabled Multiplier = 1.2 Emission = 2000000 Decay = 1.7
Photographic exposure control	*The photographic exposure control lets you modify rendered output with camera-like controls, providing values for highlights, midtones, and shadows. Alternatively, environment presets are available.*	Enabled Preset = Indoor daylight
Light refraction	*Light refraction here is the change in direction of light passing through the 'water surface' plane (as if it were travelling from one medium to another).*	20
Light reflection	*Light reflection here is the change in direction of light at the 'water surface' plane (as if it were the interface between different media) such that the light returns to the medium from which it originated.*	0
Water surface plane noise modifier	*Noise modifier modulates the position of an object's vertices along any combination of three axes. There are several specific settings for the geometry of the object: fractal refers to the creation of similar patterns at increasingly small scales, useful for creating random rippling; the bump map makes an object appear to have a bumpy or irregular surface; strength refers to the amplitude of noise in each axis (here, the z axis of the plane). Animation controls the shape of the noise effect by overlaying a sine wave for the noise pattern to follow, the periodicity of which is set by the Frequency value.*	Fractal = On Bump map = 40 Strength (z) = 20 Animate noise = On Animation frequency = 0.05
Target camera	*A target camera views the area around the target icon that you place when you create the camera. Here, the target icon was the floor plane. The target camera represents the player's point of view; how the player sees the world.*	n/a
Alpha channel	*Alpha is a type of data, found in 32-bit bitmap files, that assigns transparency to the pixels in the image.*	n/a
Spawn	*As in to 'appear' with reference to the prey item.*	n/a

Experiment generation and format

The experimental protocol was executed in MATLAB (The Mathworks Inc, Natick, MA, USA) using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Once rendered, all stimulus clips (and their corresponding alpha clip) were proliferated using MATLAB: original clips were rotated (in 90-degree increments) and flipped (across the central vertical axis) to create seven additional stimulus clips per original (eight total). Several folders of stimulus (and their alpha) clips were created and categorised by treatment, with each varying in prey item movement, prey item texture and/or the presence or absence of water caustics. A stimulus clip was then chosen at random by MATLAB from the relevant treatment folders and displayed on screen, while simultaneously playing the corresponding alpha clip behind. The alpha clip allowed MATLAB to locate the prey item (as the only white pixels present) and translate this location to the displayed stimulus clip. Participants then had the duration of the clip to find and capture (by way of touch) a single prey item within the scene: all stimulus clips were viewed at ~40 - 50 cm from a gamma-corrected 15″ ELO Entuitive LCD touch monitor (305 x 230 mm; Elo Touch Solutions, Inc., Milpitas, CA, USA), with a refresh rate of 75 Hz and a resolution of 1024 × 768 pixels. Each clip displayed represented a trial. Two primary measures were recorded for each trial: outcome (hit the prey item or time out) and response time (for hits). It was necessary for the participant to touch the prey item directly, as the outcome 'hit' was only recognised by MATLAB if the corresponding white pixels (of the prey item) were touched. I was unable to log the number of (missed) touches prior to capturing a prey item or the distance of each missed touch (from the prey item).

Ten practice trials were provided prior to the main experimental body to ensure the participant was familiar with the prey item appearance and trial format. Individual task success was fed back to the participant auditorily: if a prey item was successfully hit, a beep (2100 Hz for 0.1 s) was heard through headphones provided. Each trial was separated by a break screen, which was blank but for the instructions for continuing. Touch input was required to continue to the next trial. Upon continuing, participants were briefly presented (1 s) with a central fixation cross overlaying binary white noise. Information regarding the specific task, prey item appearance, prey item motion (either stationary or moving), experimental scene motion (either stationary or moving) and trial format (above) were relayed to the participant with an information sheet (see Appendix; prior to the practice trials) and repeated verbally (prior to beginning the experiment).

Prey item, treatments and participants

The prey item for this experiment had a texture which matched the mean luminance of the scene (108 cd/m^2). The combination of prey item movement (stationary and moving) and scene dynamism (water caustics absent and present) formed a two-by-two factorial design. Each participant completed 256 trials (64 replicates per treatment). A total of 32 participants (27 females; aged 18-21) were recruited. Each participant was naïve, had normal/corrected-to-normal vision and provided written consent in accordance with the Declaration of Helsinki. The experiment was approved by the Ethics of Research Committee of the Faculty of Science, University of Bristol.

Statistical analysis

All statistical analyses were performed in R (R Foundation for Statistical Computing, www.R-project.org) and utilized linear mixed models and generalized linear mixed models (functions lmer and glmer, respectively, in the lme4 package; Bates et al., 2017). The response variables were response time (RT, Gaussian error) and the proportion of trials with time-outs (Time-outs, binomial error). Note that response time data were first aggregated to the median for each participant-treatment combination and then these were analysed using a model with Gaussian error. The full model included the fixed effects illuminant (water caustics absent or present) and prey item (stationary or moving), plus their interaction, and the random effect of participant. The change in deviance between models with and without the predictors of interest was tested against a χ^2-distribution with degrees of freedom equal to the difference in degrees of freedom between the models.

2.4 Results

There was a significant interaction between the presence of water caustics and motion of the target for both response variables (RT: $\chi^2 = 94.86$, d.f. = 1, $p < 0.001$, Time-outs: $\chi^2 = 14.34$, d.f. = 1, $p < 0.001$). To explore the cause of this interaction, trials with prey item movement and trials with stationary prey items were analysed separately. During trials with moving prey items, participants spent significantly longer ($\chi^2 = 23.67$, d.f. = 1, $p < 0.001$) and were timed out more often ($\chi^2 = 93.51$, d.f. = 1, $p < 0.001$), when in the presence of caustics than when in the absence of caustics (Figure 2.3). The same effect was seen when trials contained stationary prey items, but to a greater extent (RT: $\chi^2 = 89.89$, d.f. = 1, $p < 0.001$; Time-outs: $\chi^2 = 326.56$, d.f. = 1, $p < 0.001$).

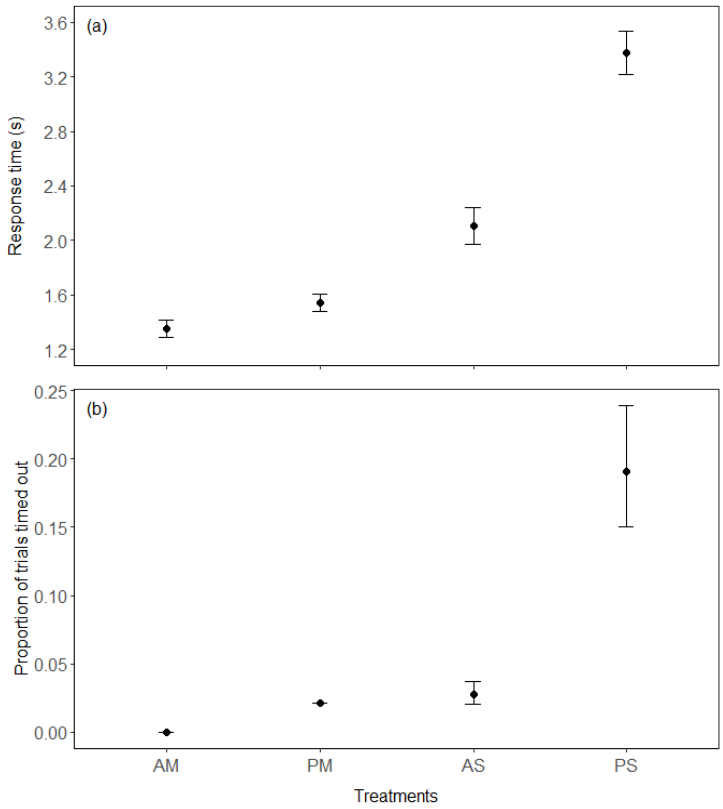

Figure 2.3 Plots for both response variables: mean response time (a) and the proportion of trials timed out (b) for the treatments. Treatment abbreviations: AM (water caustics absent, moving prey item), PM (water caustics present, moving prey item), AS (water caustics absent, stationary prey item) and PS (water caustics present, stationary prey item). Error bars indicate 95% confidence intervals derived from the linear mixed models (a) and generalised linear mixed models (b). Confidence intervals for the two moving treatments with proportion of time-outs (AM and PM) could not be estimated because the model for moving items did not converge. This was because there were never any time-outs for moving items in the absence of water caustics. Without any variance in one treatment, the maximum likelihood could not be estimated with confidence.

2.5 Discussion and methodological limitations

Both objectives for the pilot experiment were met. Underwater scenes with dynamic water caustics were successfully simulated and presented to participants, while the presence of said illuminant adversely affected prey detection: both response times and the number of time-outs were significantly greater in the presence of dynamic water caustics than in their absence. Crucially, this finding was consistent

when searching for both stationary *and* moving prey items, inferring that dynamic features within a habitat can indeed mask prey item motion to some degree.

However, while the experiment appears informative, there were methodological limitations which needed to be addressed prior to further experimentation. The first limitations to consider are those associated with the use of a software (3D Studio Max) that is primarily used for standalone graphical modelling: 3D Studio Max has no ability to independently host a psychophysical experiment and the necessary features that this entails, such as the generation of random loci for prey items or the ability to receive input from a participant. Instead, the use of a MATLAB script was necessary to introduce an experimental format post hoc. In addition, while features of 3D Studio Max could be manipulated to create realistic water caustics, there is no existing infrastructure within the software to extend its use to easily create other forms of dynamic illumination, such as dappled light, which would involve the creation of thousands of individual vegetative meshes. Indeed, the computational power required to render a caustic-emitting water surface incurred a severe time constraint itself, a caveat that was especially costly when editing, whereby minor edits to a scene would require several hours to render. Any attempts therefore to render more complex scenes (e.g. a realistic forest habitat for dappled light) would be unlikely within a limited timeframe.

Secondly, the current experiment presented a stimulus that could appear within either the presence or absence of water caustics. While this division is most representative of natural habitats, it may be more beneficial to include a static form of water caustics, despite the latter not existing in natural habitats. In this way, one can control for the difference in spatial complexity between scenes, which ensures that the witnessed effect is limited to the feature of interest (i.e. motion) and not a result of non-motion-based noise. Indeed, visually complex environments have already been shown to reduce the search efficiency in birds and humans (Dimitrova & Merilaita, 2010; Merilaita et al., 2017; Xiao & Cuthill, 2016).

Lastly, due to the lack of psychophysics-friendly parameters and lengthy render times, the stimulus clips had (eight) fixed start locations for the prey items (Figure 2.2). While beneficial in the time-limited circumstances, anecdotal participant feedback suggested that the fixed locations made the task quick to learn. This increases the susceptibility that, in subsequent experiments, one may encounter a ceiling effect and therefore an inability to detect specific and subtle effects of differing treatments. It must also be noted that the inability to register ‘misses’ (either in terms of ‘miss distance’ or ‘number of missed

touches') may be a significant methodological omission: it may be that the presence of dynamic illumination disrupts both the latency *and* accuracy of capture attempts, a finding which would go unnoticed in the current setup. Overall, it was necessary to find alternative software which enabled interactivity within a host of realistic environmental simulations.

Chapter 3. Common methodology.

3.1 Creating natural scene simulations

The solution to the methodological issues outlined in the previous chapter was a switch to the software Unreal Engine 4 (Epic Games, Cary, NC, USA; www.unrealengine.com): a games platform with generated scenes that are totally interactive and deemed realistic, and rendered in real time. Unreal Engine 4 is also supported by swathes of documentation, online community forums and assets packages. This includes the free demonstration assets package, 'Kite Demo', which contains a host of premade realistic scene components, such as tree, plant and rock meshes, and substrate textures. While Epic Games boast of "photorealistic rendering, dynamic physics and effects, lifelike animation, [and] robust data", how closely such components match to counterparts in real scenes is unclear. However, scenes judged to be realistic by human observers should be sufficient for the purpose of this thesis: the focus here is the effect of general scene motion upon prey detection (rather than fine scene detail), while the poor visual acuity of the non-human species addressed in later chapters means that such detail is less pertinent (Champ, Wallis, Vorobyev, Siebeck, & Marshall, 2014; Over & Moore, 1981). More importantly, by switching software, the issue of consistency of masking effect of water caustics across software platforms could be addressed; if the masking effect is indeed robust, then it should occur across platforms, irrespective of the method of creation.

There are several common experimental constructs used throughout each of the following experimental chapters. To avoid repetition, these constructs are outlined here first with each following experimental chapter addressing any modifications necessary for that specific experiment. While some terminology in this section may appear unfamiliar, or even ambiguous, it derives directly from Unreal Engine 4 and therefore, to maintain clarity and replicability, the same terminology has been retained (see Table 3.1 for a glossary of terms). There were seven key components that formed the core of each experimental zone: (from bottom up) floor, spawn areas, prey item, camera, "illuminant creation" and the lighting systems. Each had specific settings and connections, underpinned by the Blueprint Scripting System, which could be coded in various ways to alter interactivity and behaviour.

The floor component was a standard plane static mesh coated in a default material acquired from the free demonstration asset package, 'Kite Demo'. A material was attached to the floor component that,

when repeatedly tiled, would provide a background to the trials in all experiments. Backgrounds comprised one single image, sourced from the software's default asset package: leaf litter ('forest_path_001A') and river pebbles ('pebbly_river') were used for forest and underwater simulations respectively (Figure 3.1). I used the selected background scenes "out of the box", with range and mean of RGB values as supplied by Unreal Engine, as these were already judged to be realistic. The target luminance was then adjusted to match the mean background luminance. The monitor settings, and thus the luminance experienced by the study organism, was adjusted so that there was no clipping (saturation at the lower or upper end of the luminance range).

Set upon the background were two transparent box static meshes that would act as 'spawn' (appearance) areas (Figure 3.2). For any given trial, a prey item would appear at a random location within one appearance area (the 'origin' point), while another random location would be selected from the opposite appearance area (the 'destination' point) to create a random movement vector for the prey item. The randomness of loci was based on values selected from discrete uniform distributions using Unreal Engine's random integer generator. Once they appeared, prey items could be set to remain stationary or begin to move. Movement could occur at any desired speed along the random vector. Upon arrival at the destination point, the prey item would reverse the movement (at the same speed) back towards the origin point. This process would repeat until the end of the trial. The location constraint was chosen such that the item never left the screen during a moving trial. It must be noted that, with motion vectors crossing the centre of the scene, there may be some spatial search bias: most participants are likely to look at the centre of the scene before scanning outward. While it would have been beneficial to have random appearance locations that could occur across the entirety of the screen (in any random direction and for any distance), the sheer complexity of such installation within Unreal Engine far outweighed the risk of spatial bias, especially if the prey item is to be kept within the scene at all times and if the movement vector is to be long enough to constitute as a sustained motion signal.

The prey item was a three-dimensional sphere with a matt surface and mean luminance equal to that of the background, identical to that illustrated in Chapter 2 (see Figure 2.1). When viewed from above, as in the experiment, the prey item was circular but retained apparent depth due to the realistic projection of shadows upon a three-dimensional object (Cook, Qadri, Kieres, & Commons-Miller, 2012). Encapsulating the prey item was a collision mesh of equal shape, which extended the interactivity of the prey item to a wider space (e.g. by a third) without increasing its visible size. For example, a visible

sphere with a diameter of 18 pixels (the prey item) with the interactivity extending to a diameter of 24 pixels. This afforded participants a slight margin of error with regards to what constituted a 'hit' and enabled some control regarding the variation in participant touch techniques (i.e. fingertip size, contact point).

Figure 3.1 Screenshots of the 'Kite Demo' textures that were used to create the relevant experimental backdrops: leaf litter (left) was used as a substrate for dappled light in Experiment 1, while river pebble (right) was used as a substrate for water caustics in Experiment 2. Each image was converted to monochrome for the purpose of the experiment.

Above this activity, a camera was positioned perpendicular to the floor component, which would provide the view for each trial. The camera had equalised RGB values, creating a monochrome birds-eye perspective of the backdrop. At the highest point of the scene was a directional light with an intensity scale that could alter both the light intensity (brightness) and the shadow intensity (darkness). Between the camera and lighting systems was the region within which the illuminant could be created (below). The simulated illuminant could be either static or dynamic (with the parameters controlling dynamism kept consistent throughout all dynamic trials).

3.2 Illuminant creation: dappled light

For experiments using simulated dappled light, the region between the camera and lighting system utilised a collection of randomly positioned, pre-made model tree static meshes, sourced from the 'Kite Demo' assets package. When paired with the directional lighting systems above, characteristic dappled light could be cast across the floor component below (Figure 3.3). Crucially, a highly editable wind function ('SimpleGrassWind' function) could be added to the tree static mesh that mimicked the

presence of a natural breeze, subsequently creating a range of dappled light flickers and dynamic shadows. Conversely, the wind function could be switched off to allow for static dappled light treatments. Due to the restricted localisation of dappling, the floor component was compartmentalised into four zones, each with its own camera that captured a unique arrangement of tree shadows. Prior to each trial, an experimental zone (and the corresponding camera) was selected at random. The diversity of scenes viewed was therefore maximised, which in turn minimised learning effects.

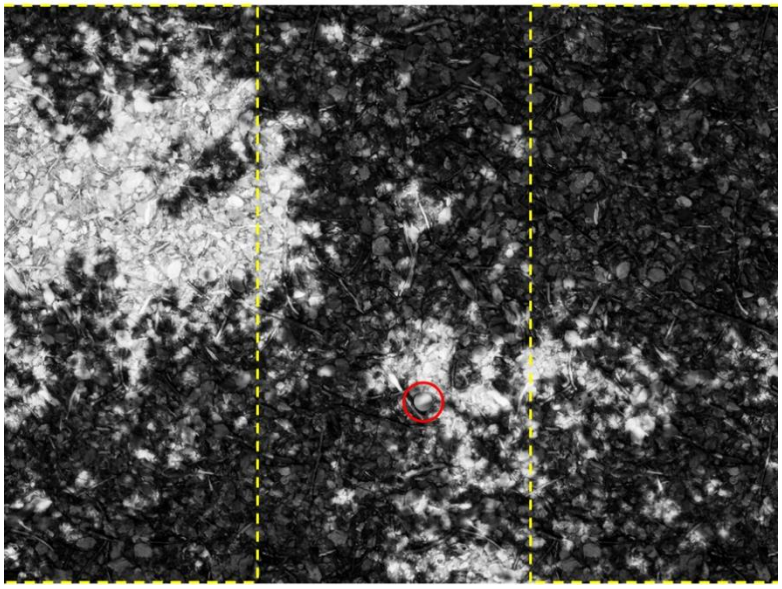

Figure 3.2 Screenshot of experimental trial illustrating prey item and spawn areas. The two regions denoted by the dashed yellow lines are the possible prey item appearance areas (no lines were present in the actual trials). The prey item (artificially highlighted by a red circle) is mid-way through moving from one appearance area towards the other.

3.3 Illuminant creation: water caustics

For experiments using simulated water caustics, the necessary component between camera and lighting systems was a plane. The material for this plane comprised a flipbook that contained a series of frames. The necessary frames were created using the free 'Caustics Generator' (Dual Heights SoftwareAB, Linköping, Sweden; www.dualheights.se/caustics) and pieced together in a single square image, tiled as in a storyboard with the first frame located in the top left corner and the last frame in the bottom right (GlueIt, www.github.com/Kavex/GlueIT). This tiled image was then edited in GIMP2 (The GIMP Development Team, www.gimp.org): first converted to monochrome, then the black-white contrast was increased and finally white pixels were converted to the alpha (transparency) channel.

The result was an image that was transparent in only the regions that corresponded to the caustic network, which could then be read in sequence by the 'flipbook' component (that creates the sequence of frames which constitute the animation). As the flipbook component reads the tiled image in sequence (at any given frequency, from left to right and top to bottom), the visualised material of the plane subtly changes accordingly. Paired with the scenes' directional light passing through the newly transparent regions of the plane, the effect is a caustic flicker projected upon the substrate. For treatments involving static caustics, the material used for the plane component was simply held as the first frame in the sequence.

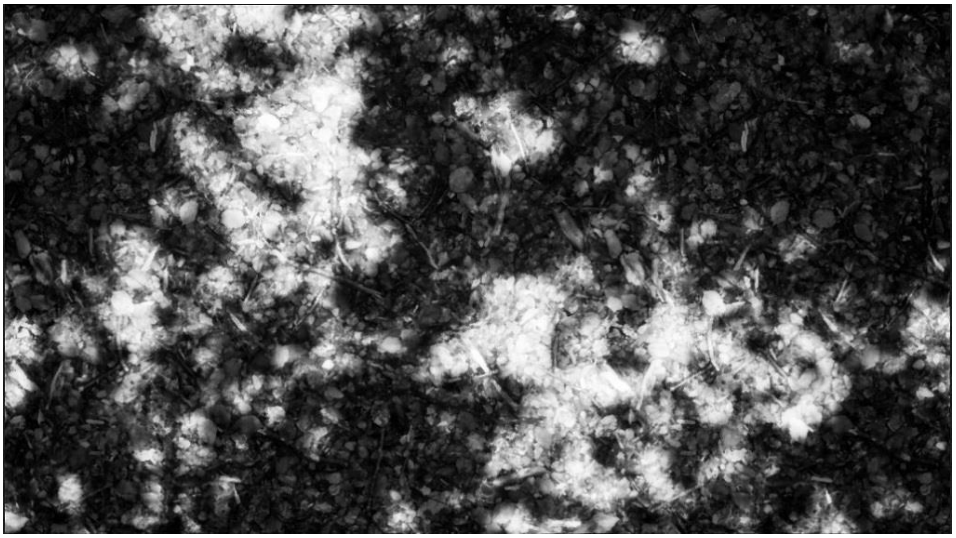

Figure 3.3 A screenshot of an example scene with simulated dappled light overlaying a leaf litter background.

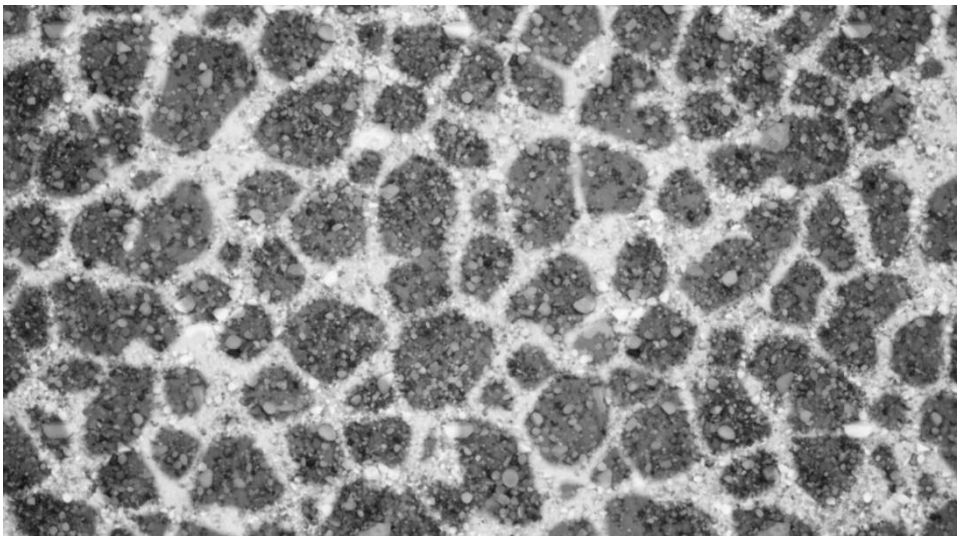

Figure 3.4 A screenshot of an example scene with simulated water caustics overlying a river pebble background.

Table 3.1. Glossary of terms derived from Unreal Engine 4.

Term	Description	Chosen settings
Blueprints Visual Scripting system	*The Blueprints Visual Scripting system in Unreal Engine is a complete gameplay scripting system based on the concept of using a node-based interface to create gameplay elements from within Unreal Editor. By connecting Nodes, Events, Functions, and Variables with Wires, it is possible to create complex gameplay elements.*	n/a
Static meshes	*Static Meshes are one of the foundational types of renderable geometry in Unreal Engine 4. Several shapes are available, including planes, boxes and, even, constructed trees.*	n/a
Collision mesh	*A simple transparent shape that is used as the bounds of what can and cannot be blocked or overlapped ('interacted with') by an accompanying static mesh.*	n/a
Spawn areas	*The denoted spawn areas were transparent box static meshes that utilised a SpawnActor node within their Blueprints. With this, the prey item could spawn (appear) anywhere within the area of the box.*	n/a
Directional light	*The Directional Light simulates light that is being emitted from a source that is infinitely far away. This means that all shadows cast by this light will be parallel, making this the ideal choice for simulating sunlight.*	Intensity = 20.0
Camera	*The Camera represents the player's point of view; how the player sees the world.*	n/a
SimpleGrassWind function	*The SimpleGrassWind function applies a basic wind operator to foliage, giving the ability to specify a wind intensity and wind speed.*	Intensity = 2.0 Speed = 1.0
Flipbook component	*The Flipbook component inputs a grid of images (8 x 8) that consecutively differ and 'flips' through them (read from left to right, top to bottom at a desired rate) to produce the appearance of image motion.*	n/a

Chapter 4. Assessing the effect of dappled light and water caustics upon prey detection and capture: humans.

Abstract

The environment plays a significant role in shaping the visibility of signals both to and from an organism. For example, against a static background movement is highly conspicuous, which favours staying still to optimise camouflage. However, backgrounds can also be dynamic, such as areas with wind-blown foliage or frequent changes in illumination. I propose that these dynamic features act as visual noise which could serve to mask otherwise conspicuous movement. Two forms of illumination change were simulated - water caustics and dappled light - to represent dynamic aquatic and terrestrial environments respectively. When asked to capture moving prey items within the simulated scenes, human participants were significantly slower and more error prone when scenes had dynamic illumination. This effect was near identical for both the aquatic and terrestrial environment. In the latter, prey item movement was also found to be masked most often when the pathway taken involved movement across the dynamic dappled areas of the scene. This could allow moving prey to reduce their signal-to-noise ratio by behaviourally favouring the relative safety of environments containing dynamic features.

4.1 Introduction

The methodological improvements outlined in Chapter 3 allowed further investigation regarding the influence of dynamic illumination, including the introduction of different forms of dynamic illumination (see 1.2 in Chapter 1). This is key because dynamic illumination is a common phenomenon, occurring in both terrestrial (e.g. dappled light) and aquatic (e.g. water caustics) environments, and little is known about the ecological impacts of its presence. As outlined in 1.4 of Chapter 1, dynamic components within a habitat have the potential to mask motion signals (Ord et al., 2007; Ord & Stamps, 2008; Peters et al., 2007) and therefore could be pertinent for organisms that balance a priority to remain concealed with the necessity to move; hence the long-standing problem that motion can break camouflage could be ameliorated (Cott, 1940; Hailman, 1977; Hall et al., 2013; Rushton et al., 2007; Stevens et al., 2008; Zylinski et al., 2009). Within the framework of SNR, provided a motion signal falls within the distribution of noise then some degree of concealment will occur, irrespective of the source of that noise (Merilaita et al., 2017).

Two examples of dynamic illumination, water caustics and dappled light, were simulated in computer based experiments to investigate the extent to which they influence human perception of both moving and stationary prey items. In addition to creating fully dynamic, realistic simulations, static examples of both illuminants were used to determine which effects are specific to movement as opposed to just the static pattern. The primary difference between water caustics and dappled light is the scope of influence, a feature determined by the source of each illuminant. Because dappled forest light is created by the shadows of vegetation that is, although moving, fixed in mean location, the dapple patterns occur around those locations (Théry, 2001). With this localisation of noise, one may predict that prey item movement needs to interact with these locations to gain full masking potential, rather than through some distractive effect of general noise. Conversely, because caustics are created by the entire, moving, water surface, they are more global in effect.

The current experiment also provides an opportunity to reaffirm whether the masking effect of water caustics highlighted in the pilot experiment is consistent across software platforms for human observers. If there is minimal disparity between the two experiments' results, then one can be confident that the reduced detectability of moving prey items within dynamic underwater scenes is not due to

methodological artefacts. This is particularly pertinent as the method of water caustic creation differs between each experiment and the illuminant is the primary feature of interest.

4.2 Methods

Trial protocol

Forty participants (37 female and 3 male, aged 18-22) were recruited opportunistically from the Psychology undergraduate population of the University of Bristol, with half for each experiment: each was naïve, had normal/corrected-to-normal vision and provided written consent in accordance with the Declaration of Helsinki. The experiment was approved by the Ethics of Research Committee of the Faculty of Science, University of Bristol.

All stimuli were viewed at 40-50 cm from a gamma-corrected 15″ ELO Entuitive 1525L LCD touch monitor (305 x 230 mm; Elo Touch Solutions Inc., Milpitas CA, USA), with a refresh rate of 75Hz and a resolution of 1024 × 768 pixels. On each trial, participants were presented with one prey item within a simulated scene. Their task was to search for and then capture, by touching, the prey item. Participants had eight seconds and one opportunity to touch the prey item. There were two experiments: Experiment 1 used simulated dappled light upon a leaf litter background while Experiment 2 used simulated water caustics upon a pebbly seabed background (Figure 3.3 and 3.4). The scene covered a screen area of 1024 x 568 pixels and had a mean luminance of 88 cd/m^2 (Experiment 1) and 97 cd/m^2 (Experiment 2). Prey items remained as a sphere static mesh that, when viewed from above, appeared circular (9.1 pixels radius; 0.9° visual angle) and was realistically shaded, encapsulated by a spherical collision mesh (12.1 pixels radius). Prey items could appear anywhere in one of two regions (384 x 568 pixels) within this scene (Figure 3.1) and could either remain stationary or begin to move, with movement fixed at a speed of 30 mm/s (3.4 degrees/s at viewing distance of participants). The simulated dappled light and water caustics were either static or dynamic (with the parameters controlling dynamism kept constant throughout all dynamic trials). The combination of prey item and scene dynamism formed a two-by-two factorial design.

There were 200 trials per participant (50 replicates of each of the four treatments), in an order independently randomised for each participant. A single practice trial for each participant prior to testing was used to demonstrate the features of the scene and trial, as well as to ensure that they could

correctly identify the prey item. Each trial was separated by a break screen, which was blank but for the trial number and instructions for continuing. The trial number was displayed in either green or red font depending upon whether the participant succeeded or failed to capture the prey item in the previous trial. The scenes chosen contained elements that were similar in size and shape to the prey item (e.g. leaves and pebbles) and therefore I wished to provide feedback on detection success to ensure that participants were attending closely to the task. Touch input was required to continue to the next trial. Each trial was completed in darkness (to remove screen glare) and with headphones on (to remove unnecessary auditory distractions). An information sheet (relevant for the current experiment) and verbal instructions were provided in a manner identical to that outlined in Chapter 2).

Two primary measures were recorded for each trial: outcome (hit, miss or time out) and response time to the nearest 10 ms (for hits and misses). A participant touch that fell within the confines of the prey item's collision mesh constituted as a 'hit', while a 'miss' was any touch that failed to do this. An additional measure for Experiment 1 was the path followed for moving prey items in relation to the levels of shade and open light encountered. Water caustics, being generated by light passage through waves, have a more regular spatial distribution than the dappled forest light, which is necessarily clustered under leafy branches. Therefore, there was greater variation in the extent to which prey movement paths passed through varying illumination in Experiment 1 (forest) than 2 (underwater). I therefore predicted within-treatment differences in Experiment 1, with search being more difficult in trials where paths crossed greater mixtures of shade and light. These paths were classified with respect to the time in direct light (versus shade) into one of five bins: 0-5% - shade only, 5-45% - mostly shade, 45%-55% - shadelight mix, 55%-95% - mostly light, 95-100% - light only. Bins were asymmetric to ensure a similar amount of data was captured in each.

Post hoc measures: Experiment 1

For Experiment 1, it was necessary to ascertain the pathway or location used by the prey item in each of the four experimental zones. This could only be achieved post hoc. Screenshots of all experimental zones were captured and resized to the resolution of the trials with Microsoft Paint (Microsoft Paint, https://www.microsoft.com/en-gb/). Using GIMP2 (GIMP, https://www.gimp.org/), these screenshots were converted to binary (black and white) images using a threshold of 0.5. With a script in Matlab (The Mathworks Inc, Natick, MA), the images were called in turn with the according trial and the zone used,

as well as the starting XY and ending XY coordinates of prey items. Matlab then created a temporary vector, which it searched along for white pixels: the output for this search was the percentage of white pixels encountered and was recorded as such when fed back into the data table.

Analysis

All statistical analyses were performed in R (R Foundation for Statistical Computing, www.R-project.org) and utilized linear mixed models and generalized linear mixed models (functions lmer and glmer, respectively, in the lme4 package; Bates et al., 2017). Participant was included as a random effect to account for the repeated measurements from the same subjects. The response variables were response time (RT, Gaussian error), proportion of trials with time-outs (Time-outs, binomial error) and proportion of trials when the prey item was missed (Misses, binomial error). Note that response time data were first aggregated to the median for each participant-treatment combination and then these were analysed using a model with Gaussian error. For each experiment, the full model included the fixed effects illuminant (static/moving) and prey item (static/moving), plus their interaction, and the random effect of participant. The change in deviance between models with and without the predictors of interest was tested against a χ^2-distribution with degrees of freedom equal to the difference in degrees of freedom between the models. If there was insufficient variance present for the full model to converge (e.g. 100% detection success for some conditions), a minimal adequate model was fitted and a likelihood-ratio test (LRT) applied.

4.3 Results

In both experiments, there was a significant interaction between motion of the illuminant and motion of the target for all response variables (Experiment 1: RT: $\chi2 = 18.82$, $p < 0.001$, Time-outs: $\chi2 = 85.72$, $p < 0.001$, Misses: $\chi2 = 24.69$, $p < 0.001$; Experiment 2: RT: $\chi2 = 24.19$, $p < 0.001$, Time-outs: $\chi2 = 44.33$, $p < 0.001$, Misses: $\chi2 = 6.15$, $p = 0.013$; d.f. = 1 in all cases). To explore these interactions, stationary and moving prey trials were analysed separately (Table 4.1). For moving prey, participants spent significantly longer, were timed out more often, and missed the target more often, when in the presence of dynamic dappled light than when in the presence of static dappled light (Figure 4.1). With static prey items there was typically either no effect of motion of the illuminant light (RT, both experiments; Time-outs and Misses, Experiment 2) or a reduced effect (Time-outs, Experiment 1); but for Misses in

Experiment 2, the effect was greater, although still in the same direction as for moving prey (more misses with moving dappled light).

Table 4.1. Effects of motion of the illuminant on prey item detection, when prey are static or moving.

Experiment 1 (dappled)	Moving prey	Static prey
RT	$\chi^2 = 35.51$, $p < 0.001$	$\chi^2 = 0.10$, $p = 0.763$
Time-outs	$\chi^2 = 58.01$, $p < 0.001$	$\chi^2 = 4.11$, $p = 0.0427$
Misses	$\chi^2 = 4.72$, $p = 0.030$	$\chi^2 = 10.78$, $p = 0.001$
Experiment 2 (caustics)		
RT	$\chi^2 = 50.58$, $p < 0.001$	$\chi^2 = 0.34$, $p = 0.559$
Time-outs	$\chi^2 = 42.00$, $p < 0.001$	$\chi^2 = 2.59$, $p = 0.107$
Misses	$\chi^2 = 4.59$, $p = 0.032$	$\chi^2 = 1.39$, $p = 0.239$

The response variables are response time (RT), proportion of trials with time-outs (Time-outs) and proportion of trials when the prey item was missed (Misses). D.f. = 1 for all tests.

Path (Experiment 1 only)

Response time, the proportion of timeouts and proportion of misses are plotted against the paths of moving prey items (Figure 4.2). There was a significant interaction between the presence of dapple and the path bin for response time (LRT = 38.78, $p < 0.001$) and the proportion of trials timed out ($\chi 2 = 40.93$, $p < 0.001$), but not for the proportion of trials missed ($\chi 2 = 3.52$, $p = 0.475$. The slowest response times and highest proportion of time-outs were associated with paths that crossed a larger mix of shade and light pixels (‘mostly shade’, ‘shadelight mix’, ‘mostly light’), while the highest proportion of misses was associated with regions of light only.

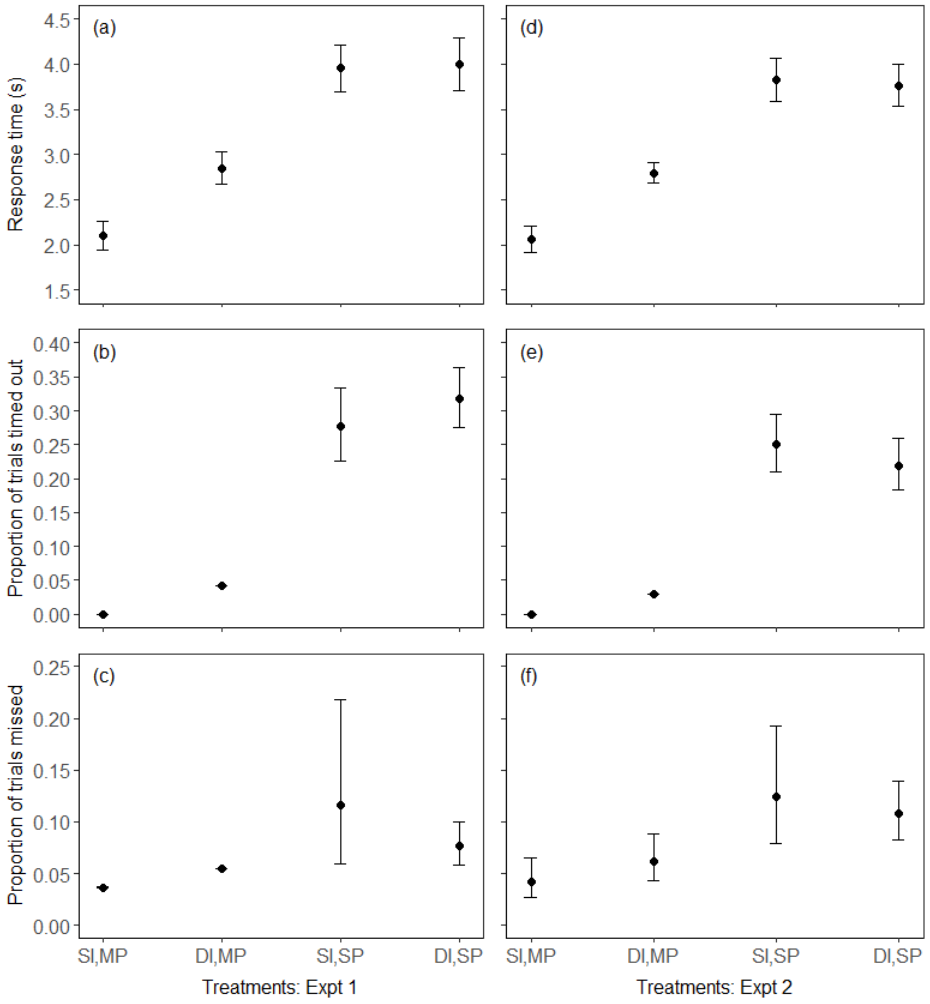

Figure 4.1 Plot grid for all response variables for Experiment 1 and 2. Treatment abbreviations: SI (static illuminant), DI (dynamic illuminant), SP (stationary prey) and MP (moving prey). Mean response times for the treatments (a, d). Error bars indicate 95% confidence intervals derived from the linear mixed models. The proportion of trials timed out (b, e) and of trials missed (c, f) for each treatment. Error bars indicate 95% confidence intervals derived from generalised linear mixed models. Confidence intervals for the two moving treatments with proportion of time-outs (b, e) could not be estimated because the model for moving items did not converge. This was because there were never any time-outs for moving items and no caustics, and very few for moving and caustics. Without any variance in one treatment, the maximum likelihood could not be estimated with confidence.

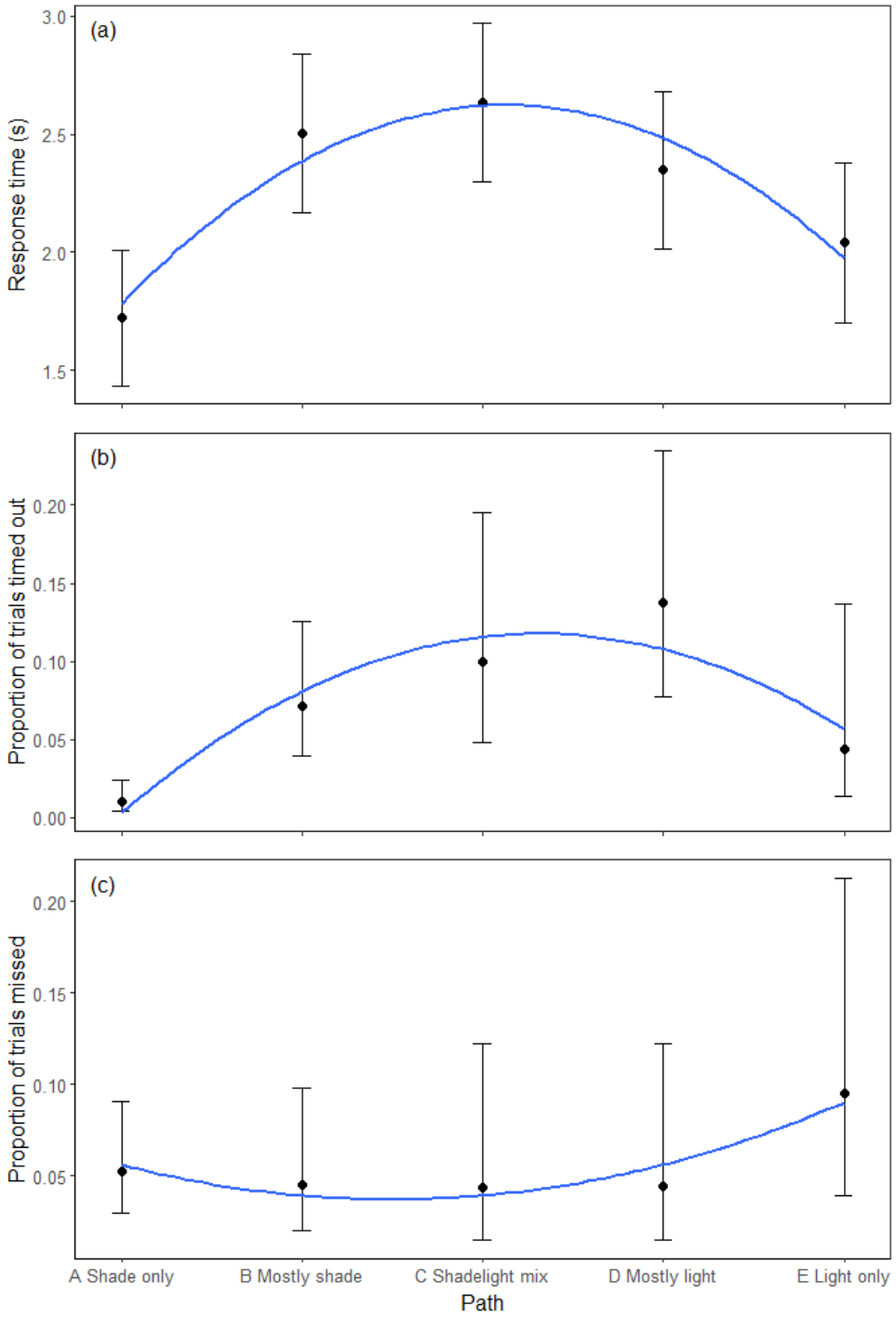

Figure 4.2 Pathway comparisons for moving prey items in the presence of dynamic dappled light by mean response time (a), proportion of time-outs (b) and proportion of misses (c) for Experiment 1. Error bars indicate 95% confidence intervals derived from linear mixed models (a) and generalised linear mixed models (b, c). All datasets are fitted with a quadratic (blue line).

4.4 Discussion

Prey detection was adversely affected in the presence of simulated dynamic dappled light and water caustics. Confirming the pilot data, the results highlight the large effect that dynamic illumination has upon the perception of *moving* prey: an effect that is near-identical for both the terrestrial and aquatic simulations. For moving prey items within dynamic scenes, the response time for finding the item, as well as the number of time-outs and misses associated with the task, were significantly greater than trials with a static scene. This demonstrates how dynamic illumination, as with dynamic visual noise caused by movement of background objects (New & Peters, 2010; Peters et al., 2007), can mask motion signals. As with background complexity (Dimitrova & Merilaita, 2010, 2012; Merilaita, 2003; Xiao & Cuthill, 2016), the SNR is reduced (Merilaita et al., 2017). Although movement 'breaks' camouflage (Cott, 1940; Hailman, 1977; Hall et al., 2013; Rushton et al., 2007; Stevens et al., 2008; Zylinski et al., 2009), an effect also seen in the slower response times and detection probabilities for static prey in our experiments, movement is safer in an environment with dynamic illumination than one without. The significance of this masking effect, over a timescale that represents a fleeting encounter in nature, may be important for providing prey additional time to (i) flee and reach the safety of shelter, or (ii) prepare secondary antipredator defences, for example startle displays (Cott, 1940; Edmunds, 1974; Umbers, Lehtonen, & Mappes, 2015), thanatosis (Edmunds, 1974; Gallup, 1977; Ratner & Thompson, 1960; Rovee, Kaufman, Collier, & Kent, 1976) or retaliatory behaviour (Edmunds, 1974; Ruxton, Sherratt, & Speed, 2004). Moreover, this masking effect appears consistent not only in both simulated aquatic and terrestrial environments but can also influence dynamic illumination at a local and global scale.

The influence of dynamic illumination is also apparent when one considers its effect upon the paths of the prey items (Figure 4.2). For prey items moving in the presence of dynamic dappled light, the slowest response times and the most recorded time-outs were found for paths that involved movement through a mix of light and shaded ('mostly shade', 'shadelight mix', 'mostly light') as opposed to purely through shade and light ('shade only', 'light only'). In addition, no recorded time-outs were found for the 'shade only' pathways, or for all paths in the static dappled light treatment. Indeed, when moving along paths with minimal visual change, the environment is relatively static and therefore movement is more conspicuous. This demonstrates that, at least for localised dynamic illumination such as dappled light, the presence of dynamism in the wider visual scene is not enough to mask movement; rather,

movement needs to occur across the boundaries of illumination change for it to be disguised. A perhaps surprising finding here was that the greatest proportion of misses didn't also occur for movement paths that involved a mix of light and shaded regions. This implies that, once a prey item was detected, participants were more accurate if the prey item moved along dappled paths than 'light only' paths. However, without more specific parameters (e.g. the distance from a prey item that a participant missed by), I cannot deduce whether misses were a consequence of a misidentification (participants falsely identifying a part of the scene as the prey item; prey item remains undetected) or due to an inaccurate capture attempt (participants 'snatch' at the prey item; prey item detected). While both possibilities remain interesting, resonating with existing anti-predator defence strategies, further investigation is necessary to assess the role of dappled light in this regard.

Remaining stationary maximised concealment in both experiments. This was not a floor effect, because more prey items were detected within the time limit than not. Unlike in the pilot experiment, however, the masking effect for stationary prey was relatively unaffected by the presence of dynamic or static illumination. This suggests that the effect of dynamic lighting is not via a non-specific increase in visual complexity, but enhanced noise in the domain that renders prey most salient: motion. While the success of remaining stationary is evident (consistent across experiments), the remaining data chapters will be limited to moving prey items. In this way, the emphasis can remain upon the extent to which motion signals (e.g. organism movement) can be masked by environmental motion noise.

There were consistently faster response times and fewer time-outs and misses for prey items found in shaded locations in Experiment 1. There are two reasons why this may be the case. Firstly, it could be an effect of participants optimising search efficiency, which, in part, is a consequence of the properties of the backgrounds used: there was a greater proportion of shade than light in the simulated scenes. Participants, therefore, could optimise their visual search by (i) searching in relatively homogenous regions (either shade or light) and (ii) searching in the most common background first (shade). Secondly, and not mutually exclusively, participants may have become adapted to a relatively dark background and so their contrast detection may become impaired when switching to fixate on an entirely light area of the scene. This would additionally explain the slower response times found for 'light only' paths for moving prey items (versus 'shade only' paths) and why they were never as slow as the mixed light pathways, as well as the greater proportion of misses for 'light only' paths. The difference in

detection levels for items in the open light areas of the scene remains interesting, as it runs counter to the expected benefit of easier detection in areas that are better illuminated (Théry, 2001).

Overall, these results emphasise the importance of considering the surrounding environment, as well as the target, and suggest a novel way in which camouflage and behavioural strategies can be directly influenced.

Chapter 5. Assessing the effect of pattern upon prey detection in the presence of water caustics.

Abstract

Organism movement is a highly conspicuous feature and, as such, can serve to increase predation risk. Yet, in Chapter 4, I demonstrate that this conspicuousness can be masked, and the costs of motion lessened under certain conditions, namely in the presence of dynamic illumination (e.g. water caustics or dappled light). Can the presence of dynamic water caustics similarly reduce the detectability of prey items that are both moving *and* patterned? Contrasting and repetitive patterns are a common feature of many reef fish which, at least to the human eye, appear highly salient. Participants searched for moving prey items with one of three repetitive patterns (parallel stripes, orthogonal stripes and chequerboard; low and high contrast) or a uniform mean luminance control. Prey items were presented within simulated scenes containing water caustics, which could be moving or static. The presence of dynamic water caustics (relative to static scenes) significantly increased response times when searching for prey items, irrespective of pattern. However, within such scenes, participants spent significantly longer searching for prey items with particular patterning: low contrast patterns were consistently harder to find and capture than high contrast forms, while one-dimensional (parallel and orthogonal) patterns were harder to find and capture than two-dimensional (chequerboard) patterns. However, no prey pattern influenced response times as effectively as the mean luminance control, which remained the hardest prey treatment to locate within dynamic scenes. There is evidence therefore that dynamic illumination can, to some extent, mask otherwise conspicuous prey items that are both moving and patterned, but further investigation is needed to fully assess the interaction between pattern and changing illumination.

5.1 Introduction

In Chapter 4, I demonstrate that the presence of dynamic illumination (e.g. water caustics or dappled light) can, to some degree, mask organism movement, a typically salient feature that predators can use in prey detection. The former, water caustics, dominate most shallow marine habitats, including coral reefs. Such habitats attract many mobile organisms that range in shape, size and, importantly, patterning. Many marine organisms have repetitive and contrasting patterning that, to the human-eye, appear visually conspicuous, driven, for example, by sexual selection, social signalling or aposematism; patterning such as high contrast stripes, bands and reticulations are common amongst reef fish (Alonso, 2015; Loew & McFarland, 1990; McFarland & Loew, 1983). Here, I wished to investigate (a) whether the presence of dynamic water caustics could reduce the detectability of prey items that were both moving and patterned and (b) whether specific forms of patterning influenced prey detection to a greater extent than other forms.

Following the same paradigm as the previous experiment, human participants tried to find moving prey items, with varying patterns, within simulated scenes of water caustics. Three distinct repetitive prey item patterns were used; one-dimensional parallel-to-motion stripes and orthogonal-to-motion stripes were chosen for their prevalence in natural systems, while two-dimensional chequerboard contains both forms of stripe, but is less common in nature (Figure 5.1). Each pattern was represented by a low and high contrast form. While one would expect objects that more closely match the relatively low contrast backdrop to receive least visual attention, the fact that water caustics consist of high contrast, repetitive edges suggests that objects with similarly high contrast components could also be masked (Figure 5.1). The six prey patterns were compared to a control prey item which was uniform mean luminance. Note the exclusion of chromatic prey patterns and backgrounds in this experiment, even though most patterned reef fish are simultaneously colourful. The latter remains a crucial component in visually guided marine organisms, and indeed may influence the noisiness of water caustics (Maximov, 2000), but will not be addressed here in an attempt to isolate the effect of pattern *per se* and to reduce the number of pattern treatments required.

5.2 Methods

Stimulus scene differences

Everything was identical to the methodology in Chapter 4, except for the prey item's appearance and motion: here it was a flattened three-dimensional plane (18 x 18 x 1 pixels; 0.9° visual angle; Figure 5.1) with a matt surface and mean luminance equal to that of the background (river pebbles, 1024 x 568 pixels). The prey item was accompanied by a square collision mesh (24 x 24 x 1 pixels). When viewed from above, as in the experiment, the prey item had a square area of 324 pixels. Though lacking apparent depth, the use of a plane as a prey item (versus hemisphere, as in the previous experiment) allowed the presentation of patterns upon the plane face without incurring three-dimensional pattern distortion. In this way, one can limit the extent to which the data could be explained by anything other than the pattern treatment group. There were three different pattern types used, each with a low and high contrast form: one-dimensional orthogonal stripes, one-dimensional parallel stripes and two-dimensional chequerboard, with 'orthogonal' and 'parallel' denoting the relationship with the direction of travel (Figure 5.1). While the orientation of each prey item (relative to the viewer) was largely determined by the random motion vector and therefore changed trial to trial, the orientation of pattern relative to the prey item motion remained. This was important given the suggestion that the orientation of patterns, such as stripes, can alter the way we perceive their motion parameters (e.g. speed; Allen, Baddeley, Scott-Samuel, & Cuthill, 2013; Hogan, Cuthill, et al., 2017; Murali & Kodandaramaiah, 2016). These six patterns were then compared to a control prey item with a hue equal to the mean luminance of the scene. One of the seven stimulus configurations was chosen at random prior to the appearance of the prey item for each trial. As Chapters 2 and 4 highlight, stationary prey items are always the most difficult to detect and so, while that is informative, this experiment is limited to moving prey items only, the focus for this thesis.

A total of 21 participants (19 female and 2 male, aged 18-22) were recruited opportunistically from the Psychology undergraduate population of the University of Bristol: each was naïve, had normal/corrected-to-normal vision and provided written consent in accordance with the Declaration of Helsinki. The experiment was approved by the Ethics of Research Committee of the Faculty of Science, University of Bristol. There were 350 trials per participant (50 replicates of each of the seven pattern treatments), in an order independently randomised for each participant. Participants had 5 seconds per

trial to detect and capture the prey item. An information sheet (relevant for the current experiment) and verbal instructions were provided in a manner identical to that outlined in Chapter 2).

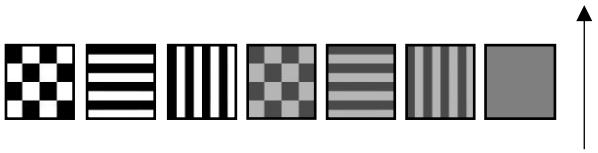

Figure 5.1 The prey item patterns and the direction of prey item movement (arrow). The prey item patterns include (from left to right) high contrast checkerboard, high contrast orthogonal, high contrast parallel, low contrast chequerboard, low contrast orthogonal, low contrast parallel and mean luminance (97 cd/m^2).

Analysis

All statistical analyses were performed in R 3.3.2 (R Foundation for Statistical Computing, www.R-project.org) and utilised linear mixed models (function lmer in the lme4 package; 24). The response variable was response time (RT), which were first aggregated to the median for each participant-treatment combination and then these were analysed using a model with Gaussian error. The full model included the fixed effects illuminant (static/dynamic), pattern (LCO, HCO, LCP, HCP, LCC, HCC) and their interaction, as well as the random effect of participant. The change in deviance between models with and without the predictors of interest was tested against a χ^2-distribution with degrees of freedom equal to the difference in degrees of freedom between the models. Pair-wise comparisons of pattern were carried using the Tukey-type correction for multiple testing provided by the multcomp package (Hothorn, Bretz, & Westfall, 2008).

5.3 Results

A significant interaction was found between the presence of water caustics and prey item pattern ($\chi^2 = 94.86$, d.f. = 1, $p < 0.001$). To establish why this interaction arose, dynamic and static caustics treatments were analysed separately: response times were significantly influenced by prey item pattern when in the presence of dynamic water caustics ($\chi^2 = 384.85$, d.f. = 9, $p < 0.001$) and, to a lesser extent, when water caustics were static ($\chi^2 = 64.42$, d.f. = 9, $p < 0.001$). Overall, the presence of dynamic water caustics with a scene reduces the detectability of moving prey items irrespective of pattern, relative to scenes with static water caustics (Table 5.1). However, pair-wise comparisons highlight how the efficacy of such reduction varies with pattern form (Table 5.2). In the presence of dynamic caustics, participants

spent longest searching for prey items with a mean luminance hue, while the low-contrast pattern forms took participants longer to detect than high-contrast pattern forms (Figure 5.2). Furthermore, one-dimensional pattern forms (orthogonal and parallel stripes) were less detectable than two-dimensional pattern forms (chequerboard), irrespective of contrast level. When water caustics were static, all prey items were equally rapidly detected.

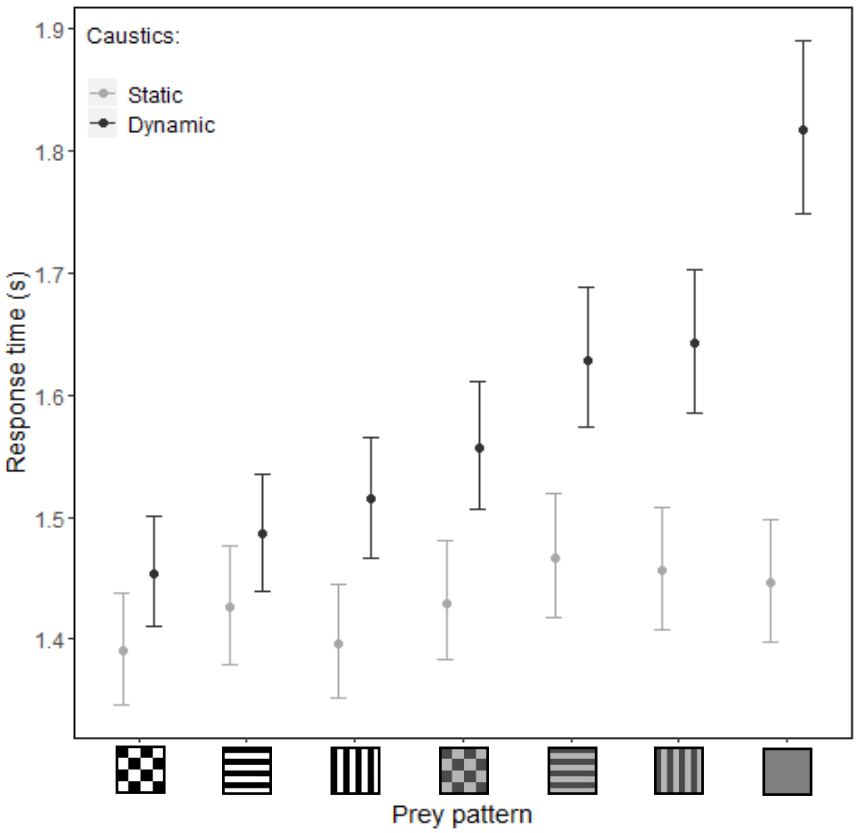

Figure 5.2 Mean response time (s) for patterned prey that moved within the presence of static and dynamic water caustics. Error bars indicate 95% confidence intervals derived from the linear mixed models. Prey item patterns were (from left to right) high contrast checkerboard, high contrast orthogonal (to motion), high contrast parallel, low contrast chequerboard, low contrast orthogonal, low contrast parallel and mean luminance (97 cd/m^2).

Table 5.1. Comparison of response times for each pattern treatment when in the presence of static and dynamic simulated caustics, with corresponding χ^2 and p values.

		ML	HO	HP	HC	LO	LP	LC
Response time (s):	*Static*	1.45	1.43	1.40	1.39	1.47	1.46	1.43
	Dynamic	1.81	1.49	1.52	1.45	1.63	1.64	1.56
χ^2		263.94	15.78	60.98	21.57	77.96	105.28	71.40
p		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Abbreviations for prey pattern treatments are ML: mean luminance; HO: high-contrast orthogonal stripes; HP: high-contrast parallel stripes; HC: high-contrast chequerboard; LO: low-contrast orthogonal stripes; LP: low-contrast parallel stripes; LC: low-contrast chequerboard.

Table 5.2. Pair-wise treatment comparisons for response time when in the presence of (a) static and (b) dynamic simulated caustics.

(a) Static caustics

	ML	HO	HP	HC	LO	LP	LC
ML	—	0.682	0.002	<0.001	0.676	0.981	0.855
HO	1.601	—	0.197	0.037	0.021	0.170	1.000
HP	3.930	2.403	—	0.998	<0.001	<0.001	0.107
HC	4.619	3.050	0.544	—	<0.001	<0.001	0.016
LO	-1.610	-3.229	-5.508	-6.256	—	0.986	0.057
LP	-0.838	-2.472	-4.799	-5.534	0.795	—	0.324
LC	1.293	-0.295	-2.668	-3.314	2.905	2.149	—

(b) Dynamic caustics

ML	—	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
HO	15.043	—	0.709	0.502	<0.001	<0.001	0.003
HP	13.489	-1.558	—	0.009	<0.001	<0.001	0.281
HC	17.356	1.867	3.470	—	<0.001	<0.001	<0.001
LO	7.79	-7.239	-5.677	-9.315	—	0.997	0.008
LP	7.19	-7.818	-6.277	-9.916	-0.594	—	0.001
LC	11.448	-3.801	-2.227	-5.815	3.528	4.126	—

Lower-left-hand triangle of both matrices are Tukey-type t-tests; upper-right-hand triangles are corresponding p-values. Abbreviations for prey pattern treatments are ML: mean luminance; HO: high-contrast orthogonal stripes; HP: high-contrast parallel stripes; HC: high-contrast chequerboard; LO: low-contrast orthogonal stripes; LP: low-contrast parallel stripes; LC: low-contrast chequerboard.

5.4 Discussion

The overall detectability of prey items was significantly reduced by the presence of moving water caustics, irrespective of pattern, which highlights that dynamic illumination can mask both movement *and* relatively conspicuous patterning. Moreover, some pattern forms were more difficult to detect than others under such conditions. All low contrast textured prey items were significantly more difficult to detect in the presence of moving, rather than static, water caustics; only one high contrast form (parallel stripes) followed this pattern. Presumably this is due to the former more closely matching the low contrast background relative to the high contrast light network which dominated the foreground, an effect accentuated if the latter is moving. Indeed, the efficacy of low contrast forms may infer that the introduction of colour (which, if not comprising black and white, would similarly reduce the pattern contrast) may not greatly hinder the masking effect. Crucially however, the optimal pattern treatment was uniform mean luminance, which may be due to the lack of internal luminance boundaries that would trigger motion detectors (Umeton et al., 2019). A number of prior studies, interested in the interaction between pattern, motion and detection, have highlighted a similar finding (Bekers, De Meyer, & Strobbe, 2016; Hughes et al., 2015, 2014; Santer, 2013; Stevens et al., 2008; von Helversen, Schooler, & Czienskowski, 2013). Indeed, the fact that cuttlefish often adopt a uniform pattern when moving may be indicative of a similar motion signal reduction strategy, though this is yet to be directly demonstrated (Zylinski et al., 2009).

The patterns used here have also received a lot of attention within the literature for dazzle colouration (see 1.4 in Chapter 1) and flicker-fusion camouflage (see below), two types of putative defensive colouration that depend on motion (Stevens & Ruxton, 2019). As discussed previously, dazzle camouflage is a mechanism by which perceived motion signals can be disrupted or distorted so as to reduce targeting accuracy (Behrens, 1999, 2012; Hogan, Cuthill, et al., 2016, 2017; Hogan, Scott-Samuel, et al., 2016; Hughes et al., 2015, 2014; Murali & Kodandaramaiah, 2018; Murali et al., 2018; Scott-Samuel et al., 2011; Stevens et al., 2011, 2008). This may be interesting as water caustic flicker, much like dazzle colouration, serves to create erroneous motion signals, hence there may be an accentuation of erroneous signals when the two are combined. One may also draw parallels between the repetitive high contrast boundaries of water caustics and the stripes necessary for inducing flicker-fusion camouflage, whereby orthogonally striped objects that are moving at a sufficient speed blur into

a uniform and featureless object, and reduce overall visibility (Endler, 1978; Stevens, 2007; Umeton, Read, & Rowe, 2017; Umeton et al., 2019). Here, if the directionality of water caustic flicker passing over a striped object matches that object's directionality, then the flicker fusion threshold may be reduced, or the effect enhanced.

An underlying criticism with such literature, however, is that findings are often sensitive to the task type and context, especially with the study of dazzle camouflage (see Hughes et al., 2014). This is unsurprising given that the concept of dazzle camouflage is based on the assumption that, due to the movement, the object in question is already detectable, and therefore the strategy instead concerns the vital period between detection and interception. So, while there may appear to be similarities between mine and previous findings, the context of the current study means generalisations may not be appropriate. Indeed, studies of the effect of different pattern types on distortions of perceived speed have found chequerboards to induce a greater bias than stripes (Scott-Samuel et al., 2011), whereas in my experiment, the chequerboard pattern was most rapidly detected. While these could be categorised as separate phenomena, it must be noted however that the spatial complexity of chequerboard here is lower than the striped pattern forms: this was a methodological oversight and will therefore require subsequent investigation.

Overall, the masking of pattern by dynamic illumination remains an interesting finding, particularly when one considers the prevalence of conspicuous fish patterning in shallow water habitats (Alonso, 2015; McFarland & Loew, 1983). While this experiment has been informative, more investigation is needed to draw firm conclusions. It may be better to use more ecologically relevant experiments, to assess how such patterning is viewed. For example, one could replace human observers with organisms of interest (e.g. reef fish) to search and capture patterned prey within simulated scenes. Similarly, one could measure the salience of patterned prey moving across a scene in relation to a specific visual system in question, both in terms of visual acuity (using software such as AcuityView; Caves & Johnsen, 2018) or in terms of chromatic sensitivity if colour is introduced to the prey items and scene. Moreover, an investigation that includes a more diverse spectrum of pattern contrasts (beyond 100% and 50%) should allow for a more reliable conclusion regarding its interaction with dynamic illumination.

Chapter 6. Assessing the effect of dappled light upon prey capture: domestic fowl (*Gallus gallus domesticus*).

Abstract

Dappled light is a common feature of sunny, vegetated habitats and can, when conditions are windy, become a source of dynamic visual noise. Here, I test the idea that the latter could mask movement and thereby reduce the risk of detection. Newly-hatched domestic fowl chicks (*Gallus gallus domesticus*), a proxy for wild forest-floor birds, were trained to peck moving, on-screen prey presented amongst two sources of dynamic dappled light: computer-simulated and created with a mirror ball. Dynamic dapple, however produced, increased the chick's latency to both fixate and peck the prey. Furthermore, dynamic visual noise masked motion in a way that static visual noise did not. This reduction in foraging efficiency should, I predict, have significant consequences for an organism's choice of habitat (as prey), foraging area (as predator) and its pattern of movement within a habitat (both).

6.1 Introduction

The findings outlined thus far are limited to human observers and therefore it is impossible to generalise to other species and other visual systems. Such systems may differ significantly from our own and, therefore, so will the perception of a given habitat and its features. Indeed, the impact of dynamic illumination upon non-human visual systems has never been directly quantified. Therefore, the next step was to extend the experiment outlined in Chapter 4 and focus on how dappled light may affect the foraging behaviour of domestic fowl chicks (*Gallus gallus domesticus*), which act as a useful proxy for wild foraging birds (Figure 6.1). Chicks are omnivorous, with a diet that includes moving invertebrate prey (Marino, 2017), and will, soon after hatching, stalk and peck appropriately at moving objects (Fantz, 1957; Over & Moore, 1981). As such, domestic fowl are easily trained and, together with their commercial availability, have since become a common model system for general bird vision, cognition and behaviour (Lisney et al., 2011; Marino, 2017; Miller & Hollander, 2010; Skelhorn & Rowe, 2006; Skelhorn, Rowland, Speed, et al., 2010). Crucially, the visual system of domestic fowl is also well characterised (Fantz, 1957; Ham & Osorio, 2007) with key disparities relative to human vision: domestic fowl are tetrachromatic (Miller & Hollander, 2010) and typically have a higher CFF (critical flicker fusion frequency) than humans (Jarvis, Taylor, Prescott, Meeks, & Wathes, 2002; Lisney et al., 2011) but a poorer visual acuity (Over & Moore, 1981). It is therefore possible that the perception of dynamic illumination will differ for humans and chicks, meaning that the resultant behavioural differences (when the latter is faced with such visual noise) are of prime interest.

Figure 6.1 Domestic fowl chicks (Gallus gallus domesticus) in the housing arena (Photo © S. Matchette). Upon arrival, each chick was given a unique combination of head, upper back and lower back markings using varying colours of non-toxic paint.

6.2 Methods

Pre-training and setup

Forty newly-hatched female domestic fowl chicks were obtained from Hy-Line International (www.hyline.com) and housed in the poultry facility of the University of Bristol Veterinary School for the duration of the experiment. By obtaining chicks within 24 hours of hatching, one could assume that they had no prior associations (either good or bad) with the type of lighting and screens used. All procedures were approved by the Animal Welfare and Ethical Review Body, University of Bristol.

Upon arrival, each chick was given a unique combination of head, upper back and lower back markings using varying colours of non-toxic paint (Kruuse, www.kruuse.com) for identification (Figure 6.1) and were housed in the same, 250 x 150 x 50 cm (L x W x H), arena with wood chip as substrate. The housing arena was subject to a light cycle that matched the ambient day-light cycle, achieved using ceiling daylight mimicking lamps (GEWISS, www.gewiss.com; twin 26 W LED) running in high-frequency (30 kHz+) ballasts, well above the CFF of domestic fowl (e.g. an average of 71.4 Hz; Jarvis et al., 2002, and 87.0 Hz; Lisney et al., 2011). The ambient temperature was maintained at 25-28 °C using multiple 175 W infrared heat lamps (General Electric, www.gelighting.com) positioned on a light rail c.60 cm above the arena. Any initial handling by experimenters was paired with a mealworm (*Tenebrio molitor*); this established a positive association with handling and familiarised chicks with the reward food item used in training and experimentation. The latter took place in a separate arena. Water and food were provided *ad libitum*, via water feeders and trays of chick starter crumb at substrate level (Farmgate, www.forfarmers.co.uk/poultry). The only exception to this was the removal of food trays for a short (30 min) pre-trial food deprivation period to increase the chick's motivation to forage in training and experimental trials. In addition to food and water, the housing arena also contained multiple objects that the chicks would encounter in the experimental arena, including a low perch, a hanging mirror ball and a computer monitor (details below). This exposure minimised any neophobic responses to these items when placed in the experimental arena. For example, the computer monitor was buried into the substrate such that chicks could walk over the screen in an identical manner to the experimental arena. Videos of training background scenes could then be presented on a continuous loop for the duration of the daylight hours.

The experimental arena, located across the room from the housing arena, was a cage measuring 120 x 50 x 50 cm (L x W x H) with wood chip substrate (Figure 6.2). At one end of this cage was a section (20 x 50 x 50 cm; L x W x H) partitioned off using wire mesh. This created an independent 'buddy area': in all training and experimental trials, two chicks were placed in this space to reduce any potential distress for the experimental chicks due to social isolation. A quarter of the chicks were allocated a buddy chick role and played no part as experimental chicks. Throughout training and experimentation, buddy chicks were changed every 25 trials, or sooner if they themselves started to emit distress calls (<5% of trials). At the opposite end to the monitor and buddy arena was a horizontal wooden perch used to loosely segregate a 'start pen' from which chicks could begin each trial. To ensure the correct ambient temperature, as in the housing arena, a 175 W infrared heat lamp was also present. An Akaso Brave 4 action camera (Akaso, www.akaso.org) was attached to the wire mesh above the monitor to record each trial from above. Recordings (4K resolution, 24 fps and 170° viewing angle) were then viewed post-hoc to analyse the chick's behaviour and to measure their responses.

Stimulus scene differences

The illuminant in question here was dappled light (see Common Methodology for the creation). The prey item for this experiment, like those in Chapters 2 and 4, was a sphere static mesh that, when viewed from above, appeared circular and was realistically shaded. To account for differences in visual system and motivation, the prey item size was increased (from a radius of 9.1 pixels to one of 18.7 pixels; 6.1° visual angle), the trials lengthened (from 8 to 60 seconds) and treatments using stationary prey were removed. The prey item had a mean luminance equal to that of the background. Movement was fixed at 24 mm/s (9.2 degrees/s at a viewing distance of 15 cm) and the prey item continued to move back and forth along its given vector for the duration of the trial. In addition to the simulated dappled light (henceforth, 'screen dapple') used in the previous experiment, another source of dappled light was introduced: a mirror ball (Showtec, www.showtec.co.uk; 500 mm diameter with 10 x 10 mm facets, suspended from a light rail) was used in conjunction with a spotlight (Arrilite 800, www.arri.com/lighting) to bathe the entire experimental arena in dappled light (Figure 6.2). The mirror ball could be left stationary or gently spun to create either static or dynamic dappled light. There were

therefore five treatments in total, in a 2x2+1 design: static mirror-ball dapple, dynamic mirror-ball dapple, static simulated dapple, dynamic simulated dapple, and no dapple illumination.

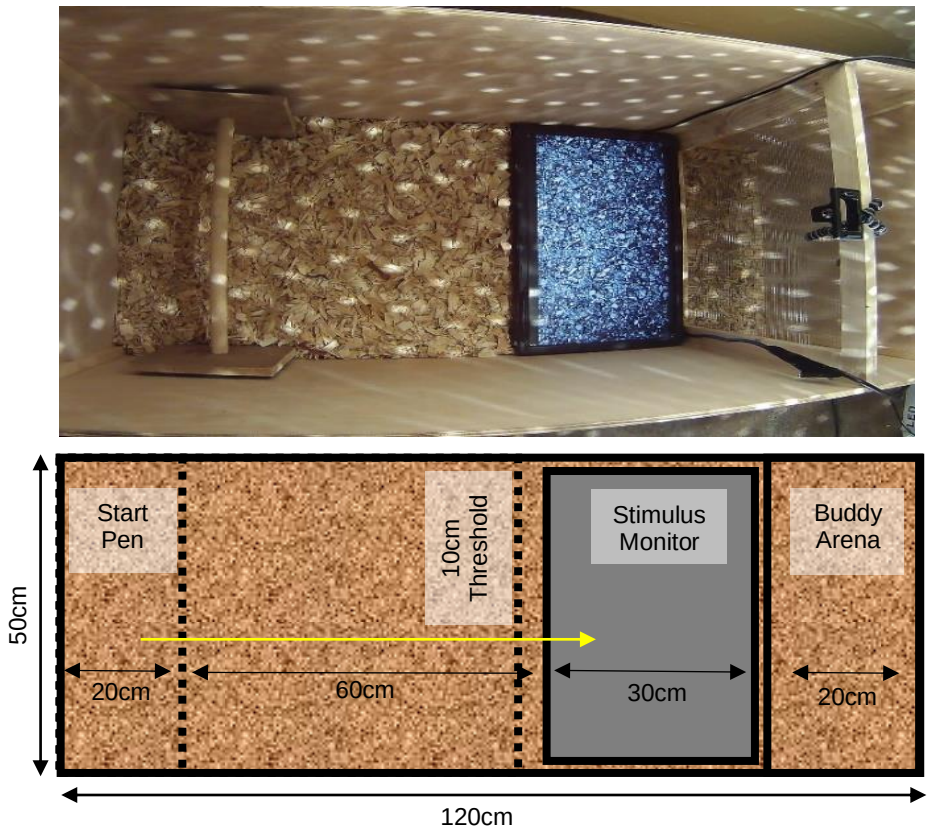

Figure 6.2 A photograph (above; Photo © S. Matchette) and diagram (below) of the experimental arena, viewed from above. Measurements not to scale. Chicks were lowered in at the start pen (denoted by the horizontal perch) and moved towards the stimulus monitor to forage. The buddy arena (beyond the monitor) was physically, but not visually, divided from the experimental arena with wire mesh. The recording device position can be seen on top of the wire mesh divider. Post-hoc video analysis determined the attack latencies from the start of trial to first successful peck, the former initiating when the chick passed within 10 cm of the monitor ("10cm Threshold"). This threshold was marked externally in pen on both flanks of the arena, though this is unseen in the photograph. The photograph also illustrates how the arena was viewed when in the presence of mirror ball dappled light.

Stimulus scenes were viewed at ~10-20 cm from a gamma-corrected 20″ Philips 200WS monitor (Philips, www.philips.co.uk), with a refresh rate of 75 Hz, an active LCD matrix and a resolution of 1680 x 1050 pixels. Because the Flicker Fusion Frequency of domestic fowl can sometimes exceed 90 Hz (Lisney et al., 2011), the use of a monitor with an active LCD matrix was desirable to ensure that any

aversion to the screen (due to visible flicker) was avoided (Oliveira et al., 2000). This monitor was positioned adjacent to the wire mesh and buried flush to the substrate. Each scene covered a screen area of 1680 x 950 pixels with a mean luminance of 80 cd/m^2 and had two spawn regions (210 x 650 pixels).

Protocol

Chicks were placed in the start pen and allowed to move towards the monitor to forage for the prey item. If a chick correctly pecked the prey item, a food reward was immediately dropped next to the chick and the trial stopped. A time limit of 2 min was given per trial. This process was repeated five times sequentially for each chick for a given treatment.

Response measures were derived from video recordings. Once a chick had passed a threshold of 10 cm from the screen (Figure 6.2), at which point it was possible to detect the prey item, a timer was initiated which marked the start of the trial. The time of first binocular fixation 'stalking' the prey was recorded, as well as the time of the subsequent peck at the prey. Attack Latency (AL) was defined as the overall time from trial start to first correct peck. This comprised Fixation Latency (FL), the time from trial start to first fixation, and Peck Delay, the difference in time between the first fixation and the first correct peck. To check the response measures for experimenter bias, as well as their replicability, a panel of nine independent raters recorded several response measures from a random sample of videos spanning all treatments which could be compared to the original experimenter recordings.

Training and experimental phase

Several training steps were necessary to introduce the experimental task, as well as each component of the experiment. The training phase involved four steps with stimuli displayed upon the monitor, with the screen set to white (Table 6.1). Each step was conducted within the experimental arena and aimed to introduce key elements of the later experiment. The first step introduced the computer-generated, spherical prey item. This step was critical to establish an association between the prey on the screen and reward. To achieve this, prey items remained stationary with a mealworm placed beside (so as not to obscure the target). The second step introduced a moving prey item; a food reward was initially given once the chick had approached the prey item, which encouraged later pecking. The third and fourth steps then introduced a moving prey item in the presence of dappled light created via the mirror ball and computer simulations respectively. Both forms of dappled light were initially introduced statically,

then later dynamically. Each chick completed no more than three training blocks in a day, with at least a 1.5 -h gap between each block. Each training phase continued until chicks could reliably search for the prey item and consume the reward; any chicks that consistently failed to reach this criterion were converted to ‘buddy’ chicks. Eighteen chicks met the criterion and entered the experiment.

The experimental phase mimicked the format of the training phase, but with a more complex and context-relevant background (Figure 3.3). The selected background was used “out of the box”, with RGB range and mean values as supplied by Unreal Engine, as these were already judged to be realistic and, in any case, precise simulation of a real forest-floor background (that these chicks had never experienced) was unimportant for the experiment’s goals. The target luminance was then adjusted to match the mean background luminance. All treatments were run twice and in a randomised order, totalling 10 trials (2 x 5) per chick for each treatment. If a chick did not peck the target within 1 min, the trial was ended and the chick was returned to the home arena. Throughout the experimental phase, chicks pecked the target within 1 min in 82% of trials (mean Attack Latency 3.2 s, median 2.1 s, range 0.6 - 45.3 s) and all chicks did so in at least five of the 10 trials per treatment. Failures to peck were associated with specific chicks rather than particular treatments (only two chicks completed as few as five trials for a treatment and these two chicks completed < 10 trials for all, and four of the five, treatments respectively). Once the experimental phase was complete, all chicks were donated to free-range small holdings.

Table 6.1. The number of trials completed by each chick during both the training and experimental phases of the study.

Training phase:	Screen:	Prey item:	Dappled light:	No of trials per chick:
Step 1	White	Stationary	Absent	25
Step 2	White	Moving	Absent	15
Step 3:				
a	White	Moving	Mirror ball: static	5
b	White	Moving	Mirror ball: dynamic	10
Step 4:				
a	White	Moving	Simulated: static	5
b	White	Moving	Simulated: dynamic	10
Experimental phase:				
Treatment 1	Leaf litter	Moving	Absent	10
Treatment 2	Leaf litter	Moving	Mirror ball: static	10
Treatment 3	Leaf litter	Moving	Mirror ball: dynamic	10
Treatment 4	Leaf litter	Moving	Simulated: static	10
Treatment 5	Leaf litter	Moving	Simulated: dynamic	10

Analysis

All statistical analyses were performed in R 3.3.2 (R Foundation for Statistical Computing, www.R-project.org) and utilised generalized linear mixed models (function glmer in the lme4 package; Bates et al., 2017). The response variables were Attack Latency, Fixation Latency and Peck Delay, all with Gamma error and inverse link functions. The gamma link was used because of positive skew in the raw time data. The full model included the fixed effect treatment and the random effect of chick ID. The change in deviance between models with and without the predictors of interest was tested against a χ^2 distribution with degrees of freedom equal to the difference in degrees of freedom between the models. Treatment effects were examined using a custom contrast matrix that represented the a priori comparisons of interest: the main effects of Display (mirror-ball vs screen dapple), Motion (static vs dynamic) and their interaction), plus a set of pairwise comparisons between each treatment and the dapple-absent control. This matrix has more contrasts than there are degrees of freedom, so the single step method provided by the multcomp package (Hothorn et al., 2008) was used to correct for multiple testing. The test statistic for these contrasts was the standardised normal deviate (z). For those interested in other comparisons, the full set of pair-wise comparisons, using the Tukey procedure in multcomp, is also provided.

To check the response measures for experimenter bias, as well as their replicability, nine, naive, independent volunteers estimated both fixation latency and pecking delay from 25 sample videos spanning all treatments. The 10 sets of timings for each of the response measures were then compared using the intra-class correlation coefficient (Shrout & Fleiss, 1979); function ICC from the R package psych (Revelle, 2017). Because bias is of interest as well as correlation, I also compared these nine volunteers' data to those of the original experimenter using paired t-tests.

6.3 Results

Repeatability and bias

For fixation latency, the intra-class correlation coefficient was 0.82 (95% c.i. 0.73 - 0.90; $F_{24,216} = 47.0$, $P < 0.001$). In pair-wise tests, there was no difference between my data and those of the nine naive volunteers (range of mean differences: -0.05 to 0.04 s, five means being negative and 4 positive; $0.12 < t_{24} < 0.99$; $0.334 < P < 0.907$). For pecking delay, the intra-class correlation coefficient was 0.98 (95% c.i. 0.96 - 0.99; $F_{24,216} = 462.0$, $P < 0.001$). In pair-wise tests, there was no difference between my data and those of eight of the nine naive volunteers (range of mean differences: -0.04 to 0.05 s, five means being negative and 4 positive; $0.05 < t_{24} < 1.84$; $0.079 < P < 0.962$). One rater's pecking delay times were significantly longer than mine (mean difference: 0.25 s; $t_{24} = 4.19$, $P < 0.001$), but this rater's times were also significantly longer than those of the eight other naive raters (range of mean differences: 3.13 to 0.30 s; $3.13 < t_{24} < 4.79$; all $P < 0.005$). Therefore, this rater was considered to be an outlier and my data to be unbiased compared to those of the others. My data were therefore considered suitable for further analysis.

Main analyses

When domestic fowl were presented with moving prey items, the Attack Latency was significantly longer when in the presence of dynamic computer-simulated dappled light than dynamic mirror ball dapple light, and both of these treatments had longer latencies than any other treatments (treatment $\chi^2_4 = 269.87$, $P < 0.001$; Figure 6.3 & Table 6.2: Attack Latency). Breaking down this overall treatment effect, there was a significant interaction between Display and Motion ($z = 3.95$, $P < 0.001$) so, to establish why, mirror-ball and screen dapple treatments were analysed separately. Dynamic dapple increasing attack latency in both conditions, but more than twice as much with screen dapple (104% increase; $\chi^2_1 = 178.77$, $P < 0.001$) than with mirror-ball dapple (41% increase; $\chi^2_1 = 56.07$, $P < 0.001$). Attack latency

for both dynamic dapple treatments was significantly longer than in the dapple-absent control (mirror: z = 5.31, P = 0.111; screen: : z = 9.64, P = 0.111). The Attack Latency under static mirror-ball dapple did not differ from that in the absence of dappled light (z = 2.30, P = 0.111), but latency in the absence of dappled light was longer than in the static screen-dapple treatment z = 4.30, P < 0.001).

Table 6.2. Pair-wise treatment comparisons for overall Attack Latency and its components (Fixation Latency and Peck Delay).

	Abs	MS	MD	SS	SD
Attack Latency:					
Abs	—	0.780	<0.001	0.136	<0.001
MS	1.15	—	<0.001	0.779	<0.001
MD	-5.66	-6.76	—	<0.001	<0.001
SS	2.33	1.15	8.01	—	<0.001
SD	-10.39	-11.46	-4.71	-12.77	—
Fixation Latency:					
Abs	—	0.712	<0.001	0.986	<0.001
MS	1.27	—	<0.001	0.380	<0.001
MD	-4.23	-5.46	—	0.002	<0.001
SS	-0.52	-1.79	3.75	—	<0.001
SD	-17.61	-18.74	-13.29	-17.23	—
Peck Delay:					
Abs	—	0.562	<0.001	0.001	0.684
MS	-1.50	—	<0.001	0.158	1
MD	4.19	5.65	—	<0.001	<0.001
SS	-3.80	-2.26	-7.99	—	0.103
SD	-1.31	0.19	-5.46	2.45	—

Lower-left-hand triangle of each matrix are Tukey-type t-tests; upper-right-hand triangles are corresponding p-values. Abbreviations for dapple treatments are Abs: absent; MS: mirror static; MD: mirror dynamic; SS: screen static; SD: screen dynamic.

The above treatment differences were largely driven by Fixation Latency, with the pattern and significance of treatment differences matching those for Attack Latency (treatment χ^2_4 = 601.87, P < 0.001; Figure 6.3 & Table 6.2: Fixation Latency). There was a significant interaction between Display and Motion (z = 7.09, P < 0.001). Analysing mirror-ball and screen dapple treatments separately, dynamic dapple increased Fixation Latency in both conditions, but far more with screen dapple (164% increase; χ^2_1 = 247.70, P < 0.001) than with mirror-ball dapple (19% increase; χ^2_1 = 15.35, P < 0.001).

Attack latency for both dynamic dapple treatments was significantly longer than in the dapple-absent control (mirror: $z = 3.06$, $P = 0.013$; screen: : $z = 16.43$, $P < 0.001$). The Attack Latencies under static mirror-ball dapple and screen dapple did not differ from that in the absence of dappled light ($z = 0.48$, $P = 0.984$, $z = -0.55$, $P = 0.975$, respectively).

The treatment differences in the delay from fixation to pecking were significant but simpler ($\chi^2_4 = 108.58$, $P < 0.001$; Figure 6.3 & Table 6.2: Peck Delay). There was no significant interaction between Display and Motion ($z = 0.184$, $P = 1.000$) but main significant main effects of Screen and Motion. Dynamic dapple increased peck delay by 53% compared to static ($z = -7.47$, $P < 0.001$) and mirror dapple increased delay by 86% compared to screen-based dapple ($z = -5.26$, $P < 0.001$). Compared to the dapple-absent control, dynamic mirror dapple increased peck delay ($z = -4.45$, $P < 0.001$), static screen dapple reduced it ($z = 5.50$, $P < 0.001$), and both static mirror ($z = 2.39$, $P = 0.093$) and dynamic screen dapple ($z = 0.78$, $P = 0.916$) showed no significant difference.

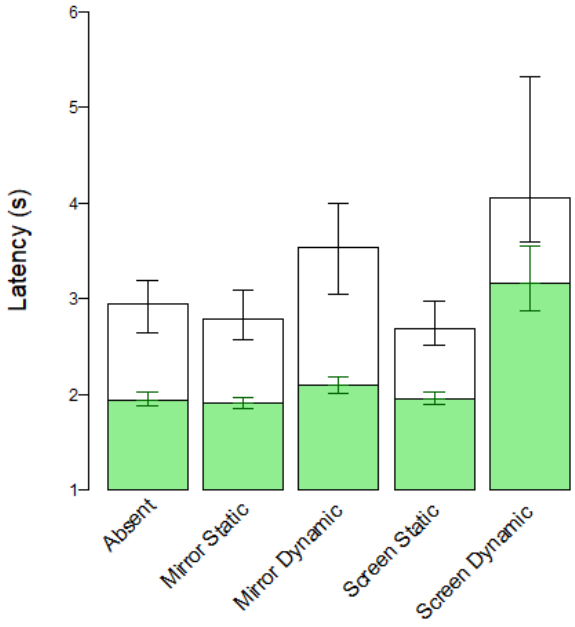

Figure 6.3 Mean fixation latency (green) and overall attack latency (white) of chicks across the five treatments. The difference between the two latencies represents Peck Delay. Error bars for Fixation Latency (dark green) and Attack Latency (black) indicate 95% confidence intervals derived from bootstrapping the linear mixed models (1000 simulations, function confint.merMod(method='boot) from the R package lme4).

6.4 Discussion

The ability of domestic fowl to forage for on-screen prey is influenced by the presence of dynamic dappled light in the same manner as in humans. Moreover, this effect is consistent irrespective of the method used to create the dynamic dappled light: both screen dapple and mirror ball dapple increased the latency to fixate and to attack relative to their static counterparts.

There are four obvious explanations for these data. Firstly, they could be a consequence of a neophobic response to the dynamic dappled light. Neophobia is a common response of domestic fowl and, therefore, efforts were made to ensure this was minimised: chicks were familiarised with each independent experimental feature during training and only chicks that reached a consistent response threshold were taken on to the experimental phase. Secondly, the data could be explained in terms of a non-specific visual distraction from the task at hand induced by the dappled light. This seems unlikely given that the latency to fixate was higher for screen dapple treatments than for mirror dapple (median of 2.3 > 1.1 s), which suggests that the interference of visual field was localised to the search area rather than a non-specific distraction. Thirdly, it could be that the regions of dappled light represent a more visually complex environment and therefore reduce search efficiency, an effect already highlighted in birds and humans (Dimitrova & Merilaita, 2010; Merilaita et al., 2017; Xiao & Cuthill, 2016). However, this is unlikely given that there is no effect of static dapple treatments upon successful foraging, despite static dapple representing a comparably spatially complex environment. The most convincing explanation is that dappled light lowers the SNR: the specific features of the prey that are used for detection and the subsequent attack are drowned out by the moving dappled light (Merilaita et al., 2017). Both sources of dappled light create motion, luminance and edge noise, all features used to discriminate a target from the background. The greater effect of screen dapple versus mirror ball dapple is consistent with this, because the former creates more moving false luminance edges in the specific area the target is to be found.

In contrast, static dapple, whether produced by mirror ball or only on the computer screen, has little, if any, effect. This might seem surprising because a scene with dappled light has a higher contrast range than without and therefore would appear more visually complex (Dimitrova & Merilaita, 2010; Dimitrova, Stobbe, Schaefer, & Merilaita, 2009; Xiao & Cuthill, 2016). Further, these multiple high contrast light points, particularly for static mirror ball dapple, might act as distractors (Dimitrova et al., 2009).

Nevertheless, the chicks did not appear to be affected: indeed, the peck delay was slightly but significantly longer for scenes with an absence of dappled light than static screen dappled light. A key take-home message is therefore that static noise does not mask dynamic signals (the moving target), but dynamic noise does.

An important methodological note is that, although two sources of dappled light were used that differed in their 'scope of influence' (global or limited to screen), they also differed in terms of spatial structure and the dynamic of dappling (Figure 3.2 versus that seen in Figure 6.2). Of the two, screen dapple is more realistic as it is modelled to match the spatiotemporal properties of real forest dapple flicker. In contrast, mirror ball dapple represented a more predictable light flicker, a product of the uniform mirror ball facets: light spots that move along a parallel trajectory at roughly a constant speed and spacing. In addition, due to its top-down projection, mirror ball dapple could be momentarily occluded by the chick itself and may not consistently project upon an area that the chick is investigating, possibly resulting in a ceiling effect. Indeed, this may be the reason for the differences in fixation latency between the two dynamic treatments and why there was minimal effect of static mirror ball dapple versus the absent control. Nevertheless, mirror ball dapple provides an alternative form of dapple that, when dynamic, still exerts an influence over the ability of chicks to forage successfully.

Chapter 7. Assessing the effect of water caustics upon prey capture: triggerfish (*Rhinecanthus aculeatus*).

Abstract

Dynamic illumination is common in terrestrial and aquatic environments, but is particularly relevant to the animals that inhabit coral reefs where the reticulate patterns known as 'water caustics' play chaotically in the shallows. In behavioural experiments with a wild-caught reef fish, the Picasso triggerfish (*Rhinecanthus aculeatus*, family: Balistidae), the presence of dynamic water caustics is shown to affect prey detection and attack latency of moving prey items negatively. Manipulating two features of water caustic form (clarity and scale) reveals that the masking effect is likely to be most effective in shallow water. This investigation is the first to (1) address the impacts of dynamic underwater illumination upon fish behaviour and (2) directly assess how visual features of water caustics can affect visually guided behaviour.

7.1 Introduction

While the use of domestic fowl chicks offered an insight into the influence of dynamic illumination upon non-human visual systems, the ability to draw strong conclusions about ecologically valid impact is limited: domestic fowl have a recent wild ancestor and act as a good proxy, but can no longer be considered 'wild'. It was therefore desirable to turn the attention towards an organism that has more ecologically pertinence: *Rhinecanthus aculeatus*, commonly known as the blackbar, Picasso or lagoon triggerfish (Figure 7.1). Triggerfish have a broad distribution in shallow marine environments across the Indo-Pacific region, typically associating with coral reefs or rubble (Witte & Mahaney, 2001) and feeding upon a variety of (primarily) benthic organisms (Randall, 1985). Moreover, the visual system of *R. aculeatus* has been extensively studied (Champ, Vorobyev, & Marshall, 2016; Champ et al., 2014; Cheney, Newport, McClure, & Marshall, 2013; Pignatelli, Champ, Marshall, & Vorobyev, 2010).

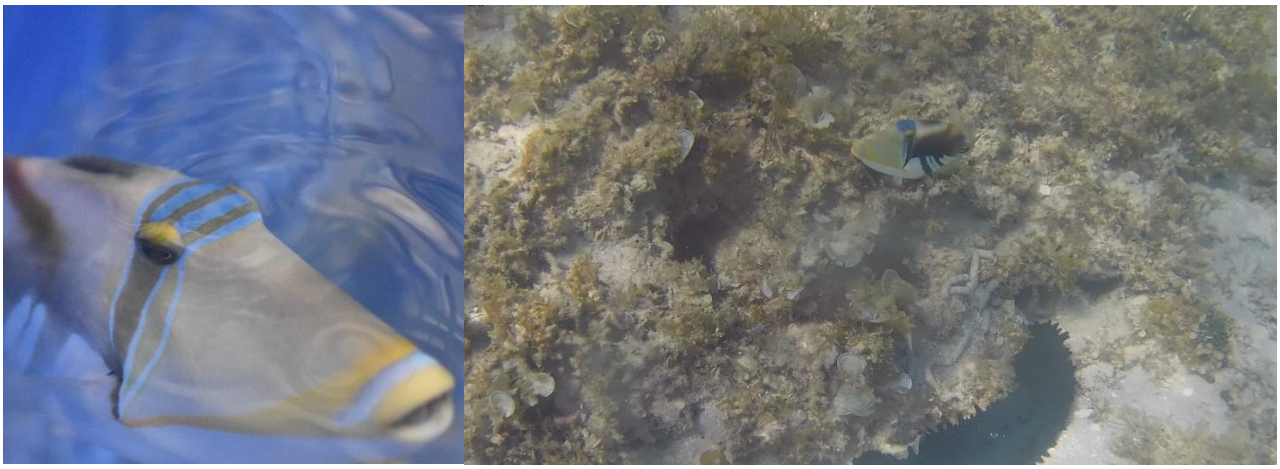

Figure 7.1 A close-up (left) of a Picasso triggerfish, Rhinecanthus aculeatus, as well as a video frame (right) of an individual within the shallow reef flat habitats off Casuarina Beach, Lizard Island, Great Barrier Reef, Australia (14°40 8 S, 145°27 34 E; Photos © S. Matchette).

The primary aim of the experiment was to highlight that, as in humans and domestic fowl, dynamic illumination (here water caustics) can hinder visual detection by masking simulated prey item movement. Water caustics are a common phenomenon within the shallow habitats that Picasso triggerfish, and countless other reef fish, grow and live in (Figure 7.1). The caveat here is that many pelagic marine organisms have visual systems that have evolved in the presence of water caustic flicker; putatively as a consequence, the contrast sensitivity of these organisms arise from frequency

responses that fall within the frequency of water caustic flicker, facilitating the detection of reflective objects in midwater (Loew & McFarland, 1990; McFarland & Loew, 1983; Sabbah et al., 2012). Here, however, I test the assumption that near to the substrate, where a reflective object is viewed against a flickering background, the organism is no longer able to distinguish signal from noise, and detection is hindered. If this is the case, it would suggest an underlying visual trade-off that is limiting the temporal vision of some fish for certain visual tasks, including prey detection. This experiment also offered an opportunity to begin exploring whether the disruptive effect of varying illumination is relative to specific visual features of water caustics (beyond general motion). Two features of water caustics are manipulated in this experiment, the scale of caustic shade and the sharpness of caustic boundary, both of which are broadly associated with a change in water and focal depth (Lythgoe, 1979; McFarland & Loew, 1983). In deeper water, the spatial scale of caustics is larger and they have more blurred edges (Lythgoe, 1979; McFarland & Loew, 1983). I use scenes with static caustics as control treatments that, while non-existent in nature, provide an opportunity to isolate illuminant motion and control for spatial complexity, as the latter has been shown to reduce search efficiency in some taxa (Dimitrova & Merilaita, 2010; Merilaita et al., 2017; Xiao & Cuthill, 2016).

7.2 Methods

Animals

Sixteen wild-caught *R. aculeatus* were caught using hand nets and clove oil from shallow reef flats off Casuarina Beach, Lizard Island, Great Barrier Reef, Australia (14°40 8 S, 145°27 34 E) and released at the same location once the study was completed. Fish were collected under a Great Barrier Reef Marine Park Authority Permit G16/38497 and Queensland General Fisheries Permit 183990. All procedures were approved by the Animal Welfare and Ethical Review Body of the University of Bristol (UIN/UB/18/084) and the Animal Ethics Committee at the University of Queensland (QBI/304/16). Fish were measured upon capture and ranged from 65 – 130 mm (standard length; excludes caudal fin): individuals were deemed to be subadults and adults, and displayed similar levels of motivation to peck at prey items of the size presented.

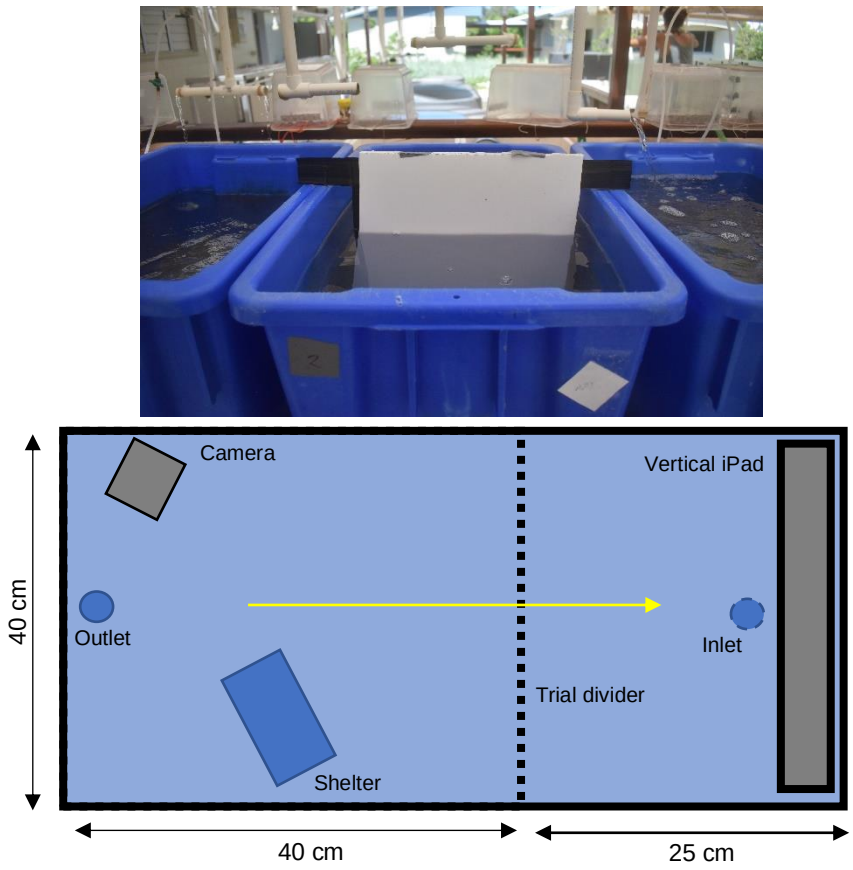

Figure 7.2 A photograph (above; Photo © S. Matchette) and diagram (below) of the individual aquaria. The trial divider was initially inserted to isolate the fish in the left-hand side (or near side in the photo) of the aquaria. The iPad was then lowered into the opposite side and the stimulus video file was loaded. When the iPad was ready, the camera was attached and recording started. The trial divider was then lifted (denoting the start of the trial) and the fish moved from the left side to the right side, to search for and peck on the prey item presented on the iPad (denoting the end of the trial). The shelter was necessary for well-being of the fish throughout the duration of the study and remained in the left-hand side of the aquaria during experimental trials. The water inlet tube, suspended above the right-hand side, was switched off prior to any training or experimental trial.

Fish were housed individually in experimental aquaria (blue plastic tanks; 68 L volume; 65 cm x 40 cm x 40 cm; L x W x H) exposed to ambient daylight (Figure 7.2). Shade nets were fitted around the workbench to reduce the impact of direct sunlight during the early morning and late afternoon hours. Each aquarium had a seawater inlet (from the source of capture), an outlet pipe and an appropriately sized shelter. All tanks were labelled with the date and location of capture, individual ID and number. An acclimatisation period of 24 h was permitted before beginning any feeding regime. Fish were initially

fed thrice daily (morning, noon and afternoon) to habituate to human presence and introduce their reward food item: a small (2mm) piece of diced squid (*Doryteuthis opalescens*; Qualy-Pak Inc, CA, USA) which was offered with tweezers or, if not eaten directly, dropped to await later consumption (no longer than 30 min). Fish only began training once they consistently and readily took food directly from the tweezers.

Stimulus scene differences

The illuminant of interest here was water caustics (see Common Methodology for the creation). With the exception of the illuminant simulated, the experimental scenes presented in this experiment mirrored that of the previous chapter, necessary to account for non-human visual systems and motivation. Prey items remained as sphere static meshes that, when viewed from above, appeared circular (radius of 18.7 pixels; 3.7° visual angle) and was realistically shaded. Movement was fixed at 24 mm/s (5.5 degrees/s at a viewing distance of 25 cm). While the use of prey items with the exact size and speed of wild triggerfish prey would have been ideal, the choice was made difficult by their broad diet, which ranges from slow-moving molluscs to fast-moving fish (of varying sizes). Instead, as with domestic fowl in the previous chapter, the size and speed of prey item presented was such that fish would readily respond to, and be capable of pecking at, in nearly all trials. Screen recordings (60 s) of each simulated scene running in Unreal Engine 4 were made (via Bandicam, www.bandicam.com) to create an external bank of stimulus videos. All stimulus videos were presented on an iPad Air I (Apple, CA, www.apple.com), which has an LCD capacitive touchscreen (disabled) with a resolution of 1536 x 2048 pixels and a refresh rate of 60 Hz. The iPad had waterproof housing (LifeProof, www.lifeproof.com) and was placed in a transparent waterproof bag (Overboard, www.over-board.co.uk) with its long dimension horizontal. Each scene was monochromatic, covered a screen area of 1680 x 1020 pixels and was viewed from a bird's-eye perspective. There were a total of eight treatment groups (2^3 factorial design), distinguished by the scale, sharpness and motion of caustics present (Figure 7.3): fine scale diffuse moving, fine scale diffuse static control, fine scale sharp moving, fine scale sharp static control, coarse scale diffuse moving, coarse scale diffuse static control, coarse scale sharp moving, coarse scale sharp static control. The four treatments in which the motion of caustics was static acted as experimental controls, allowing for equal spatial complexity across scenes with and without motion. Mean luminance of the scene varied with treatment background (fine sharp: 110 cd/m^2, coarse sharp: 138 cd/m^2, fine diffuse: 151 cd/m^2, coarse diffuse: 139 cd/m^2).

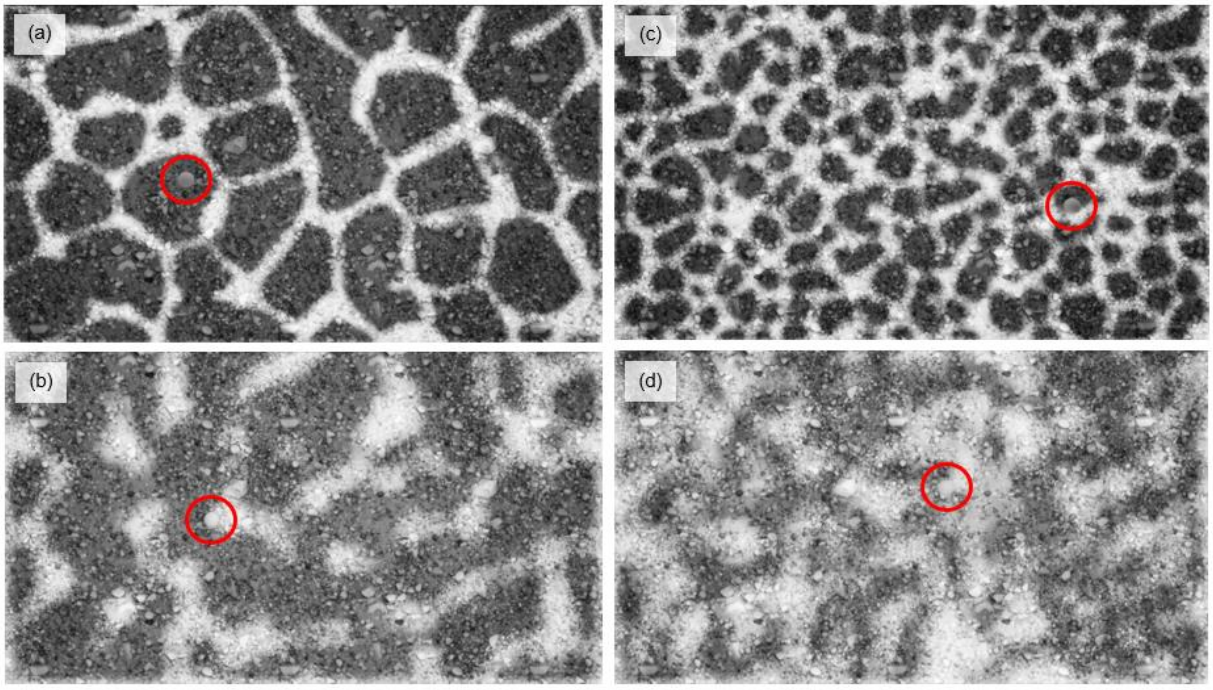

Figure 7.3 Screenshots of the four static treatment groups that, with four identical but dynamic groups, made up the eight experimental groups. Each screenshot shows the prey item (artificially circled in red) midway through a trial, moving across the scene. Caustic shade could be either coarse (a, b) or fine (c, d) scale, while caustic boundaries could be sharp (a, c) or diffuse (b, d) in contrast.

Training phase

A total of seven training stages were required to introduce each experimental aspect in turn (Table 7.1). First, fish were presented with a static prey item hand-drawn on to a white PVC feeding board, identical in dimensions to the simulated prey item and iPad respectively. The pieces of squid used as a reward were naturally adhesive and could be stuck onto the feeding board or iPad screen, as appropriate. Fish were initially encouraged to approach the feeding board and prey item by positioning some squid next to the prey item (five sessions). For fish that did not immediately approach, the board could be left in the tank for an extended period to allow food to be taken in their own time and to reduce the novelty of the board. Second, the prey item with accompanying squid was presented on an iPad displaying a white background (seven sessions). Third, fish approached and pecked the prey item without food present (six sessions), with fish being tweezer-fed a squid reward immediately after a successful peck. At this point fish could then progress on to attacking a moving prey item (seven sessions).

The final three stages of training introduced (1) the trial divider and camera for recording behaviour (six sessions), (2) an example set of simulated caustics overlaid on a white background (six sessions) and (3) the experimental scene substrate without caustics (four sessions). Fish moved on to the next training stage when they had completed at least four sessions and achieved at least an 80% cumulative success rate. A total of 10 trials were completed for each session, with two sessions daily (morning and afternoon).

The procedure for the final training sessions remained the same throughout experimentation. The trial divider was positioned in the aquaria to restrict the fish to the non-iPad end of the aquaria, together with the camera which was set to record. The trial divider was a large section of white plastic that, when placed in the tank (25 cm from iPad), isolated the fish from the iPad and blocked the view of the camera. The camera, an Akaso V50 Pro (Akaso, www.akaso.net; 4K resolution, 30 fps and 170° viewing angle), was housed in a waterproof case and attached with a suction clip onto the left wall of the aquaria, 10 cm from the non-iPad aquarium wall. The video files of a given treatment were queued and shuffled on the iPad. The divider was lifted (trial start) to allow the fish to find the prey item (Figure 7.4). Upon a successful peck (trial end), fish were rewarded with the food item and the trial divider refitted. The next video file was loaded, and the process repeated. Post-hoc video analysis was used to measure the latency of attack (trial start to trial end).

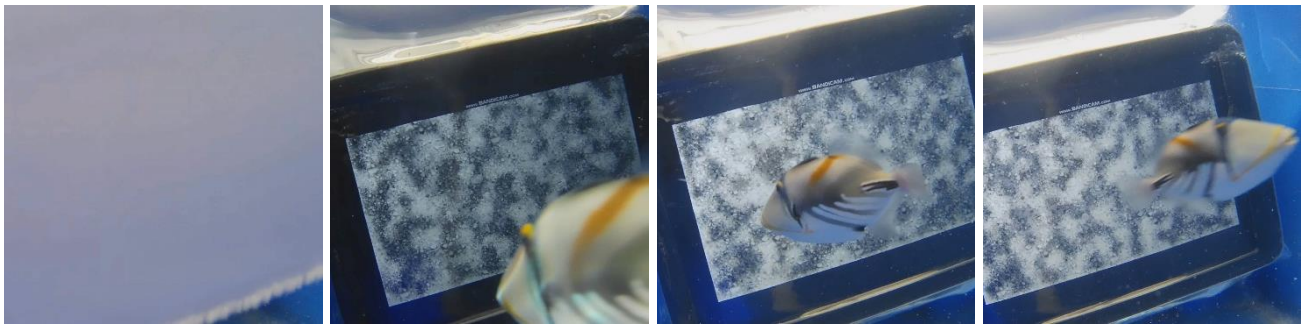

Figure 7.4 Frames taken from an experimental trial video post-hoc (Photos © S. Matchette). The trial divider is first removed (a), at which point the fish quickly swims towards the iPad (b) and the trial timer is initiated. The fish searches for the prey item on the iPad screen within the simulated scene (c), here presenting fine scale and diffuse water caustics. Once successfully pecked, the trial timer is stopped, and the fish immediately swims back to the researcher to collect a food reward (d).

Both feeding board and iPad were presented in the same way: lowered in on a modified hand net to the far end of the aquaria, perpendicular to the base. Though caustics in nature would differ in form if viewed

from this perpendicular angle (McFarland & Loew, 1983), it minimised the influence that angle of attack had on the ability to see the target: most fish would approach a face on target in a more uniform manner, whereas controls of entry would need to be installed if approached top-down. Water input was also shut off for every feed and training session to (1) avoid washing the squid off the board, and (2) to act as a cue for the fish that food was imminent – most fish would leave their homes at this cue.

Table 7.1. The number of trials completed by each fish during the training phases of the study.

Training phase:	Purpose:	No of trials per fish:
I	Introduce feeding board, squid in view, static prey	50
II	Introduce iPad, squid in view, static prey	70
III	Squid as reward on successful peck, static prey	60
IV	Introduce moving target, squid on peck	70
V	Introduce camera and divider	60
VI	Introduce simulated caustics (on white background)	60
VII	Introduce experimental substrate (no caustics)	40

Experimental protocol

Each fish completed ten trials for each treatment block, with two treatment blocks a day (am and pm), for four days. The order of treatment blocks was different for all fish. After four days, this process was repeated, staggering the treatment order by one to minimise any influence that pm vs am sessions may have upon motivation and satiation levels. Another repeat (of only five trials each) ensured that each fish had 25 trials per treatment. Throughout the experimental phase, fish pecked the prey item within a range of 0.6 and 52 s after presenting the stimulus, and within 1 min for 99% of trials (median Attack Latency 3.2 s, IQR 4.4 s).

Statistical analysis

All statistical analyses were performed in R 3.3.2 (R Foundation for Statistical Computing, www.R-project.org) and utilised linear mixed models (function lmer in the lme4 package; Bates et al., 2017). The response variable was Attack Latency (log transformed) with Gaussian error and identity link function. The transformation was necessary to normalise residuals in the face of skew in the raw time data. The primary model included the fixed effects caustic motion (static versus dynamic), caustic scale

(fine versus coarse) and caustic sharpness (diffuse versus sharp), the three- and two-way interactions and the random effect of fish ID. Initially, the change in deviance between the model with and without the predictors of interest was tested against a χ^2-distribution with degrees of freedom equal to the difference in degrees of freedom between the models. A secondary model included the fixed effect treatment and the random effect of fish ID. Pair-wise comparisons were carried out using the Tukey-type correction for multiple testing provided by the multcomp package (Hothorn et al., 2008).

7.3 Results

The data demonstrate that the detection of moving prey items by *R. aculeatus* is significantly disrupted by the presence of dynamic illumination (Fig. 2). This effect can be directly attributed to changes in the three features of water caustics which were manipulated: fish were significantly slower to attack the prey item when caustics were moving ($\chi^2 = 290.0$, d.f. = 1, $p < 0.001$), when caustic boundaries were sharper ($\chi^2 = 27.6$, d.f. = 1, $p < 0.001$) and when the scale of caustic shade was fine ($\chi^2 = 15.1$, d.f. = 1, $p < 0.001$; Figure 7.5 and Table 7). The fastest attack latencies arose when the presented caustics were static, irrespective of scale and sharpness, with these four (control) treatments indicating a baseline for triggerfish responses for this task. There were no statistically significant interactions between any factors (three-way interaction: $\chi^2 = 0.7$, d.f. = 1, $p = 0.410$; two-way interactions: *scale:sharpness*: $\chi^2 = 2.7$, d.f. = 1, $p = 0.100$; *scale:motion*: $\chi^2 = 0.1$, d.f. = 1, $p = 0.820$; *motion:sharpness*: $\chi^2 = 1.8$, d.f. = 1, $p = 0.180$).

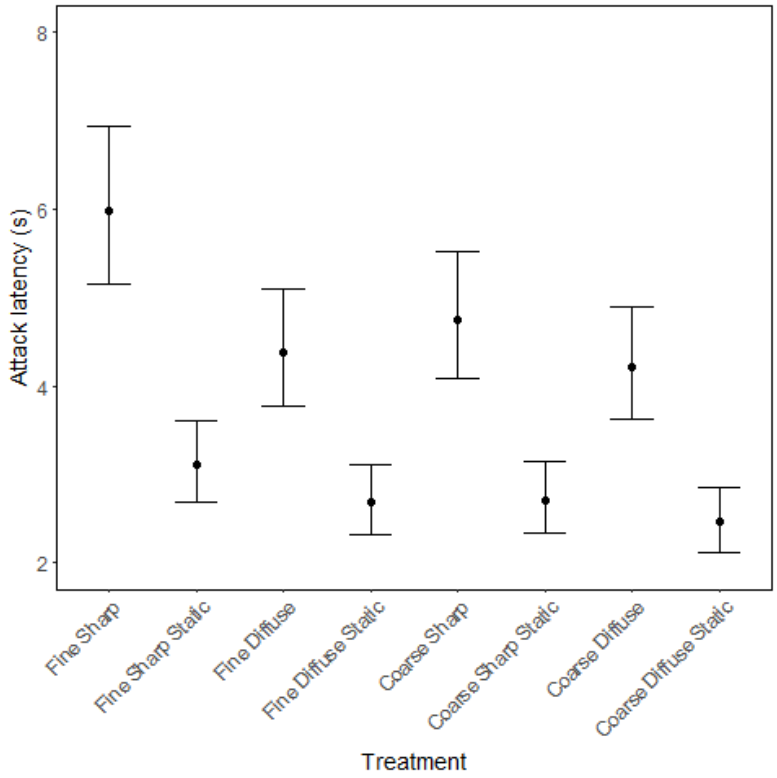

Figure 7.5 Mean Attack latency (s) of fish across the eight treatments. Error bars for Attack latency indicate 95% confidence intervals derived from the linear mixed models.

Table 7.2. Pair-wise treatment comparisons for overall Attack Latency (AL)

	FDS	FD	FSS	FS	WDS	WD	WSS	WS
FDS	—	<0.001	0.284	<0.001	0.873	<0.001	1.000	<0.001
FD	7.71	—	<0.001	<0.001	<0.001	0.999	<0.001	0.921
FSS	2.32	-5.39	—	<0.001	0.005	<0.001	0.367	<0.001
FS	12.6	4.86	10.3	—	<0.001	<0.001	<0.001	0.007
WDS	-1.37	-9.07	-3.68	-13.9	—	<0.001	0.803	<0.001
WD	7.09	-0.62	4.77	-5.47	8.46	—	<0.001	0.584
WSS	0.14	-7.56	-2.17	-12.4	1.51	-6.95	—	<0.001
WS	8.94	1.24	6.63	-3.62	10.3	1.85	8.80	—

The lower-left-hand triangle contains Tukey-type t-tests; the upper-right-hand triangle contains the corresponding p-values. Abbreviations for treatments are FDS: Fine Diffuse Static; FD: Fine Diffuse; FSS: Fine Sharp Static; FS: Fine Sharp; WDS: Wide Diffuse Static; WD: Wide Diffuse; WSS: Wide Sharp Static; WS: Wide Sharp.

7.4 Discussion

This experiment tested the assumption that water caustic flicker (like other forms of dynamic illumination) presented upon a substrate masks the motion of a target prey item. Not only does the motion of water caustics negatively affect attack latency, as in previous chapters, but so too does an increase in caustic boundary sharpness and a reduction in caustic shade scale, a combination most likely in the shallowest waters (McFarland & Loew, 1983). As with motion, the influence of scale and clarity can be understood within the framework of SNR: fine scale caustic shade and sharp caustic boundary edges both introduce noise that more closely matches the scale and edges of the prey item, respectively. Overall, the difficulty that triggerfish experience in distinguishing signal from noise illustrates an evident trade-off within their temporal vision: while some speculate that the temporal vision of many marine organisms is tuned to detect prey that is illuminated by caustic flicker in midwater (McFarland & Loew, 1983), I demonstrate that prey detection can be impeded by caustic flicker in shallow benthic zones. For organisms that negotiate both pelagic and benthic zones, it is therefore likely that their temporal vision has reached an optimal compromise for the two visual tasks, detecting prey near the surface or near the substrate; though this is yet to be tested.

One primary prediction is that three-dimensionality of the substrate would serve to accentuate the negative effect of caustics on detection by increasing spatial complexity (McFarland & Loew, 1983), an effect that should be paralleled by dynamic illumination in terrestrial habitats. The habitats within which water caustics and dappled light are common contain a host of three-dimensional structures: shallow marine habitats can be dominated by rocks, aquatic vegetation and coral, while many smaller vegetative structures reside beneath a forest canopy. When light flickers across such structures, the resultant visual form will become stretched and distorted, as well as flickering simultaneously between different substrate heights (McFarland & Loew, 1983; Partridge, 1990). Such visual complexity and unpredictability should serve to enhance the noise present in such habitats and constrain some visual tasks. This would certainly be true for those marine organisms, as discussed previously, with apparent visual adaptations for using caustic flicker to detect three-dimensionality in non-descript midwater (Loew & McFarland, 1990; McFarland & Loew, 1983; Sabbah et al., 2012). While the current experiment used tiled backgrounds that aimed to induce a perception of three-dimensionality (i.e. seabed rubble), when such organisms are forced to distinguish three-dimensionality from genuine three-dimensionality, one expects visual detection to suffer greatly. It may even be that, in this way, dynamic illumination may

accentuate the safety of three-dimensional structures for vulnerable organisms; mangroves and coral reef systems, for example, play a key role as nurseries for many marine organisms due to their physical complexity (Laegdsgaard & Johnson, 2001; Nagelkerken et al., 2000).

Chapter 8. Future exploration and conclusions.

8.1 Thesis summary

In this thesis I have demonstrated, across humans, birds and fish, that dynamic illumination significantly impedes the detection of moving objects. I initially tested this hypothesis in Chapter 2 using one form of dynamic illumination (water caustics) and human participants, while Chapter 3 outlined the methodological adjustments necessary for subsequent investigation and the inclusion of a second form of dynamic illumination (dappled light). In Chapter 4, I demonstrated that these illuminants, when dynamic, negatively affect the ability of human participants to find and capture moving prey. I extended this paradigm in Chapter 5 to assess whether dynamic illumination could impede the detection of objects that were moving and conspicuously patterned: the presence of dynamic water caustics primarily increased search times for mean luminance prey items, but also prey items with patterns that are low contrast and one-dimensional. In Chapters 6 and 7, I expanded the investigation to address two non-human visual systems. The presence of dynamic dappled light, however created, increased the time taken for domestic fowl chicks (Chapter 6) to find and peck moving prey items, while dynamic water caustics had a similar effect upon Picasso triggerfish (Chapter 7).

8.2 Features of the methodology and simulated environment

All data chapters have involved stimulus scenes that were generated by software made primarily for graphical creation (Chapter 2) or gaming (Chapters 4-7), rather than strictly for psychophysics. That said, Unreal Engine 4 is a highly successful, multi-award-winning, games platform *because* the generated scenes are perceived as realistic and immersive. It is because of this regard that computer simulations and scene modelling should prove highly fruitful in the future study of animal behaviour. For example, realistic environments can now be modelled that allow total control over both the environmental conditions and the modelled organism, which in nature is neither practical nor possible (Bian et al., 2018, 2019). Indeed, the use of 'serious' games (Michael & Chen, 2005) has become an important tool for understanding human foraging and attention, especially when presented in three spatial dimensions (Prpic et al., 2019). I believe such methods provide a useful intermediate step between, for example, a traditional computer-based laboratory experiment on visual search and a relatively uncontrollable, but ecologically valid, field experiment. Moreover, such simulations are not

limited to screens but can extend to the creation of fully immersive virtual reality environments. Here, human, and maybe even animal, observers can freely 'roam' through a simulated habitat in search of a given stimulus, while real-time data is simultaneously accrued (e.g. behavioural responses, eye-tracking, search techniques, type of movement). When faced with a search task in the presence of distractive dynamic illumination within a scene, the use of eye-tracking software to quantify where visual organisms are looking and what they are looking at remains of key interest and is yet to be tested. It must also be noted that, for experiments involving human participants, the type of task the participant completes can also be easily altered within such models to address alternative hypotheses: for example, one may investigate whether the presence of dynamic illumination influences an onlooker's assessment of prey item speed or trajectory. Specifically, computational modelling will allow experiments to address the impact of dynamic illumination across a host of environmental contexts, which can then lay the foundations for behavioural observations in the field to consolidate the findings.

Natural observations, nevertheless, remain a crucial methodological component for assessing the influence of dynamic illumination upon behaviour, as well as revealing whether there are other impacts on behaviour connected to dynamic illumination. This primarily concerns how visually 'noisy' habitats are perceived and subsequently used by organisms in the wild, such as when and where organisms choose to live and forage. During periods of dynamic illumination, when movement is safer relative to periods when illumination is absent/static, do prey organisms increase activities associated with foraging or commuting? Is the need for group or protean movement lessened? Conversely, under noisy conditions, is there a shift towards non-foraging behaviours or foraging techniques associated with non-visual senses in predators? A collection of relevant video footage taken from appropriate habitats for candidate organisms across a host of conditions would provide a useful foundation for addressing these questions. Alternatively, one could induce a change in behavioural state by experimental means and analyse the subsequent responses to dynamic illumination; for example, inducing satiation or hunger would favour an organism to act either as prey (and therefore reduce one's detectability) or predator (to then emphasise prey detection) respectively, while dynamic illumination influences both outcomes differently.

Indeed, this methodology could come full circle, whereby video frames of the real illuminant (e.g. water caustics) could replace the generated frames currently used in the environmental simulations. Illuminant frames recorded in a host of differing environmental conditions can be seamlessly fed into Unreal

Engine 4 and used to test further visual tasks for varying taxa. There were several environmental conditions that were standardised in the experiments in this thesis, which could otherwise be highly variable in nature (Hannah et al., 1995; McFarland & Loew, 1983; Peters, 2013): vegetation composition, light type and orientation, and wind strength and direction were all kept constant, while substrates were kept perceptually flat and unchanging. Each feature warrants further investigation to examine the wider implications of dynamic illumination within behavioural ecology. For example, as highlighted in Chapter 7, one feature that deserves further exploration is the presence of three-dimensionality within the scene and how such structuring interacts with a given illuminant (Figure 8.1).

Lastly, it would be beneficial to further tease apart specific spatial and temporal elements of water caustics, the illuminant with the most extreme scale of change. By extracting data from natural footage (via video analysis), one can begin to assess how water caustics change in space from one frame to the next, and therefore infer how these changes may affect the relevant visual system. In this way, more can be understood about why the visual disruption illustrated by the previous data chapters occurs, beyond the generic idea of irrelevant motion noise. Moreover, the parameters extracted can be used to align simulated water caustics with natural ones, increasing the efficacy of such software.

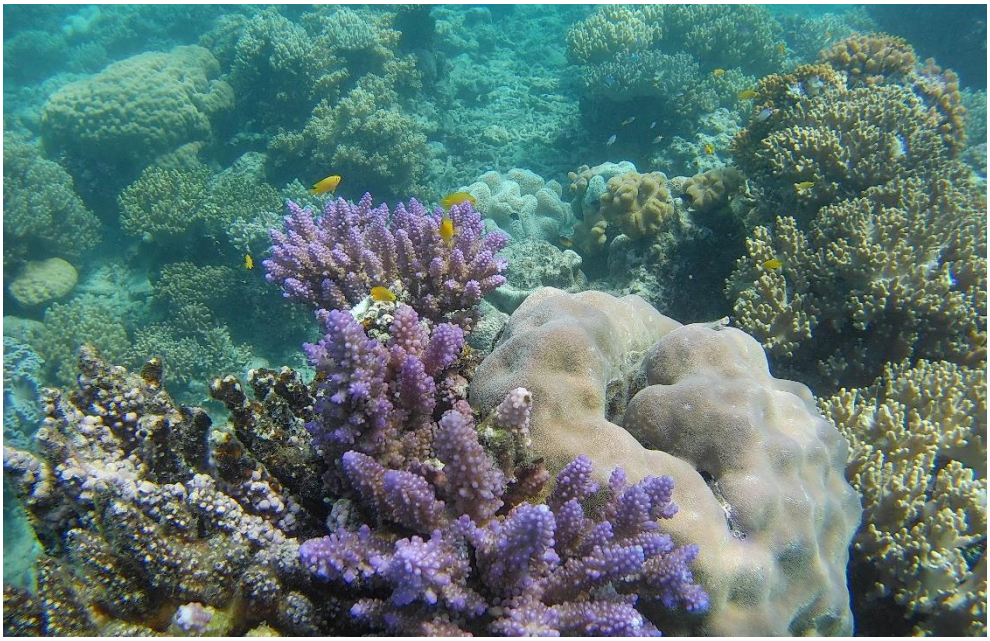

Figure 8.1 Coral reefs exhibit a great diversity of three-dimensional form and, when healthy, can appear highly colourful in shallower waters (Photo © S. Matchette).

8.3 Features of the prey item

In conjunction with environmental standardisation, several prey ("organism") features remained constant throughout the experiments documented. Firstly, prey item motion was simplified to linear pathways, which may not always be optimal for wild organisms, because predictability of motion may increase predation risk. As highlighted in Chapter 1, other movement pathways, such as protean (Humphries & Driver, 1970; Richardson et al., 2018) or punctate (Freyd & Finke, 1984), would offer more complexity and affect detection efficacy.

Secondly, only single experimental prey items were used, while many organisms exhibit shoaling behaviour or aggregation. When paired with a complex light flicker, which inconsistently illuminates an organism or feature, group movement would increase the difficulty that an onlooker has in isolating and capturing individuals; signals that exhibit visual inconsistency while moving affect individual prey detection, and this effect is amplified for larger groups (Murali et al., 2019). This effect will be maximised if prey items have features that are highly reflective, such that there is a greater extent of visual inconsistency; for example the use of mirrors or silvering by shoaling pelagic fish (Herring, 1994; McFall-Ngai, 1990). The assessment of prey density is also likely to be distorted by the interaction of unpredictable flicker and motion parallax. Similarly, dynamic illumination may play a key role for group movement in that it may lessen the oddity effect (Landeau & Terborgh, 1986; Parrish, Strand, & Lott, 1989; Theodorakis, 1989): the oddities of some group members are masked and the associated predatory attention is less discriminatory. The perception of group movement is also affected by prey pattern. Though less effective for solitary prey items than mean luminance (Chapter 5), the use of dazzle-like patterning for a group of prey items, for example, may be more effective: dazzle colouration can influence group level 'confusion effect' (Landeau & Terborgh, 1986) provided prey density and motion pathway unpredictability are sufficiently high (Hogan, Cuthill, et al., 2016; Scott-Samuel et al., 2015). The presence of dynamic illumination, especially underwater with multi-directionality water caustics, is likely to enhance the latter and therefore aid prey organism survival.

Thirdly, the stimulus scenes and prey items throughout the data chapters were all standardised to be achromatic. The initial interest in dynamic illumination, as a source of motion noise, could be addressed effectively in the absence of colour and hence the experiments proceeded accordingly. In this way, one could eliminate the need for multiple colour controls and the need to accommodate for differences in

colour vision between organisms. However, for most visual systems, natural scenes will appear chromatic (Figure 8.1). For example, in shallow marine environments, where water caustics are most common and acute, a full colour spectrum is typically present with few wavelengths lost to attenuation (Cronin, Johnsen, Marshall, & Warrant, 2014; Lythgoe, 1979). Whether the visual disruption attributed to dynamic illumination is maintained with chromatic scenes and prey is open to further exploration. Indeed, there is speculation that early colour vision arose as a means to counter the intense light flicker common in marine environments (Maximov, 2000), in part because colour vision provides information about the structure and material properties of objects and surfaces, that is robust to the luminance noise created by shadows and a varying illuminant (Kingdom, 2019). If this were true, one would therefore expect improved attack latencies for treatments that previously proved difficult. That said, given that the creation of water caustics is underpinned by refraction, there may be evidence of chromatic dispersion at the fringes of the caustic boundaries. Indeed, dispersion is a crucial difference between the use of 'real' caustics versus simulated caustics, with its recreation being most difficult in the latter. While it is not yet known whether the introduction of potentially minute colour signals such as these would serve to increase or decrease the SNR, the perceived hue of a prey item as it moves through water caustics may become inconsistent. Chromatic signal inconsistencies like these impair capture success and capture accuracy of moving targets (Murali et al., 2019, 2018; Pike, 2015) and colour discrimination (Simpson, Marshall, & Cheney, 2016), and may also interfere with individual recognition because of interference with feature binding (Espinosa & Cuthill, 2014). This effect will be dependent upon the spectral properties of the microhabitat within which the organism is present: the perception of chromatic contrast (as with achromatic contrast) greatly differs between microhabitats in both forest (Endler, 1993; Théry, 2001) and marine environments, the latter accentuated by the attenuation of different wavelengths of light with increased depth (Cronin et al., 2014). These spectral differences will serve to shape signal and colouration properties (Gomez & Théry, 2007), and therefore detectability, given that colour-contrast and brightness are major components of visual conspicuousness (Théry, 2001). Relative to the addition of colour, one could extend the findings of Chapter 5 with stimuli with chromatic patterning, given that many reef fish possess bands and reticulations (Alonso, 2015; Loew & McFarland, 1990; McFarland & Loew, 1983) that are also highly chromatic. An interesting experimental step here could be to analyse the skin responses of cuttlefish to the presence of varying water caustics, given

their fame for rapid colour and pattern change with respect to context and habitat (Hanlon & Messenger, 2018).

8.4 A note on context

The experimental chapters in this thesis address camouflage and concealment. However, the SNR framework also encompasses scenarios where the opposite is required: communication and signalling require SNR enhancement, rather than its diminishment (Merilaita et al., 2017). Many colour-based visual signals utilise high optical contrast, either chromatic or achromatic, to increase signal efficacy within a given microhabitat (Gomez & Théry, 2007): for example, the use of 'super black' to frame chromatic sexual signals in birds of paradise (McCoy, Feo, Harvey, & Prum, 2018; Wilts, Michielsen, De Raedt, & Stavenga, 2014). The conspicuousness of a signal is highly dependent upon the signalling environment, such as the spectral composition of the background (Gomez & Théry, 2007), and hence some organisms may enhance signals with behavioural adjustments within a microhabitat, such as birds that orientate within sunlit patches to increase an iridescent effect (Dakin & Montgomerie, 2009; Sicsú, Manica, Maia, & Macedo, 2013).

Crucially, some visual signals are dynamic and therefore, if the signalling environment is equally dynamic, then some level of adjustment is required to maintain signal conspicuousness. Peters *et al.* (2007) reported that the duration of aggressive tail flicks between rival Jacky dragon lizards, *Amphibolurus muricatus,* dramatically increased when the leafy surroundings were subjected to artificially increased wind, versus ambient wind conditions; this response differentiated the tail flicking signal from the surrounding moving foliage (Peters et al., 2007). Moreover, this behavioural change was found to be reversible: it was adjusted as the artificial wind was added or removed (Peters et al., 2007). Note that tail flick duration increased and not angular speed of tail flick, a compromise attributed to the biomechanical or energetic costs associated with creating the angular speed necessary for maximal signal conspicuousness (Peters et al., 2008). Similarly, Ord *et al.* (2007) observed that the speed of vertical head-bobs and dewlap expansion displayed by territorial Anole lizards, *Anolis cristatellus* and *Anolis gundlachi*, strongly correlated with the varying speed of wind-blown background vegetation. As with all signals, there are benefits from maintaining SNR, the failure to do so here being a potential loss of territory or resources to a rival (Ord et al., 2007; Peters et al., 2007).

Given this evidence, together with the data reported in this thesis, it is likely that dynamic illumination should have a similar effect as physical motion in terms of disrupting visual signalling. Thus far, this remains untested. The most relevant observations come from a series of computer simulations that modelled an individual Jacky dragon lizard (*A. muricatus)* and the effect of different environmental conditions (e.g. wind speed and luminance profiles) upon tail flick display saliency: when the luminance contrast was greatest, the saliency of display was greater when wind speeds were low, whereas the opposite was true when the luminance profile was flat (Bian et al., 2019). Overall, investigating the effect of dynamic illumination upon motion-based visual signalling will incorporate many of the features discussed here; for example, the type of motion signal used and the effect of colour (particularly for sexually selected signals). One would also expect dynamic illumination to influence motion signals associated with groups: for example, the subtle motion cues used in the coordination of shoal movement would become more difficult to distinguish in the presence of flicker, especially if the shoal comprised highly reflective fish.

8.5 A note on visual systems

The last major consideration to address is that, while water caustics are busy and chaotic to the human eye, some organisms have visual mechanisms that lessen the effect of, or indeed remove, intense illumination flicker. This is particularly common for those within marine environments. For example, the visual system of the sabellid fan worm, *Acromegalomma vesiculosum*, has apparent adaptations to filter out high-frequency caustic flicker while remaining sensitive to rapidly moving threats (Bok, Nilsson, & Garm, 2019). Similarly, many crustacean and most cephalopod species have a multitude of visual channels that are sensitive to many aspects of light (the energy, polarisation and intensity; Horváth & Varjú, 2004; Wehner, 1983), permitting organisms to utilise different channels where necessary. Indeed, fiddler crabs (*Uca stenodactylu*) use polarisation vision to detect the polarisation contrast generated by the bodies of conspecifics (rivals or otherwise), predators and objects even within the (relatively polarised) glare of the surrounding mud flats (How et al., 2015). The presence of water caustics may also prove useful for solving the 'correspondence problem', the inability of a binocular visual system to correctly interpret the disparity between the left and right eye when viewing three-dimensional structures (Nieder, 2003; Swirski et al., 2009). Some marine organisms even have temporal frequency responses that specifically fall within that of water caustics (McFarland & Loew,

1983), as discussed in Chapter 7. However, there remains an important (and still untested) interaction between organisms that can eliminate the caustic flicker and those that cannot, especially concerning predator-prey interactions within visually noisy habitats. If such disparity does exist regarding the perception of dynamic illumination, selection for traditional camouflage strategies may become relaxed for some organisms in particularly noisy habitats; though the temporality of dynamic light in most habitats means selection for anti-predator colouration should remain. Moreover, visual systems differ greatly in their visual acuity and therefore the distance at which visual tasks are achieved will differ, subsequently shaping their behaviour. For many, the effect of dynamic illumination will be distance-dependent, with the high contrast luminance changes becoming patchy and diffuse (i.e. random arbitrary noise) at greater distances. To this end, the use of specific visual system filters (e.g. AcuityView; Caves & Johnsen, 2018) to assess the saliency of dynamic illumination at different viewing distances would be an appropriate and necessary next step. Similarly, one would expect the responses to and perception of dappled light by birds, rodents and other small mammals to vary according to the differences in the number and sensitivity of photoreceptors i.e. whether they were dichromatic, trichromatic or tetrachromatic. Overall, these considerations form an interesting foundation for visual interaction, either between conspecifics or non-specifics.

8.6 Conclusions

Using an array of model organisms, I have presented evidence that the presence of dynamic illumination within a habitat can effectively mask motion signals, such as those elicited from organism movement, which would otherwise be highly conspicuous. In this way, dynamic illumination mirrors the effect that moving background objects have in the same context. Crucially, there is an implication that certain conditions (i.e. the presence of dynamic visual noise) can ease the constraints of motion, an important ecological detail given the apparent incompatibility of most camouflage strategies and movement. Indeed, under such conditions, the selective pressure for traditional camouflage strategies may even become relaxed, instead focussing upon colouration and patterning that is important for other forms of signalling, such as for social or sexual means. While the focus for the experimentation and subsequent conclusions demonstrate the significant role that dynamic illumination can have within the context of predator-prey interactions, one would also expect wider implications of dynamic illumination within other motion-based visual and sexual signalling, though this is yet to be tested.

References.

Allen, W. L., Baddeley, R. J., Cuthill, I. C., & Scott-Samuel, N. E. (2012). A quantitative test of the predicted relationship between countershading and lighting environment. *American Naturalist*, *180*(6), 762–776.

Allen, W. L., Baddeley, R. J., Scott-Samuel, N. E., & Cuthill, I. C. (2013). The evolution and function of pattern diversity in snakes. *Behavioral Ecology*, *24*(5), 1237–1250.

Alonso, W. J. (2015). The “hyper-visible world” hypothesis for the dazzling colours of coral reef fish. *F1000 Research*, *4*, 115.

Atsumi, T., Ide, M., & Wada, M. (2018). Spontaneous discriminative response to the biological motion displays involving a walking conspecific in mice. *Frontiers in Behavioral Neuroscience*, *12*, 263.

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M., & Zdravkovic, V. (2008). Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Animal Behaviour*, *76*(1), 201–215.

Barrows, F. P., & Bartl, M. H. (2014). Photonic structures in biology: a possible blueprint for nanotechnology. *Nanomaterials and Nanotechnology*, *4*, 1–12.

Bates, D., Maechler, M., Bolker, B., Walker, S., Haubo, R., Christensen, B., Singmann, H., Dai, B., Grothendieck, G., & Green, P. (2017). *lme4: Linear Mixed-Effects Models using “Eigen” and S4*. Retrieved from https://cran.r-project.org/web/packages/lme4/index.html

Behrens, R. R. (1999). The role of artists in ship camouflage during World War I. *Leonardo*, *32*(1), 53–59.

Behrens, R. R. (2012). *Ship shape, a dazzle camouflage sourcebook : an anthology of writings about ship camouflage during world war one*. Dysart, Iowa: Bobolink Books.

Bekers, W., De Meyer, R., & Strobbe, T. (2016). Shape recognition for ships: World War I naval camouflage under the magnifying glass. *WIT Transactions on The Built Environment*, *158*, 157–168.

Berry, M. V, & Upstill, C. (1980). IV Catastrophe optics: morphologies of caustics and their diffraction

patterns. *Progress in Optics*, *18*, 257–346.

Bian, X., Chandler, T., Laird, W., Pinilla, A., & Peters, R. A. (2018). Integrating evolutionary biology with digital arts to quantify ecological constraints on vision-based behaviour. *Methods in Ecology and Evolution*, *9*(3), 544–559.

Bian, X., Chandler, T., Pinilla, A., & Peters, R. A. (2019). Now you see me, now you don't: environmental conditions, signaler behavior, and receiver response thresholds interact to determine the efficacy of a movement-based animal signal. *Frontiers in Ecology and Evolution*, *7*, 1–16.

Bian, X., Elgar, M. A., & Peters, R. A. (2016). The swaying behavior of *Extatosoma tiaratum*: Motion camouflage in a stick insect? *Behavioral Ecology*, *27*(1), 83–92.

Bok, M. J., Nilsson, D. E., & Garm, A. (2019). Photoresponses in the radiolar eyes of the fan worm *Acromegalomma vesiculosum*. *Journal of Experimental Biology*, *22*(23).

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436.

Brunyé, T. T., Martis, S. B., Kirejczyk, J. A., & Rock, K. (2019). Camouflage pattern features interact with movement speed to determine human target detectability. *Applied Ergonomics*, *77*, 50–57.

Caro, T. M. (2005). *Antipredator defenses in birds and mammals*. Chicago: University of Chicago Press.

Caro, T. M. (2013). The colours of extant mammals. *Seminars in Cell & Developmental Biology*, *24*(6–7), 542–552.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*, 1484–1525.

Caves, E. M., & Johnsen, S. (2018). AcuityView: an R package for portraying the effects of visual acuity on scenes observed by an animal. *Methods in Ecology and Evolution*, *9*(3), 793–797.

Champ, C. M., Vorobyev, M., & Marshall, N. J. (2016). Colour thresholds in a coral reef fish. *Royal Society Open Science*, *3*(9), 160399.

Champ, C. M., Wallis, G., Vorobyev, M., Siebeck, U., & Marshall, N. J. (2014). Visual acuity in a species of coral reef fish: *Rhinecanthus aculeatus*. *Brain, Behavior and Evolution*, *83*(1), 31–42.

Cheney, K. L., Newport, C., McClure, E. C., & Marshall, N. J. (2013). Colour vision and response bias in a coral reef fish. *The Journal of Experimental Biology*, *216*, 2967–2973.

Colonnier, F., Ramirez-Martinez, S., Viollet, S., & Ruffier, F. (2019). A bio-inspired sighted robot chases like a hoverfly. *Bioinspiration & Biomimetics*, *14*(3), 036002.

Cook, R. G., Qadri, M. A. J., Kieres, A., & Commons-Miller, N. (2012). Shape from shading in pigeons. *Cognition*, *124*, 284–303.

Cott, H. B. (1940). *Adaptive Colouration in Animals*. London, UK: Methuen & Co. Ltd.

Cronin, T. W., Johnsen, S., Marshall, N. J., & Warrant, E. J. (2014). *Visual Ecology*. Princeton University Press.

Cuthill, I. C. (2019). Camouflage. *Journal of Zoology*, *308*(2), 75–92.

Cuthill, I. C., Sanghera, N. S., Penacchio, O., Lovell, P. G., Ruxton, G. D., & Harris, J. M. (2016). Optimizing countershading camouflage. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(46), 13093–13097.

Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A., & Troscianko, T. S. (2005). Disruptive coloration and background pattern matching. *Nature*, *434*(7029), 72–74.

Czaja, R. A., Kanonik, A., & Burke, R. L. (2018). The effect of rainfall on predation of diamond-backed terrapin (*Malaclemys terrapin*) nests. *Journal of Herpetology*, *52*(4), 402–405.

Dakin, R., & Montgomerie, R. (2009). Peacocks orient their courtship displays towards the sun. *Behavioral Ecology and Sociobiology*, *63*(6), 825–834.

Dimitrova, M., & Merilaita, S. (2010). Prey concealment: visual background complexity and prey contrast distribution. *Behavioral Ecology*, *21*(1), 176–181.

Dimitrova, M., & Merilaita, S. (2012). Prey pattern regularity and background complexity affect detectability of background-matching prey. *Behavioral Ecology*, *23*(2), 384–390.

Dimitrova, M., Stobbe, N., Schaefer, H. M., & Merilaita, S. (2009). Concealed by conspicuousness: distractive prey markings and backgrounds. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1663), 1905–1910.

Doucet, S. M., & Meadows, M. G. (2009). Iridescence: a functional perspective. *Journal of The Royal Society Interface*, *6*, S115–S132.

Duarte, R. C., Flores, A. A. V, & Stevens, M. (2017). Camouflage through colour change: mechanisms, adaptive value and ecological significance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1724), 20160342.

Dudgeon, C. L., & White, W. T. (2012). First record of potential Batesian mimicry in an elasmobranch: juvenile zebra sharks mimic banded sea snakes? *Marine and Freshwater Research*, *63*(6), 545.

Dukas, R., & Kamil, A. C. (2001). Limited attention: the constraint underlying search image. *Behavioral Ecology*, *12*(2), 192–199.

Edmunds, M. (1974). *Defence in Animals: a Survey of Anti-predator Defences*. London, UK: Longmans.

Egan, J., Sharman, R. J., Scott-Brown, K. C., & Lovell, P. G. (2016). Edge enhancement improves disruptive camouflage by emphasising false edges and creating pictorial relief. *Scientific Reports*, *6*(1), 38274.

Endler, J. A. (1978). A predator's view of animal color patterns. In *Evolutionary Biology* (pp. 319–364).

Endler, J. A. (1981). An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society*, *16*(1), 25–31.

Endler, J. A. (1984). Progressive background in moths, and a quantitative measure of crypsis. *Biological Journal of the Linnean Society*, *22*(3), 187–231.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs*, *63*(631), 1–27.

Endler, J. A., & Théry, M. (1996). Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *The American Naturalist*, *148*(3), 421–452.

Espinosa, I., & Cuthill, I. C. (2014). Disruptive colouration and perceptual grouping. *PLoS One*, *9*(1), e87153.

Fantz, R. L. (1957). Form preferences in newly hatched chicks. *Journal of Comparative and Physiological Psychology*, *50*(5), 422–430.

Fleishman, L. J. (1985). Cryptic movement in the vine snake *Oxybelis aeneus*. *Copeia*, *1985*(1), 242–245.

Fleishman, L. J. (1986). Motion detection in the presence and absence of background motion in an Anolis lizard. *Journal of Comparative Physiology A*, *159*(5), 711–720.

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *10*(1), 126–132.

Frost, B. J. (2010). A taxonomy of different forms of visual motion detection and their underlying neural mechanisms. *Brain, Behavior and Evolution*, *75*(3), 218–235.

Gallup, G. G. (1977). Tonic immobility: the role of fear and predation. *The Psychological Record*, *27*(S1), 41–61.

Gans, C. (1967). The chameleon. *Natural History*, *76*, 52–59.

Gao, C., Li, J., & Jing, W. (2016). A terminal guidance law based on motion camouflage strategy of air-to-ground missiles. *International Journal of Aerospace Engineering*, *2016*, 1–7.

Gibson, J. J. (1950). *The perception of the visual world*. Boston: Houghton Miffin.

Gomez, D., & Théry, M. (2007). Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a neotropical rainforest bird community. *American Naturalist*, *169*, 42–61.

Hailman, J. P. (1977). *Optical Signals: Animal Communication and Light*. Bloomington, IN, USA: Indiana University Press.

Hall, J. R., Baddeley, R. J., Scott-Samuel, N. E., Shohet, A. J., & Cuthill, I. C. (2017). Camouflaging moving objects: crypsis and masquerade. *Behavioral Ecology*, *28*(5), 1248–1255.

Hall, J. R., Cuthill, I. C., Baddeley, R. J., Attwood, A. S., Munafò, M. R., & Scott-Samuel, N. E. (2016). Dynamic dazzle distorts speed perception. *PLoS One*, *11*(5), e0155162.

Hall, J. R., Cuthill, I. C., Baddeley, R. J., Shohet, A. J., & Scott-Samuel, N. E. (2013). Camouflage,

detection and identification of moving targets. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1758), 20130064.

Ham, A. D., & Osorio, D. (2007). Colour preferences and colour vision in poultry chicks. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1621), 1941–1948.

Hanlon, R. T., & Messenger, J. B. (2018). *Cephalopod Behaviour* (2nd ed.). Cambridge: Cambridge University Press.

Hannah, P., Paluikof, J., & Quine, C. (1995). Predicting windspeeds for forest areas in complex terrain. In M. Coutts & J. Grace (Eds.), *Wind and trees* (pp. 113–129). Cambridge: Cambridge University Press.

Herring, P. J. (1994, November 1). Reflective systems in aquatic animals. *Comparative Biochemistry and Physiology*, Vol. 109, pp. 513–546.

Hogan, B. G., Cuthill, I. C., & Scott-Samuel, N. E. (2016). Dazzle camouflage, target tracking, and the confusion effect. *Behavioral Ecology*, *27*(5), 1547–1551.

Hogan, B. G., Cuthill, I. C., & Scott-Samuel, N. E. (2017). Dazzle camouflage and the confusion effect: the influence of varying speed on target tracking. *Animal Behaviour*, *123*, 349–353.

Hogan, B. G., Hildenbrandt, H., Scott-Samuel, N. E., Cuthill, I. C., & Hemelrijk, C. K. (2017). The confusion effect when attacking simulated three-dimensional starling flocks. *Royal Society Open Science*, *4*(1), 160564.

Hogan, B. G., Scott-Samuel, N. E., & Cuthill, I. C. (2016). Contrast, contours and the confusion effect in dazzle camouflage. *Royal Society Open Science*, *3*(7).

Horváth, G., & Varjú, D. (2004). *Polarized light in animal vision: polarization patterns in nature*. Springer.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363.

How, M. J., Christy, J. H., Temple, S. E., Hemmi, J. M., Marshall, N. J., & Roberts, N. W. (2015). Target detection is enhanced by polarization vision in a fiddler crab. *Current Biology*, *25*(23), 3069–3073.

Huffard, C. L., Boneka, F., & Full, R. J. (2005). Underwater bipedal locomotion by octopuses in disguise. *Science*, *307*(5717), 1927.

Hughes, A. E., Jones, C., Joshi, K., & Tolhurst, D. J. (2017). Diverted by dazzle: perceived movement direction is biased by target pattern orientation. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1850), 20170015.

Hughes, A. E., Magor-Elliott, R. S., & Stevens, M. (2015). The role of stripe orientation in target capture success. *Frontiers in Zoology*, *12*.

Hughes, A. E., Troscianko, J., & Stevens, M. (2014). Motion dazzle and the effects of target patterning on capture success. *BMC Evolutionary Biology*, *14*(1), 201.

Humphries, D. A., & Driver, P. M. (1970). Protean defence by prey animals. *Oecologia*, *5*(4), 285–302.

Huveneers, C., Holman, D., Robbins, R., Fox, A., Endler, J. A., & Taylor, A. H. (2015). White sharks exploit the sun during predatory approaches. *The American Naturalist*, *185*(4), 562–570.

Ioannou, C. C., Guttal, V., & Couzin, I. D. (2012). Predatory fish select for coordinated collective motion in virtual prey. *Science*, *337*(6099), 1212–1215.

Ioannou, C. C., & Krause, J. (2009). Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biology Letters*, *5*(2), 191–193.

Ioannou, C. C., Rocque, F., Herbert-Read, J. E., Duffield, C., & Firth, J. A. (2019). Predators attacking virtual prey reveal the costs and benefits of leadership. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(18), 8925–8930.

Jarvis, J. R., Taylor, N. R., Prescott, N. B., Meeks, I., & Wathes, C. M. (2002). Measuring and modelling the photopic flicker sensitivity of the chicken (Gallus g domesticus). *Vision Research*, *42*, 99–106.

Joets, A. (2012). Optical caustics and their modelling as singularities. In V. Blanlœil & T. Ohmoto (Eds.), *Singularities in Geometry and Topology* (pp. 1–17).

Johnsen, S. (2012). *The Optics of Life: A Biologist's Guide to Light in Nature*. Princeton: Princeton University Press.

Kelty-Stephen, D. G. (2018). Multifractal evidence of nonlinear interactions stabilizing posture for phasmids in windy conditions: A reanalysis of insect postural-sway data. *PLoS One*, *13*(8), e0202367.

Kim, J. (2019). Three-dimensional multi-robot control to chase a target while not being observed. *International Journal of Advanced Robotic Systems*, *16*, 1–11.

Kingdom, F. A. A. (2019). Colour vision helps distinguish light from material. *Current Opinion in Behavioral Sciences*, *30*, 15–20.

Kjernsmo, K., Hall, J. R., Doyle, C., Khuzayim, N., Cuthill, I. C., Scott-Samuel, N. E., & Whitney, H. M. (2018). Iridescence impairs object recognition in bumblebees. *Scientific Reports*, *8*(1), 8095.

Kleiner, M., Brainard, D. H., Pelli, D. G., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in psychtoolbox-3. *Perception*, *36*(14), 1–16.

Koch, D. D. (1989). Glare and contrast sensitivity testing in cataract patients. *Journal of Cataract & Refractive Surgery*, *15*(2), 158–164.

Krakauer, D. C. (1995). Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. *Behavioral Ecology and Sociobiology*, *36*(6), 421–429.

Krasky, D. A., & Takagi, D. (2018). Diffusion of swimmers jumping stochastically between multiple velocities. *Journal of Statistical Mechanics: Theory and Experiment*, *2018*(10), 103201.

Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.

Kristjánsson, T., Thornton, I. M., Chetverikov, A., & Kristjánsson, Á. (2020). Dynamics of visual attention revealed in foraging tasks. *Cognition*, *194*, 104032.

Laegdsgaard, P., & Johnson, C. (2001). Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology*, *257*(2), 229–253.

Landeau, L., & Terborgh, J. (1986). Oddity and the 'confusion effect' in predation. *Animal Behaviour*, *34*(5), 1372–1380.

Lisney, T. J., Rubene, D., Rózsa, J., Løvlie, H., Håstad, O., & Ödeen, A. (2011). Behavioural

assessment of flicker fusion frequency in chicken *Gallus gallus domesticus*. *Vision Research*, *51*(12), 1324–1332.

Loew, E. R., & McFarland, W. N. (1990). The underwater visual environment. In R. Douglas & M. Djamgoz (Eds.), *The Visual System of Fish* (pp. 1–40). London: Chapman and Hall.

Londoño, G. A., García, D. A., & Sánchez Martínez, M. A. (2015). Morphological and behavioral evidence of Batesian mimicry in nestlings of a lowland Amazonian bird. *The American Naturalist*, *185*(1), 135–141.

Lynch, D. K. (2015). Snell's window in wavy water. *Applied Optics*, *54*(4), B8.

Lythgoe, J. N. (1979). *The Ecology of Vision*. Oxford: Clarendon Press.

Mappes, J., Marples, N. M., & Endler, J. A. (2005). The complex business of survival by aposematism. *Trends in Ecology & Evolution*, *20*(11), 598–603.

Marino, L. (2017). Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken. *Animal Cognition*, *20*(2), 127–147.

Martin, G. R., & Katzir, G. (2000). Sun shades and eye size in birds. *Brain, Behavior and Evolution*, *56*(6), 340–344.

Maximov, V. V. (2000). Environmental factors which may have led to the appearance of colour vision. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *355*(1401), 1239–1242.

McCoy, D. E., Feo, T., Harvey, T. A., & Prum, R. O. (2018). Structural absorption by barbule microstructures of super black bird of paradise feathers. *Nature Communications*, *9*(1), 1.

McFall-Ngai, M. J. (1990). Crypsis in the pelagic environment. *American Zoologist*, *30*(1), 175–188.

McFarland, W. N., & Loew, E. R. (1983). Wave produced changes in underwater light and their relations to vision. *Environmental Biology of Fishes*, *8*(3–4), 173–184.

Melin, A. D., Kline, D. W., Hiramatsu, C., & Caro, T. M. (2016). Zebra stripes through the eyes of their predators, zebras, and humans. *PLoS One*, *11*(1), e0145679.

Mély, D. A., Kim, J., McGill, M., Guo, Y., & Serre, T. (2016). A systematic comparison between visual cues for boundary detection. *Vision Research*, *120*, 93–107.

Merilaita, S. (2003). Visual background complexity facilitates the evolution of camouflage. *Evolution*, *57*(6), 1248–1254.

Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1724), 20160341.

Merilaita, S., & Stevens, M. (2011). Crypsis through background matching. In M. Stevens & S. Merilaita (Eds.), *Animal Camouflage: Mechanisms and Function* (First, pp. 17–33). Cambridge: Cambridge University Press.

Michael, D. R., & Chen, S. (2005). *Serious games: games that educate, train and inform* (First). Mason, OH, USA: Course Technology.

Miller, C. W., & Hollander, S. D. (2010). Predation on heliconia bugs, *Leptoscelis tricolor*: examining the influences of crypsis and predator color preferences. *Canadian Journal of Zoology*, *88*(1), 122–128.

Mizutani, A., Chahl, J. S., & Srinivasan, M. V. (2003). Motion camouflage in dragonflies. *Nature*, *423*(6940), 604.

Molkov, A. A., & Dolin, L. S. (2019). The Snell's window image for remote sensing of the upper sea layer: results of practical application. *Journal of Marine Science and Engineering*, *7*(3), 70.

Murali, G., & Kodandaramaiah, U. (2016). Deceived by stripes: conspicuous patterning on vital anterior body parts can redirect predatory strikes to expendable posterior organs. *Open Science*, *3*(6).

Murali, G., & Kodandaramaiah, U. (2018). Body size and evolution of motion dazzle coloration in lizards. *Behavioral Ecology*, *29*(1), 79–86.

Murali, G., Kumari, K., & Kodandaramaiah, U. (2019). Dynamic colour change and the confusion effect against predation. *Scientific Reports*, *9*(1), 274.

Murali, G., Merilaita, S., & Kodandaramaiah, U. (2018). Grab my tail: evolution of dazzle stripes and colourful tails in lizards. *Journal of Evolutionary Biology*, *31*(11), 1675–1688.

Nagelkerken, I., Van Der Velde, G., Gorissen, M. W., Meijer, G. J., Van't Hof, T., & Den Hartog, C. (2000). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for

important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science*, *51*, 31–44.

New, S. T. D., & Peters, R. A. (2010). A framework for quantifying properties of 3-dimensional movement-based signals. *Current Zoology*, *56*(3), 327–336.

Nieder, A. (2003, May 13). Stereoscopic vision: solving the correspondence problem. *Current Biology*, Vol. 13, pp. R394–R396.

Nye, J. F. (2018). Symmetrical optical caustics. *Journal of Optics*, *20*(7), 075612.

Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I. C., Endler, J. A., … Waas, J. R. (2000). Considerations on the use of video playbacks as visual stimuli: The Lisbon workshop consensus. *Acta Ethologica*, *3*, 61–65.

Ord, T. J., Peters, R. A., Clucas, B., & Stamps, J. A. (2007). Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1613), 1057–1062.

Ord, T. J., & Stamps, J. A. (2008). Alert signals enhance animal communication in “noisy” environments. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(48), 18830–18835.

Ordemann, A., Balazsi, G., & Moss, F. (2003). Pattern formation and stochastic motion of the zooplankton Daphnia in a light field. *Physica A: Statistical Mechanics and Its Applications*, *325*(1–2), 260–266.

Ortolani, A., & Caro, T. M. (1996). The adaptive significance of color patterns in carnivores; phylogenetic tests of classic hypotheses. In J. Gittleman (Ed.), *Carnivore Behavior, Ecology, and Evolution* (2nd ed., Vol. 2, pp. 132–188). Ithaca, NY: Cornell University Press.

Over, R., & Moore, D. (1981). Spatial acuity of the chicken. *Brain Research*, *211*(2), 424–426.

Pan, J. S., Bingham, N., Chen, C., & Bingham, G. P. (2017). Breaking camouflage and detecting targets require optic flow and image structure information. *Applied Optics*, *56*(22), 6410.

Parrish, J. K., Strand, S. W., & Lott, J. L. (1989). Predation on a school of flat-iron herring, *Harengula thrissina*. *Copeia*, *1989*(4), 1089.

Partridge, J. C. (1990). The colour sensitivity and vision of fishes. In P. J. Herring, A. K. Campbell, M. Whitfield, & L. Maddock (Eds.), *Light and Life in the Sea* (pp. 167–184). Cambridge, UK: Cambridge University Press.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Penacchio, O., Harris, J. M., & Lovell, P. G. (2017). Establishing the behavioural limits for countershaded camouflage. *Scientific Reports*, *7*(1), 13672.

Penacchio, O., Lovell, P. G., Cuthill, I. C., Ruxton, G. D., & Harris, J. M. (2015). Three-dimensional camouflage: exploiting photons to conceal form. *The American Naturalist*, *186*(4), 553–563.

Peters, R. A. (2013). Noise in visual communication: motion from wind-blown plants. In H. Brumm (Ed.), *Animal Communication and Noise* (Vol. 2, pp. 311–330).

Peters, R. A., Clifford, C. W. G., & Evans, C. S. (2002). Measuring the structure of dynamic visual signals. *Animal Behaviour*, *64*(1), 131–146.

Peters, R. A., & Evans, C. S. (2003). Design of the Jacky dragon visual display: signal and noise characteristics in a complex moving environment. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *189*(6), 447–459.

Peters, R. A., Hemmi, J. M., & Zeil, J. (2007). Signaling against the wind: modifying motion-signal structure in response to increased noise. *Current Biology*, *17*(14), 1231–1234.

Peters, R. A., Hemmi, J. M., & Zeil, J. (2008). Image motion environments: background noise for movement-based animal signals. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *194*(5), 441–456.

Pignatelli, V., Champ, C. M., Marshall, N. J., & Vorobyev, M. (2010). Double cones are used for colour discrimination in the reef fish, *Rhinecanthus aculeatus*. *Biology Letters*, *6*(4), 537–539.

Pike, T. W. (2015). Interference coloration as an anti-predator defence. *Biology Letters*, *11*(4).

Prpic, V., Kniestedt, I., Camilleri, E., Maureira, M. G., Kristjánsson, Á., & Thornton, I. M. (2019). A serious game to explore human foraging in a 3D environment. *PLoS One*, *14*(7), e0219827.

Ramos, J. A., & Peters, R. A. (2017a). Habitat-dependent variation in motion signal structure between allopatric populations of lizards. *Animal Behaviour*, *126*, 69–78.

Ramos, J. A., & Peters, R. A. (2017b). Motion-based signaling in sympatric species of Australian agamid lizards. *Journal of Comparative Physiology A*, *203*(8), 661–671.

Ramos, J. A., & Peters, R. A. (2017c). Quantifying ecological constraints on motion signaling. *Frontiers in Ecology and Evolution*, *5*, 9.

Randall, J. E. (1985). *Guide to Hawaiian Reef Fishes*. Newtown Square: Harrowood Books.

Ratner, S. C., & Thompson, R. W. (1960). Immobility reactions (fear) of domestic fowl as a function of age and prior experience. *Animal Behaviour*, *8*(3–4), 186–191.

Revelle, W. R. (2017). *psych: Procedures for Personality and Psychological Research*. Retrieved from https://www.scholars.northwestern.edu/en/publications/psych-procedures-for-personality-and-psychological-research

Richardson, G., Dickinson, P., Burman, O. H. P., & Pike, T. W. (2018). Unpredictable movement as an anti-predator strategy. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1885), 20181112.

Rodgers, G. M., Kimbell, H., & Morrell, L. J. (2013). Mixed-phenotype grouping: the interaction between oddity and crypsis. *Oecologia*, *172*(1), 59–68.

Rovee, C. K., Kaufman, L. W., Collier, G. H., & Kent, G. C. (1976). Periodicity of death feigning by domestic fowl in response to simulated predation. *Physiology & Behavior*, *17*(6), 891–895.

Rowland, H. M. (2009). From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1516), 519–527.

Rushton, S. K., Bradshaw, M. F., & Warren, P. A. (2007). The pop out of scene-relative object movement against retinal motion due to self-movement. *Cognition*, *105*(1), 237–245.

Ruxton, G. D., Allen, W. L., Sherratt, T. N., & Speed, M. P. (2018). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry* (Second). Oxford: Oxford University Press.

Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding Attack - The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford, UK: Oxford University Press.

Ryerson, W. G. (2017). A novel form of behavioral camouflage in colubrid snakes. *Copeia*, *105*(2), 363–367.

Sabbah, S., Gray, S. M., & Hawryshyn, C. W. (2012). Radiance fluctuations induced by surface waves can enhance the appearance of underwater objects. *Limnology and Oceanography*, *57*(4), 1025–1041.

Santer, R. D. (2013). Motion dazzle: a locust's eye view. *Biology Letters*, *9*(6).

Sazima, I., Nobre Carvalho, L., Pereira Mendonça, F., & Zuanon, J. (2006). Fallen leaves on the water-bed: diurnal camouflage of three night active fish species in an Amazonian streamlet. *Neotropical Ichthyology*, *4*(1), 119–122.

Schenck, H. (1957). On the focusing of sunlight by ocean waves. *Journal of the Optical Society of America*, *47*(7), 653.

Scott-Samuel, N. E., Baddeley, R. J., Palmer, C. E., & Cuthill, I. C. (2011). Dazzle camouflage affects speed perception. *PLoS One*, *6*(6).

Scott-Samuel, N. E., Holmes, G., Baddeley, R. J., & Cuthill, I. C. (2012). Confusion: some strategies to prevent successful object tracking. *Perception*, *41*, 56–57.

Scott-Samuel, N. E., Holmes, G., Baddeley, R. J., & Cuthill, I. C. (2015). Moving in groups: how density and unpredictable motion affect predation risk. *Behavioral Ecology and Sociobiology*, *69*(6), 867–872.

Seago, A. E., Brady, P., Vigneron, J. P., & Schultz, T. D. (2009, April 6). Gold bugs and beyond: A review of iridescence and structural colour mechanisms in beetles (Coleoptera). *Journal of the Royal Society Interface*, Vol. 6, pp. S165–S184.

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: uses in assessing rater reliability. *Psychological Bulletin*, *86*, 420–428.

Sicsú, P., Manica, L. T., Maia, R., & Macedo, R. H. (2013). Here comes the sun: multimodal displays are associated with sunlight incidence. *Behavioral Ecology and Sociobiology*, *67*(10), 1633–

1642.

Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: sustained inattentional blindness for dynamic events. *Perception*, *28*(9), 1059–1074.

Simpson, E. E., Marshall, N. J., & Cheney, K. L. (2016). Coral reef fish perceive lightness illusions. *Scientific Reports*, *6*(1), 35335.

Skelhorn, J., Halpin, C. G., & Rowe, C. (2016). Learning about aposematic prey. *Behavioral Ecology*, *27*(4), 955–964.

Skelhorn, J., & Rowe, C. (2006). Taste-rejection by predators and the evolution of unpalatability in prey. *Behavioral Ecology and Sociobiology*, *60*(4), 550–555.

Skelhorn, J., & Rowe, C. (2016). Cognition and the evolution of camouflage. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1825), 20152890.

Skelhorn, J., Rowland, H. M., & Ruxton, G. D. (2010). The evolution and ecology of masquerade. *Biological Journal of the Linnean Society*, *99*(1), 1–8.

Skelhorn, J., Rowland, H. M., Speed, M. P., & Ruxton, G. D. (2010). Masquerade: camouflage without crypsis. *Science*, *327*(5961), 51.

Sokolov, A. A., Zeidman, P., Erb, M., Ryvlin, P., Friston, K. J., & Pavlova, M. A. (2018). Structural and effective brain connectivity underlying biological motion detection. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(51), E12034–E12042.

Srinivasan, M. V, & Davey, M. (1995). Strategies for active camouflage of motion. *Proceedings of the Royal Society B: Biological Sciences*, *259*(1354), 19–25.

Stevens, M. (2007). Predator perception and the interrelation between different forms of protective coloration. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1617), 1457–1464.

Stevens, M., & Cuthill, I. C. (2006). Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), 2141–2147.

Stevens, M., & Merilaita, S. (2009). Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1516), 423–427.

Stevens, M., & Ruxton, G. D. (2019). The key role of behaviour in animal camouflage. *Biological Reviews*, *94*, 116–134.

Stevens, M., Searle, W. T. L., Seymour, J. E., Marshall, K. L. A., & Ruxton, G. D. (2011). Motion dazzle and camouflage as distinct anti-predator defenses. *BMC Biology*, *9*, 81.

Stevens, M., Winney, I. S., Cantor, A., & Graham, J. (2009). Outline and surface disruption in animal camouflage. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1657), 781–786.

Stevens, M., Yule, D. H., & Ruxton, G. D. (2008). Dazzle coloration and prey movement. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1651), 2639–2643.

Swirski, Y., Schechner, Y. Y., Herzberg, B., & Negahdaripour, S. (2009). Stereo from flickering caustics. *12th IEEE International Conference on Computer Vision*, 205–212.

Thayer, A. H. (1896). The law which underlies protective coloration. *Auk*, *13*, 124–129.

Thayer, G. H. (1909). *Concealing Coloration in the Animal Kingdom, an Exposition of the Laws of Disguise Through Color and Pattern: Being a Summary of Abbott H. Thayer's Discoveries*. New York, NY, USA: The Macmillan Co.

Theodorakis, C. W. (1989). Size segregation and the effects of oddity on predation risk in minnow schools. *Animal Behaviour*, *38*(3), 496–502.

Théry, M. (2001). Forest light and its influence on habitat selection. *Plant Ecology*, *153*, 251–261.

Troscianko, J., Skelhorn, J., & Stevens, M. (2017). Quantifying camouflage: how to predict detectability from appearance. *BMC Evolutionary Biology*, *17*(1), 7.

Umbers, K. D. L., Fabricant, S. A., Gawryszewski, F. M., Seago, A. E., & Herberstein, M. E. (2014). Reversible colour change in Arthropoda. *Biological Reviews*, *89*(4), 820–848.

Umbers, K. D. L., Lehtonen, J., & Mappes, J. (2015). Deimatic displays. *Current Biology*, *25*(2).

Umeton, D., Read, J. C. A., & Rowe, C. (2017). Unravelling the illusion of flicker fusion. *Biology Letters*, *13*(2), 20160831.

Umeton, D., Tarawneh, G., Fezza, E., Read, J. C. A., & Rowe, C. (2019). Pattern and speed interact to hide moving prey. *Current Biology*, *23*, 1–5.

von Helversen, B., Schooler, L. J., & Czienskowski, U. (2013). Are stripes beneficial? Dazzle camouflage influences perceived speed and hit rates. *PLoS One*, *8*(4).

Watson, A. B., & Robson, J. G. (1981). Discrimination at threshold: labelled detectors in human vision. *Vision Research*, *21*(7), 1115–1122.

Wehner, R. (1983). The perception of polarised light. *Symposia of the Society for Experimental Biology*, *36*, 331–369.

Wilts, B. D., Michielsen, K., De Raedt, H., & Stavenga, D. G. (2014). Sparkling feather reflections of a bird-of-paradise explained by finite-difference time-domain modeling. *Proceedings of the National Academy of Sciences*, *111*(12), 4363–4368.

Witte, A., & Mahaney, C. (2001). *Hawaiian Reef Fish*. Waipahu: Island Heritage Publishing.

Woo, K. L., Rieucau, G., & Burke, D. (2017). Computer-animated stimuli to measure motion sensitivity: constraints on signal design in the Jacky dragon. *Current Zoology*, *63*(1), 75–84.

Xiao, F., & Cuthill, I. C. (2016). Background complexity and the detectability of camouflaged targets by birds and humans. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1838), 20161527.

Yin, J., Gong, H., An, X., Chen, Z., Lu, Y., Andolina, I. M., McLoughlin, N., & Wang, W. (2015). Breaking cover: neural responses to slow and fast camouflage-breaking motion. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1813), 20151182.

Zylinski, S., Osorio, D., & Shohet, A. J. (2009). Cuttlefish camouflage: context-dependent body pattern use during motion. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1675), 3963–3969.

Appendix.

The information sheet provided to participants prior to completing the experiment outlined in Chapter 2. Similar forms were provided for participants completing the experiments outlined in Chapters 4 and 5, with the relevant information adjusted accordingly (i.e. trial length, number of trials, example background). Crucially, for the latter two chapters, participants were made aware that they had only one touch opportunity to capture the target.

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EXPERIMENT INFORMATION

Your task is to 'capture' a target within a video clip.

To capture a target, simply **touch the target** on screen.

The target is a **mean luminance sphere**.

There will be **one** target per clip and each clip is only **6 seconds long**.

Try and be as fast but as accurate as possible.

The target will either be stationary or moving.

When you are successful at capturing a target, you will hear a beep (if not, no noise will be heard)

Between each trial, a touch is required to continue on to the next trial.

You will have 10 practice trials to complete first. These are aimed to get you used to the process of capturing and target motion.

You will then have 256 experimental trials to work through. The process and set-up is exactly the same as the practice trials, simply with the addition of backgrounds (example below).

Backgrounds will either be stationary or moving.

The whole experiment should last no longer than **45 minutes**.

If at any point you require a break, simply leave the screen between trials where the computer is awaiting a touch. Take as long as you need.