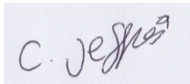# The impact of changes in snow cover on snowshoe hare camouflage.

Volume 1 of 1

Submitted by Charlotte Jeffers, to the University of Exeter
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in July 2020.

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Abstract

Climate change is regarded as a primary threat to global biodiversity. One avenue in which climate change is influencing survival is through the minimisation of the efficacy of anti-predator defences. Background matching camouflage is an anti-predator defence whereby an organism remains undetectable even when in plain sight. Within seasonal coat colour species, species which undergo a colour changing biannual moult thought to provide anti-predator colouration in their seasonally variable environment, the occurrence of camouflage mismatch is beginning to be recorded. The primary subject of this camouflage mismatch research has been the snowshoe hare (*Lepus americanus*). However, whilst this mismatch is being observed in nature and is impacting survival rate in snowshoe hares and other seasonal coat colour species, no research as of yet has examined whether these seasonal moults provide background-matching camouflage. In addition, no previous research has examined the impact of camouflage mismatch on detectability from an ecologically relevant visual system, such as the most common mammalian visual system: dichromatism. Within this thesis, both of these gaps in knowledge are explored through computer detection experiments and eye movement analysis in humans.

In chapter two, I investigate the impact of predator visual system, camouflage efficacy, background complexity, coat colour, and seasonal background type on the detection rate of snowshoe hares. Participants were displayed 15 randomly generated images of snowshoe hares on a natural landscape and located the snowshoe hares as quickly as possible. Snowshoe hares were detected more rapidly when their camouflage was ineffective, both in colour and brightness. In addition, more complex backgrounds resulted in longer search times. Although visual systems did not differ in overall detection times, simulated dichromatic vision resulted in longer search times for brightness camouflaged snowshoe hares. Within chapter three, I build upon the findings of chapter two, utilising eye-tracking equipment to examine participant visual attention and search mechanisms whilst locating snowshoe hares. I found that simulated dichromatic and trichromatic visual systems differ dramatically in the mechanisms used within the detection and discrimination of a camouflaged target. I also found that camouflage efficacy and background

complexity function primarily as a method to reduce detectability, but do not influence the discriminability of a snowshoe hare from its background.

This thesis provides support to previous research indicating that climate change will have a significant negative impact on the efficacy of seasonal coat colour camouflage and thus survival. The effects of this are already being recorded in the wild, with mismatched snowshoe hares experiencing elevated predation rates. This thesis supports that the primary reason for the increased predation is ineffective background-matching camouflage. Many aspects of camouflage and prey detection are explored within this thesis which are yet to be tested in seasonal coat colour species in the wild. In particular, how background complexity influences detectability, and the importance of considering an ecologically relevant predator visual system when examining camouflage. Overall, this thesis indicates that as the camouflage efficacy of seasonal coat colour species further decreases due to climate change, detectability, and thus predation risk, will increase.

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<u>Chapter 1: Introduction</u>

The Impact of Climate Change on Camouflage Efficacy

Climate change is negatively impacting many aspects of species fitness, including camouflage efficacy (Zimova *et al*., 2018). Camouflage is an important anti-predator defence and decreased camouflage efficacy influences fitness by reducing survival (Zimova *et al*., 2016). This thesis examines the impact of climate change on the camouflage efficacy of seasonal coat colour species, specifically examining snowshoes hares (*Lepus americanus*). Although the existence and consequences of camouflage mismatch in the wild is well recorded (Mills *et al*., 2013; Zimova *et al*., 2014; Atmeh *et al*., 2018; Wilson *et al*., 2018), gaps remain in our knowledge as to the link between camouflage and snowshoe hare detectability, and the consequences of mismatch on detectability. Most importantly, this thesis aims to answer whether seasonal coat colour moulting provides camouflage, and whether visual search behaviours explain the elevated predation rates of mismatched hares. Within this thesis I use human participants in citizen science experiments to examine whether ineffective camouflage results in snowshoe hares becoming more detectable, and why changes in detection occur.

Climate Change

The earth has natural climate cycles, characterised by extended periods of warming and cooling. However, the change in climate over the past century differs from previous natural climatic changes in rate and severity (Crowley, 2000). Recent climate change is predominantly attributed to greenhouse gas emissions, most notably CO_2 (Davis *et* al., 2010; Montzka *et al*., 2011). In general, elevated temperatures and CO_2 levels are reducing range size (Deutsch *et al*., 2008; Sekercioglu *et al*., 2008; Diamond *et al*., 2012; Sunday *et al*., 2012), foraging windows (Rohr & Palmer, 2013), and degrading habitat quality (Hoegh-Guldberg *et al*., 2007; Silverman *et al*., 2009). Alpine, sub-arctic, and arctic regions are particularly vulnerable to climate change, partly due to the rapid rate of temperature change over relatively short altitudinal distances (Marty *et al*., 2017; Rogora *et al.* 2018), and reduced snow cover duration due to warmer spring temperatures (Klein *et al*., 2016; Marty *et al*., 2017). Many species have used range shifts to compensate for temperature alterations, however for many alpine species these shifts are resulting in reduced range

sizes (Parmesan & Yohe, 2003; Diefenbach *et al*., 2016). Alpine, sub-arctic, and arctic regions are additionally vulnerable to temperature changes as the presence of black carbons, emitted from forest fires and fossil fuels (Kaspari *et al*., 2015; Resquin *et al*., 2018), increases light absorption and further elevates snow melt rate (Schmale *et al*., 2017).

Climate change is also negatively impacting life history traits, with traits experiencing a 'mismatch'. Many birds migrate to breeding grounds from cues at their wintering grounds (Cotton, 2003), however as climate change progresses these species will experience a mistiming of resource availability and requirement when breeding (Inouye *et* al., 2000; Stenseth & Mysterud, 2002). Within alpine, sub-arctic, and arctic regions, hibernation emergence is experiencing a mismatch. Marmots are emerging from hibernation earlier, likely due to elevated air temperatures (Inouye *et* al., 2000). The quantity of snowpack on marmot emergence date is increasing, extending the window between emergence and peak food abundance (Inouye *et* al., 2000). Contrastingly, Columbian ground squirrels are delaying emergence date (Lane *et al*., 2012). This late emergence is decreasing mean annual fitness, likely because of shorter active periods to prepare for the following years hibernation (Lane *et al*., 2012). One life history trait experiencing a particularly detrimental mismatch is seasonal coat colour camouflage (Mills *et al*., 2013). Seasonal coat colour (SCC) moulting occurs in 21 species across the northern hemisphere and is defined as the transition from a brown or grey summer coat, to a white, or predominantly white, winter coat (Zimova *et al*., 2018). These species include 18 species of mammals, including eight species of muroids, six species of leporids, three mustelids, and one canid (Zimova *et al*., 2018), as well as three species of bird all from the genus *Lagopus*. All 21 species known to undergo this SCC moulting are predated, suggesting these SCC moults have evolved for year-round anti-predator camouflage in a seasonally heterogeneous environment (Zimova *et al*., 2018). From this, it is theorised that the impact of camouflage mismatch in snowshoe hare populations will be similarly reflected in other SCC species, potentially excluding those that adapt behaviourally or phenotypically to the changing climate (Steen *et al*., 1992; Montgomerie *et al*., 2001; Atmeh *et al*., 2018; Davis *et al*., 2019). Due to changes in snowpack duration, these species are experiencing a camouflage mismatch, defined as a 60% difference between coat colour and background colour (Mills *et al*., 2013).

Camouflage mismatch has been shown to negatively impact survival within SCC species (Zimova *et al.*, 2014; Atmeh *et al*., 2018), with the severity expected to increase towards the end of the century as snow cover duration decreases and the duration of mismatch increases (Mills *et al*., 2013; Zimova *et al.,* 2016).

Snowshoe hares are one example of a species which undergoes a seasonal coat colour change, moulting from a white, winter coat to a brown, summer coat (Zimova *et al., 2018*). Within the literature, camouflage mismatch within SCC species has been primarily researched within snowshoe hares, although it has been observed in other species, such as weasels and ptarmigans (Steen *et al*., 1992; Montgomerie *et al*., 2001; Atmeh *et al*., 2018). Camouflage mismatch is arising within snowshoe hares due to limited phenotypic plasticity in moult initiation and rate (Mills *et al*., 2013; Zimova *et al*., 2014). However, despite the term 'camouflage mismatch' being used within the literature (Mills *et al*., 2013; Zimova *et al*., 2014; Zimova *et al*., 2016; Atmeh *et al*., 2018), no research has been conducted into examining whether these coat colour changes provide visual protection against predators. It is widely believed that the white, winter coat provides background matching camouflage for the snow-covered periods, whilst the brown coat provides camouflage throughout the summer. Although rudimentary classification of coat and background matching has been conducted in previous research (Mills *et al*., 2013), few studies have taken accurate measures of chromatic or achromatic matching (Zimova *et al*., 2016). In order to understand whether elevated predation rates are due to poor camouflage efficacy, it is first fundamental to explore whether these seasonal coat colours provide camouflage to begin with.

Camouflage

<u>Methods of Camouflage</u>

Camouflage refers to a concealment strategy to prevent the detection and recognition of an organism (Stevens & Merilaita, 2009a). Although camouflage can be attributed to disguising oneself from a number of sensory modalities (Ruxton, 2009), such as auditory (Wilson & Hare, 2006), chemical (Dettner & Liepert, 1994; Akino *et al*., 2004), and mechanical cues (Zuk *et al*., 2001), it is most commonly associated with the avoidance of visually-guided predators. The terminology surrounding the classification of visual camouflage types is debated

within the literature (Stevens & Merilaita, 2009a). However, camouflage loosely fits into three categories: crypsis, masquerade, and strategies involving motion (Stevens & Merilaita, 2009a; Merilaita *et al.*, 2017; Cuthill, 2019).

Crypsis is a catch-all term for a camouflage strategy which prevents immediate detection when an organism is in plain sight (Stevens & Merilaita, 2009a; Stevens & Merilaita, 2011). Disruptive colouration and distractive markings are two examples of crypsis using camouflage (Stevens & Merilaita, 2011). Disruptive colouration prevents the detection of an organism by disguising the outline or shape (Stevens *et al.*, 2006; Stevens & Merilaita, 2011). By breaking up the outline of an organism, disruptive camouflage reduces the distinguishability of the prey from the background, even when disruptive markings do not match the background (Stevens *et al.*, 2006; Stevens & Merilaita, 2009b). Distractive markings redirect attention away from salient features of an organism (Merilaita *et al.*, 2013). Distractive markings are conspicuous, but their conspicuousness functions to draw attention away from an organism's outline (Merilaita *et al.*, 2013).

Background matching is the most common example of crypsis, often occurring in conjunction with the aforementioned methods (Stevens & Merilaita, 2011). This form of camouflage is theorised as the most likely method of crypsis utilised by seasonal coat colour species (Zimova *et al.*, 2018). Background matching refers to when the colour, brightness, and pattern of an organism matches the background (Stevens & Merilaita, 2011; Michalis *et al.*, 2017; Cuthill, 2019). Despite background matching being common in nature, the heterogeneity of natural landscapes can often mean background matching is imperfect (Hughes *et al.*, 2019). Many species compensate behaviourally for poor background matching by selecting regions within their environment where camouflage efficacy is maximised (Hughes *et al.*, 2019; Stevens & Ruxton, 2019). Within SCC species, although some adapt behaviourally to compensate for mismatch, such as willow ptarmigans seeking out foraging areas that match their plumage (Steen *et al.*, 1992), or rock ptarmigans dirtying their white plumage after snowmelt (Montgomerie *et al.*, 2001), others do not modify behaviours and remain conspicuous. Within snowshoe hares specifically, compensatory behavioural plasticity is absent in the presence of mismatch (Zimova *et al.*, 2014). Background matching species can additionally match common features within their environment or utilise a generalist camouflage that

is effective across multiple backgrounds (Houston *et al*., 2007; Michalis *et al*., 2017; Hughes *et al*., 2019). Effective background matching camouflage typically requires both chromatic and achromatic matching (Osorio & Vorobyev, 2005; Troscianko *et al*., 2017); meaning an organism needs to match the background in both colour and luminance from the perspective of the receiver. Within previous research into SCC species, camouflage mismatch has been calculated based upon colour mismatch, with no emphasis upon luminance matching (Mills *et al*., 2013; Zimova *et al*., 2014; Zimova *et al*., 2016; Atmeh *et al*., 2018).

Masquerade camouflage is a form of camouflage where an organism is misidentified by a receiver (Skelhorn *et al*., 2010). Masquerade camouflage does not need to be cryptic as it disguises the organism as an unimportant feature of the environment, such as leaves (Lima & Salvador, 2018) or twigs (Skelhorn *et al*., 2010), rather than blending into the environment (Skelhorn *et al*., 2010). Maximising the efficacy of masquerade camouflage often requires behavioural modifications (Dockery *et al*., 2009; Buresch *et al*., 2011). In the presence of mismatch in SCC species, it is possible that masquerade could occur. Specifically, masquerade camouflage would be most likely to be present during the times of early snowmelt or snowfall, whereby a brown coat appears to a predator as a log on a snowy landscape, and a white coat appears as a patch of snow. Although apparent masquerade examples are found in nature (Buresch *et al*., 2015; Kikuchi *et al*., 2017a; Lima & Salvador, 2018), there is some controversy surrounding defining an organism as using masquerade camouflage. One of the primary concerns surrounding masquerade camouflage is that it requires misidentification (Skelhorn *et al*., 2010). From much of the research conducted, it cannot be accurately predicted whether an organism was overlooked due to misclassification, or crypsis (Font, 2019).

Motion can be split into motion dazzle and motion camouflage (Stevens & Merilaita, 2011). Motion dazzle prevents receivers being able to predict target speed and direction (Stevens *et al*., 2011; Hogan *et al*., 2016). Motion camouflage is movement behaviours that reduces the likelihood that movement will be detected (Mizutani *et al*., 2003; Stevens & Merilaita, 2011).

Background Complexity

Search difficulty is greatest when the target is similar to non-targets (Duncan & Humphreys, 1989). This simple finding has been explored more extensively in

recent years in regard to background complexity. Complex backgrounds result in slower and ineffective detection of targets (Paulmier *et al*., 2001; Uetz *et al*., 2011; Dimitrova & Merilaita, 2012). This is thought to be due to the presence of distractors within the image (Verghese, 2001). When searching for a target, environmental features that look like the target (Duncan & Humphreys, 1989), or have an attentional draw (Neider & Zelinksy, 2006), result in longer overall search times.

More complex backgrounds are thought to facilitate the evolution of camouflage (Merilaita, 2003). This is because complex backgrounds result in longer search times (Paulmier *et al*., 2001; Uetz *et al*., 2011; Dimitrova & Merilaita, 2012), and camouflage is more effective on complex backgrounds (Dimitrova & Merilaita, 2012; Xiao & Cuthill, 2016). At present, the benefits of background complexity on camouflage efficacy have been identified in both trichromatic and tetrachromatic visual systems (Dimitrova & Merilaita, 2010; Dimitrova & Merilaita, 2012; Xiao & Cuthill, 2016). As of yet, no measurements of background complexity have been used when examining mortality rates of SCC species and prior research indicates that the complexity of a background will likely play an important role in the detectability of poorly camouflaged targets by predators.

Visual Predation

Visual Search and Search Images in Predators

An important pre-requisite to the evolution of camouflage is the presence of visual predators within the environment. Camouflage functions as an anti-predator defence whereby predators do not identify, or misidentify, prey when in plain sight (Stevens & Merilaita, 2009a; Skelhorn & Rowe, 2016). If a prey item is easily identifiable, predators can have effective visual searches (Troscianko *et al*., 2008). This means that, regardless of distractors within the environment, a predator is able to rapidly locate potential prey. However, when prey is well camouflaged, visual searching becomes less effective. Ineffective searching requires a predator spend longer searching prior to locating prey (Troscianko *et al*., 2008). Therefore, ineffective searches are time consuming and produce larger windows during which prey could respond behaviourally to a potential threat.

One method utilised by predators to improve search efficacy is the production of a search image. A search image is produced over multiple encounters with a specific prey species, and aids in rapid camouflage breaking by isolating recognisable features to draw predator attention (Bond, 1983; Langley *et al.*, 1996; Skelhorn & Rowe, 2016). For camouflaged prey, a search image involves a predator identifying features that are less well camouflaged, such as edges (Troscianko *et al.*, 2008). This is likely why disruptive camouflage has been shown to strongly hinder search image formation (Troscianko *et al.*, 2018). Although a search image increases detection rates for specific prey types, the development of a search image can be costly as predators overlook other potential food sources (Pietrewicz & Kamil, 1979; Dukas, 2002). Because of this trade-off, search images are believed to only be formed for the most abundant camouflaged prey type (Bond, 2007). Snowshoe hares are the primary food source for many of their predators, therefore it is not unlikely that search images are used to increase detection success (Krebs, 2010). Search images are thought to promote the evolution of polymorphism within prey species (Bond & Kamil, 2002; Karpestam *et al.*, 2014). The evolution of polymorphism minimises species detectability by having multiple morphs which are not encompassed within the predator's search image (Karpestam *et al.*, 2014; Duarte *et al.*, 2017). Although snowshoe hares and other SCC species do exhibit polymorphism, multiple morphs rarely occur within the same time and space (Zimova *et al.*, 2020). Therefore, it is unlikely this polymorphism has evolved to minimise the efficacy of search images, but rather reduce snowshoe hare detectability (Troscianko *et al.*, 2008). Seasonal coat colour moulting may result in ineffective visual searches across all seasons by providing adaptive camouflage, resulting in longer search times (Troscianko *et al.*, 2008).

Many snowshoe hare predators are visual hunters. Snowshoe hares are predated primarily by mammals and birds, their predators including, but not limited to, coyotes, wolves, lynxes, owls, and raptors (Krebs *et al.*, 1995; O'Donoghue *et al.*, 1997; Stenseth *et al.*, 1997; Murray, 2002; Zimova *et al.*, 2019). Avian predators account for 34-40% of predation, whilst mammalian predators account for 36-66% (Krebs *et al.*, 1995; Murray, 2002). Coyotes use visual cues in prey detection, often in conjunction with olfactory stimuli (Wells, 1978; Wells & Lehner, 1978; Lawson *et al.*, 2019). Across canid predators in

general there is an emphasis on intraspecific visual communication, implying vision is an important sense and is expected to be used in hunting (Fox, 1970; Jacobs *et al.*, 1993). In regard to felid predators, vision appears to be less fundamental in predation. Lynx have been reported as having a visual acuity 6-8 times worse than humans (Maffei *et al.*, 1990). In comparison, canid visual acuity is predicted to be 3-4 times worse than humans (Miller & Murphy, 1995; Lind *et al.*, 2017). This suggests that felid predators would be less likely to visually search for prey, instead favouring an ambush predation style (Lone *et al.*, 2014). However, visual recognition of prey remains important to felid predators within the task of prey capture, even if not as important as it is for canid predators (Rockhill *et al.*, 2013; Lone *et al.*, 2014). Raptors have renowned visual acuity, relying primarily upon visual cues when hunting (Jones *et al.*, 2007; González-Martín-Moro *et al.*, 2017; Mitkus *et al.*, 2018). Owls use auditory cues to locate prey but visual cues in prey capture (Hocking & Mitchell, 1961; Knudsen, 2002; Takahashi, 2010). Overall, snowshoe hare predators use visual cues for predation, even if these cues are secondary to other sensory stimuli.

<u>Colour Vision in Predators</u>

Snowshoe hare predators are likely primarily dichromatic and tetrachromatic. Dichromacy is the most common visual system amongst mammals (Rowe, 2002). Dichromatic species have two cone cell types within the retina (Hunt *et al.*, 2009). These two cone cell types result in a sensitivity to two wavelengths of light and comparison between these wavelengths (Gouras, 2007). Dichromatic mammals typically see long and short wavelengths, resulting in yellow-blue colour vision (Jacobs, 2009). However, combinations of the wavelengths perceived by dichromats does differ across species and taxa (Jacobs, 2009). Species within the genus *Canis* (Jacobs *et al.*, 1993) and *Mustela* (Calderone & Jacobs, 2003) perceive short and long wavelengths of light. Snowshoe hare predators include Canids (such as coyotes and wolves), and Mustelids (such as weasels), suggesting they possess yellow-blue colour vision (Gouras, 2007; Zimova et al., 2019). Trichromats possess three cone cell types, and therefore perceive and compare three wavelengths of light (Gouras, 2007). In humans, these wavelengths are long (red), medium (green), and short (blue). Other trichromats are able to perceive short wavelengths into the ultraviolet spectrum

(Arrese *et al*., 2002; Kirchner *et al*., 2005). Although trichromacy is unlikely within snowshoe hare predators, prior research into snowshoe hare mismatch has utilised this visual system to classify mismatch (e.g. Mills *et al*., 2013; Zimova *et al*., 2016). Almost all bird species, including raptors, possess four cone cell types, expected to result in tetrachromatic colour vision (Lind *et al*., 2017). These four cone cells are commonly sensitive to long, medium, short, and ultraviolet wavelengths of light (Osorio *et al*., 1999b; Cuthill *et al*., 2000; Kelber, 2019). Some research has suggested that ultraviolet cues are seldom used by raptors when hunting (Lind *et al*., 2013). However, the ability of raptors to distinguish four wavebands of light suggest they are capable of perceiving far more colours than that of trichromatic or dichromatic predators. Owls lack the SWS1 gene, which produces the opsin sensitive to ultraviolet light (Bowmaker & Martin, 1978). Despite this, owls are able to detect ultraviolet light at night through their rod cells (Höglund *et al*., 2019).

In previous snowshoe hare research, camouflage mismatch has been assessed from a human perspective (Mills *et al*.,2013; Zimova et al., 2016; Wilson et al., 2018). With the majority of snowshoe hare predators being dichromatic or tetrachromatic, the severity of camouflage mismatch as perceived by predators is unknown. Trichromats are able to perceive a greater spectrum of colours than dichromats (Jacobs, 2009), and lesser spectrum than tetrachromats (Tedore & Nilsson, 2019). This suggests that mismatch is likely perceived differently by different predators. In primates, the presence of dichromacy has been linked to a greater reliance on olfactory cues when foraging, suggesting a disadvantage to dichromatic colour vision (Melin *et al*., 2019). However, trichromacy is predominantly advantageous for distinguishing between red and green stimuli, which are not relevant for the detection of SCC prey (Osorio & Vorobyev, 1996; Melin *et al*., 2019). In general, trichromats have been found to be better at breaking camouflage in comparison with dichromatic species (Troscianko *et al*., 2017; Fennell *et al*., 2019). However, under low light dichromatic predators may confer a camouflage breaking advantage (Caine *et al*., 2010; Troscianko *et al*., 2017). Therefore, trichromatic predators may be superior when breaking chromatic camouflage, especially when red and green cues are present, and dichromatic predators when breaking achromatic camouflage. Whilst this result appears logical, the perception of a greater spectrum of colour allows for easier discrimination between colours, it has been

suggested that the colours that occur in nature do not pose a disadvantage for dichromats in regard to discrimination between colours (Pastilha *et al.*, 2019). Many snowshoe terrestrial predators hunt nocturnally, suggesting a minimal reliance upon colour vision (Purves *et al.*, 2001; Heurich *et al.*, 2014). However, snowshoe hares modify behaviours under the full moon, when cone cells would be most activated for nocturnal predators (Purves *et al.*, 2001; Gigliotti & Diefenbach, 2018). Therefore, chromatic vision may be advantageous in camouflage breaking for nocturnal dichromatic predators, specifically under high illumination. Tetrachromatic species have a fourth cone cell type with which to compare with three other cone cells, resulting in an additional dimension within which colour can vary (Tedore & Nilsson, 2019). Therefore, unless camouflage has specifically evolved for defence against tetrachromatic predators (Stevens *et al.*, 2017), chromatic camouflage is likely to be less effective against tetrachromatic predators (Nokelainen *et al.*, 2017).

Thesis Methodology, Aims and Purpose

The elevated predation rates of snowshoe hares and other seasonal coat colour species have been attributed to camouflage mismatch (e.g. Mills *et al.*, 2013; Zimova *et al.*, 2014; Atmeh *et al.*, 2018). Despite this claim, little research has been conducted to test to what degree seasonal coat colours provide camouflage. Chromatic contrast between the hare and the background have been observed in previous research, but only from the perspective of a trichromatic observer (e.g. Mills *et al.*, 2013; Atmeh *et al.*, 2018). With the majority of snowshoe hare terrestrial predators likely possessing dichromatic colour vision, it is difficult to predict whether this chromatic mismatch will be perceived equally by predators as it has been by humans. In regard to brightness matching, no research has yet been conducted. Within the context of largely achromatic prey, such as seasonal coat colour prey, brightness or luminance matching is likely important in avoiding detection. Finally, the influence of background complexity on detection rates of snowshoe hares will be vital in understanding whether there is potential to mediate any occurrences of mismatching camouflage. If more complex backgrounds result in longer search times even in the absence of effective camouflage, the extended search period may introduce longer windows for predator avoidance behaviours to

occur. In order to examine these questions, I will be utilising citizen science target detection experiments and eye movement analysis.

<u>Citizen Science</u>

Citizen science uses the general public to produce databases and data that encompass the globe (Devictor *et al.*, 2010). Many of these experiments focus on using citizens to report species distribution, and the presence of endangered or invasive species (Bonney *et al.*, 2009; Lowman *et al.*, 2009; Devictor *et al.*, 2010). Although citizen science produces large quantities of data, rapid analysis, and promotes citizen interaction (Bonney *et al.*, 2009; Devictor *et al.*, 2010; McKinley *et al.*, 2017), there are some issues. Predominantly the quality of data collected and the inequality of global distribution of these projects come under scrutiny (Devictor *et al.*, 2010; Bonney *et al.*, 2014). In recent years, the production of online citizen science games has increased (Curtis, 2014). These games use engaging data collection methods, thus increasing interaction (Curtis, 2014; Prestopnik & Tang, 2015). Citizen science games can produce high quality data for research, but participant behaviours need to be accounted for (Prestopnik *et al.*, 2017).

   Citizen science experiments are increasingly popular within the field of sensory ecology. Use of these experiments has expanded our knowledge on crypsis (Karpestam *et al.*, 2014; Toh & Todd, 2017; Nokelainen *et al.*, 2019), mimicry (Hassall *et al.*, 2019), and motion dazzle (Stevens *et al.*, 2011; Hogan *et al.*, 2016). Most of these experiments examine the impact of camouflage on target detection rate (e.g. Stevens *et al.*, 2013; Nokelainen *et al.*, 2019). Using humans to mimic animal behaviours limits the ecological validity of these experiments but there are many benefits to using computer detection experiments. For example, controlling for extraneous variables, replicating multiple visual systems (Troscianko *et al.*, 2017), and acquiring vast quantities of data (Nokelainen *et al.*, 2019). This enables the concept of camouflage to be explored more in-depth than achievable in the field. The manipulation of images to mimic multiple visual systems, excluding tetrachromacy, enables the simulation of different predators' perspective of camouflage efficacy and elevates the ecological validity of studies of this kind.

Eye-Tracking Analysis

Eye-tracking has been a fundamental step in the fields of psychology and marketing to better understand human attention (Mele & Federici, 2012; Santos *et al*., 2015), providing insight into the processing and cognition of stimuli (Just & Carpenter, 1976; Morin, 2011; Orquin & Loose, 2013). In animals, optokinetic experiments have been conducted to better understand the neuroscience of these species (Scheetz *et al*., 2018). Optokinetic experiments have been used to examine visual acuity (Haug *et al*., 2010; Lev-Ari *et al*., 2017; Znotinas & Standen, 2018), colour vision (Kretschmer *et al*., 2012; Ryan *et al*., 2016), and gaze stabilisation (Daly *et al*., 2017; Daly *et al*., 2019). Within these experiments, animals are normally restrained to minimise movement and enable accurate eye tracking (Horridge & Sandeman, 1964; Thomas *et al.*, 2004; Znotinas & Standen, 2018). Restraining animals has the potential to negatively influence the ecological validity of behaviours; a factor more recently compensated for (Ryan *et al*., 2016). Although some optokinetic research examines pupil movement (Iwashita *et al*., 2001; Ryan *et al*., 2016), the majority examine head or eye movement (Kretschmer *et al*., 2012; Kretschmer *et al*., 2015; Daly *et al*., 2017). Pupil tracking enables the distinction between fine-scale alterations in attention, whilst head or eye movements are constrained to direction distinction. Fine-scale movements such as saccades, pursuit, and fixations are vital in understanding attentional variations in visual response (Young & Sheena, 1975; Gegenfurtner, 2016; Land, 2019).

Eye movements can be categorised as fixations, saccades, and smooth pursuit. Smooth pursuit eye movements are used to track moving targets (Robinson, 1965; Purves *et al*., 2001). Fixations are periods of time an organism focuses the fovea on one particular region (Purves *et al*., 2001), and are necessary for cognitive processing (Henderson & Hollingworth, 1998; Guo *et al*., 2006). Longer fixations occur when a target is less discriminable from the background, due to greater cognitive processing demands (Hooge & Erkelens, 1998; Vlaskamp & Hooge, 2006). Saccades are unidirectional eye movements and are typically involuntary, occurring between fixations (Purves *et al*., 2001). Saccades are less effective in the processing of stimuli in comparison to fixations (Henderson & Hollingworth, 1998). Shorter saccades occur when the search environment is complex, due to more fixations being required to discriminate features (Vlaskamp & Hooge, 2006). Fixations and saccades

explain visual search behaviours by indicating regions of interest, attentional draw, and the cognitive load of target discrimination.

<u>Thesis Aims and Purpose</u>

Within my first experiment, using an online detection experiment and human participants, I test whether camouflage and background complexity influences the rate at which snowshoe hares are detected. I also examine whether simple categorical classification of mismatch, coat colour, and background type are sufficient in displaying variations in detectability. In my second experiment, I test why variations in detection times occur. Using human participants and eye-tracking technology, I acquire participant eye movement data whilst searching for snowshoe hares. I aim to examine what aspects of visual search behaviour are influenced by camouflage and background complexity, to explore the reasons behind detection delays. Across both experiments, participants searched for snowshoe hares using modelled dichromatic (blue-yellow) predator vision, or trichromatic vision (red-green-blue). In the final chapter, I discuss the findings of the thesis, examine the implications, outline areas for further research, and conservation options. This thesis aims to examine whether seasonal coat colour moulting provides a camouflage advantage in SCC species by reducing their detectability or discriminability, specifically focusing upon colour difference and brightness contrast, whether mismatch influences dichromatic predatory species differently to trichromatic human experimenters, and what visual search behaviours influence detection and discrimination rate.

Chapter 2: How is snowshoe hare (*Lepus americanus)* detectability influenced by camouflage mismatch and background complexity?

Abstract

Climate change is significantly impacting the timings of snow fall and melt within temperate regions, reducing the duration of snowpack cover within these areas. As the duration of snow cover declines, the species that rely on coat colour moults to retain seasonal camouflage are becoming increasingly mismatched with their backgrounds, resulting in increased mortality. However, the effect of seasonal moulting and level of background matching camouflage on the likelihood of detection has not been directly tested. Here I use an online citizen science experiment, in which participants view images simulating dichromatic or trichromatic predator vision, to examine whether coat colour mismatch and background complexity influences snowshoe hare detectability. The results show that hares are easiest to locate when their brightness is more different from the background, and when the complexity of the background is lower. Brown hares were most difficult to locate on snowless backgrounds in comparison with other background types, whilst white hares were most difficult to find on patchy backgrounds. The results suggest that the elevated predation rates of mismatched snowshoe hares are due to faster visual detection by predators, underpinned by increased brightness contrasts and low background complexity. Overall, these results suggest that if climate change continues to reduce snowpack duration at the predicted rate, camouflage mismatch in seasonally colour-changing animals will result in heightened detectability and greater predation pressure.

Introduction

Climate change is regarded as a primary threat to biodiversity (Omann *et al.*, 2009) and is negatively influencing many fundamental life history traits, such as migration (Inouye *et al.*, 2000; Both & Visser, 2001), reproduction (Winkler *et al.*, 2002; Musolin, 2007), and hibernation emergence (Inouye *et al.*, 2000; Sherwin *et al.*, 2013), by eliciting changes in timing (Stenseth & Mysterud, 2002). These mismatches in timing are primarily due to environmental cues, such as temperature (Park *et al.*, 2000), being used for event initiation. One important life history trait effected by climate change is camouflage, specifically within species that undergo seasonal coat colour (SCC) moulting (Zimova *et al.*, 2018). Camouflage mismatch is occurring due to decreased snow duration and is elevating predation rates due to heightened detectability (Mills *et al.*, 2013; Wilson *et al.*, 2018).

Camouflage is an anti-predator defence most commonly associated with the avoidance of visually guided predators (Wallace, 1889; Cot, 1940; Stevens & Merilaita, 2009a; Cuthill, 2019). Background matching camouflage occurs when a species colour, brightness, or patterning matches their environment, or features of their environment (Endler, 1978; Stevens & Merilaita, 2011; Michalis *et al.*, 2017; Price *et al.*, 2019). Within seasonally variable regions, such as temperate areas, one coat colour may be insufficient for providing effective, year-round camouflage. As a result, some temperate species have evolved multiple phenotypic morphs to enable camouflage across environmentally distinct seasons (Zimova *et al.*, 2018). These species are termed "seasonal coat colour species" (SCC) and differ from other biannual, temperate moults in that, rather than moulting exclusively to produce a coat suitable for the coming season's climate (Ling, 1972), moulting changes coat colour; from a white winter coat to a brown or grey summer coat.

SCC moulting is observed in 21 mammal and bird species (Zimova *et al.,* 2018). Although this colour change phenomenon is assumed to have evolved in response to selection for adaptive camouflage, detection probability based upon camouflage efficacy has not been tested. Decreased snowpack duration as a result of climate change has resulted in a human-observed mismatch between SCC species coat colour and their environment (Mote, 2006; Stewart, 2009; Mills *et al.*, 2013; Pederson *et al.,* 2013). Mismatch has previously been defined as coat colour and background colour differing by 60% or more (Mills *et al.,*

2013; Zimova *et al.,* 2014; Zimova *et al.*, 2018). This percentage difference and colour contrast percentage, although arbitrary, result in significant differences in predation risk (Zimova *et al.*, 2016).

The snowshoe hare (*Lepus americanus*) undergoes SCC moulting. Snowshoe hare population dynamics are driven heavily by predation, with predation accounting for up to 100% of mortalities (Hodges, 2000). Because of this, the focus of SCC camouflage mismatch has been on snowshoe hares (e.g. Mills *et al.,* 2013; Zimova *et al.*, 2016; Wilson *et al.*, 2018). Mismatch decreases weekly snowshoe hare survival by 7-12%, in comparison with camouflaged hares (Zimova *et al.*, 2016; Wilson *et al.*, 2018). In response to this elevated predation pressure, snowshoe hares show limited phenotypic plasticity. Plasticity occurs in moult rate and initiation during spring, with no observed plasticity during the autumn moult (Mills *et al.*, 2013; Zimova *et al.*, 2014; Zimova *et al.*, 2020). Behavioural plasticity is also limited as snowshoe hares show minimal adaptation to diminish the impact of mismatch, exhibiting no differences in flight distance, concealment, or positioning within their environment (Zimova *et al.*, 2014). The increased predation rates of mismatched hares are thought to be occurring directly due to coat and background colour mismatch increasing conspicuousness to visual predators (Zimova *et al.*, 2016; Delhey & Peters, 2017; Wilson *et al.*, 2018; Lawson *et al.*, 2019).

Background matching camouflage typically requires both chromatic and achromatic matching between coat colour and the background, or common features within the background (Osorio & Vorobyev, 2005; Troscianko *et al.*, 2017). Previous research has focused upon coat and background colour matching from the experimenter's perspective (Mills *et al.*, 2013). Therefore, it is difficult to know to what extent the 7-12% decrease in weekly survival is directly associated with ineffective camouflage; especially from a predator perspective (Zimova *et al.*, 2016; Wilson *et al.*, 2018). Snowshoe hare detectability has also only been assessed under human, trichromatic, colour vision. The majority of snowshoe hare predators in the wild are likely to be dichromatic, such as coyotes or wolves, or tetrachromatic, such as raptors (Jacobs *et al.,* 1993; Kelber *et al.,* 2003; Kitchener *et al.,* 2010). Dichromatic predators possess two cone cell types, typically resulting in blue-yellow colour contrast (Gouras, 2007; Jacobs, 2009). In contrast, potentially tetrachromatic predators such as birds

(Cuthill, 2006) have four cone cell types used in colour vision, resulting in an additional dimension of colour in comparison with humans, based on responses in ultraviolet, shortwave, mediumwave, and longwave cone types (Lind *et al*., 2017). The perception of luminance also varies across species. Mammals typically use long-wavelength sensitive cones to detect luminance, in humans both long and medium-wavelength sensitive cones are used, whereas birds likely use double cones (Osorio & Vorobyev, 2005). As such, the camouflage of hares in different environments may vary with visual system, affecting detection rates.

Beyond general differences in how colour and brightness may be perceived, there is some debate within the literature as to whether dichromatic or trichromatic vision should be superior for camouflage breaking. Initially, research indicated that dichromats were superior in camouflage breaking (Anon, 1940; Morgan *et al*., 1992). Specifically, dichromatic visual systems perform better when colour discrimination is unimportant and under low lighting conditions (Melin *et al*., 2007; Smith *et al*., 2012). These conditions would be common for snowshoe hare predators, particularly nocturnal predators (Caine *et al*., 2010; Heurich *et al*., 2014; Fennell *et al*., 2019). However, more recently trichromatic visual systems are exhibiting a camouflage breaking advantage, especially within the context of detection games (Troscianko *et al*., 2017; Fennell *et al*., 2019). It can be predicted that dichromatic predators would perceive mismatch differently from trichromatic predators (Fennell *et al*., 2019), particularly when considering detection across different times of the day. With all previous research into snowshoe hare mismatch being conducted by human experimenters (e.g. Mills *et al*., 2013; Zimova *et al*., 2014), how different visual systems perceive camouflage is important when considering the impact of mismatch in the wild.

Another important aspect to consider when examining the efficacy of camouflage and its impact on detection is background complexity. Visually complex backgrounds, described as backgrounds with high variability in the shape of elements constituting the background (Dimitrova & Merilaita, 2012), are thought to reduce detectability through the presence of additional information to process prior to identifying the target (Merilaita *et al.* 2001; Merilaita, 2003). Within previous research, background complexity has been shown to significantly reduce the detectability of organisms with ineffective or

generalist camouflage (Merilaita, 2003; Xiao & Cuthill, 2016; Hughes *et al*., 2019). Although backgrounds are likely becoming more complex as a result of reduced snow cover, as snow is more uniform than grass or shrubbery, background complexity may play a role in explaining the current variations in predation rates, and complex backgrounds have the potential to mitigate the impact of ineffective camouflage (Merilaita, 2003).

Within this chapter, I use a citizen science detection game to quantify the impact of snowshoe hare camouflage mismatch on detection time and hit success. I predict that hares which differ from their background more severely in both brightness and colour will be easier to locate and therefore result in shorter detection times and greater hit success. I predict that hare coat colour will take longest to locate on the ecologically relevant background images: brown hares on snowless backgrounds, white hares on snowy backgrounds, and moulting hares on patchy backgrounds. I predict that background images that are more visually complex will have longer detection times and lower success. Even when background matching is ineffective detection times will be longer on complex backgrounds. Finally, I predict that, due to the limited chromatic signals, participants playing under the modelled dichromatic visual system will locate snowshoe hares faster than those playing under the trichromatic visual system.

Methodology

Experiment Overview

I developed an online citizen science experiment where participants were required to locate hares of different coat colours on different seasonal background types. The computer detection experiment was produced using HTML5 and JavaScript to be played by participants within the scientific community and general public. The game was based upon games used in previous research into camouflage and visual systems, following the general design outlined in previous studies (Troscianko *et al*., 2017; Troscianko *et al*., 2018; Nokelainen *et al*., 2019). Participants were shown 14 randomly selected background images, comprising of snow-cover (snowy), partial snow-cover (patchy), or no snow-cover (snowless). A randomly selected snowshoe hare image was generated and overlaid on the background - the hares could be

white, brown, or moulting (a combination of white and brown during the moulting phase). Participants were required to locate the hare as quickly as possible before clicking on the hare using a mouse or touchscreen to indicate the hare had been found. The game was playable in one of two visual systems selected by the participants: simulated generalised dichromatic predator vision, or trichromatic predator vision.

<u>Photographs</u>

All photographs were provided by the University of Montana from previous research into snowshoe hare camouflage mismatch. Approximately 24,000 images were provided, and from these the most suitable images were selected for use within the game. A total of 60 background images were selected for each of the three background type categories – snowy, patchy, or snowless – and 30 images were selected for each hare coat type – white, brown, or moulting. This resulted in a total of 180 individual background photographs, and 90 individual hare photographs.

Background Images

The 180 background images used within the experiment were manually selected, with all chosen images having roughly equivalent distance between the background and the photographer. This was to minimise potential variation in the appearance of hare size within the game. All background images selected did not have any snowshoe hares present within the original photographs. Background images were cropped to 1200 x 900 pixels. The use of a white point for colour standardisation was used as colour cards were not available within the original photographs. Standardisation was completed within Adobe Photoshop (Adobe, 2018), with the white point being selected as a region of the image expected to be white. Images were standardised to control for varying lighting conditions that might produce mismatch (Stevens *et al.*, 2007).

Hare Images

Hares in the 90 selected images had the majority or entirety of their body visible. Hares with small obscurities were used when the obstruction could be removed using the Adobe Photoshop clone stamp tool to produce a full outline. Hare images were standardised to result in uniformity of colour using a white

point within the image, using the same method as for background images (Stevens *et al*., 2007). The backgrounds of the hare images were removed within Adobe Photoshop using the lasso tool. Fine scale removal of the background was completed manually using the eraser. Hare images were resized so the pixel area of the image was as close to 18,500 pixels (the pixel area of the smallest hare image) as possible but not greater, whilst maintaining aspect ratio. All resized hares had a pixel area within 375 pixels of the target area.

Modelling Dichromatic Vision

Dichromatic images were produced in ImageJ (Schneider *et al*., 2012), using the same approach as Troscianko *et al*. (2017). For each image, the colour channels were separated into red (R), green (G), and blue (B) channels, and the average of the R and G channels were calculated to produce a yellow (Y) channel:

$$Y = \frac{(R+G)}{2} \quad 1$$

The channels were merged, with the Y channel being used for both the R and G channels of the dichromatic image. The B channel remained as the original B channel. The image was stacked to produce the final blue-yellow (dichromatic) image and exported from ImageJ.

Online Computer Game

The online game was available on all browsers and could be accessed by computer, tablet, or mobile device. Participants for the game were primarily acquired through word of mouth and online advertisement on social media.

Participants were initially shown a welcome screen providing brief instructions on how to play (Figure 1.1A). Participants next selected whether to play as a modelled generalised dichromatic predator – a coyote – or a trichromatic predator – a human. Participants were asked whether they had previously played the game, to determine naïve participants from experienced ones. Participants were lastly shown additional instructions and were required to select OK to begin the game to ensure participants were fully informed prior to beginning their trial (Figure 1.1B). Each participant was shown 14 randomly generated slides and could track their progress using a progress bar located below the game screen (Figure 1.2). Successfully locating the hare was recorded as a 'hit' and the hare was outlined by a green circle. Failure to locate

the hare within the time frame was recorded as a 'miss' and the hare was outlined by a red circle.

Participants could track hit success through a progress bar. A light grey block indicated a hit (Figure 1.2A), and a dark grey square indicated a miss (Figure 1.2B). Each slide was shown to participants for 15,000 milliseconds, a timer indicating the length of time left in seconds was visible beside the progress bar (Figure 1.2C). A time limit was used to ensure search times were realistic and long search times due to participants becoming distracted would not be included within analyses.

Figure 1.1: Online game introductory slides. *A: welcome screen with brief instructions. B: Final instructional slide before participants play the game.*

Participants were shown backgrounds and hares randomly selected from all the images for the selected visual system. The location of the hare within the slide was randomly selected from a set of pre-determined coordinates, of which there were ten possible options for each slide. The coordinates were selected as appropriate locations for a hare to be located within the background, such as ensuring all hares were positioned on the ground.

Upon completion of the game, participants were informed their mean detection time for their play attempt, and were informed which percentile of players this score placed them in. <mark>Upon submission of their score, information on the participants device type and screen size was collected and stored with their play data.</mark>

Figure 1.2: An example game slide. *A) an example of a successful hit on the progress bar; B) an example of a miss on the progress bar; C) the timer counting down from 15 seconds.*

Camouflage Efficacy

Camouflage efficacy was measured as the brightness and colour differences between the hare and a 200 x 200-pixel square of the background surrounding the hare, <mark>using a CIELAB-like colour space in ImageJ (Schneider *et al*., 2012). The CIELAB colour space best reflects the perception of colour by the human eye (Westland, 2003; Wübbeler *et al*., 2017). Due to the absence of calibration cards within the images the colours recorded are device-dependent, the resulting measurements are therefore CIELAB-like and not CIELAB (Stevens *et al*., 2009; Sharma, 2018).</mark> The size of the background area used for analysis was determined based upon the average hare size. Three colour measurements were recorded <mark>within the CIELAB-like colour space</mark>. Luminance (L), or more specifically brightness as I did not model human vision directly but used data from the images, with L scaling from 0 (black) to 100 (white). Colour

was measured using two axes: a and b. Axis a scales from -128 (green) to +127 (red). Axis b scales from -128 (blue) to +127 (yellow).

Brightness contrast between hare and background was calculated using Weber contrast, as this calculation is most suited to a small target (the hare) on a larger background (Peli, 1990). Brightness contrast was calculated as the absolute value of:

$$Absolute\ Brightness\ Contrast = |\frac{(L_h - L_B)}{L_B}|$$

2

Where L_h is the mean brightness value of the hare and L_B is the mean brightness value of the 200 x 200-pixel square of the background. Within the analysis, absolute brightness contrast was used, whereby the difference in brightness, irrespective of whether the target or the background were brighter, was positive.

To measure the colour difference between the hare and the immediate background, the euclidian distance between the a and b values for the hare and the background was calculated as:

$$Colour\ Difference = \sqrt{((a_h - a_B)^2) + ((b_h - b_B)^2)}$$

3

Where a_h and a_B refer to the mean value of the a channel for the hare and background respectively, and b_h and b_B refer to the mean values of the b channel for the hare and background respectively (Goodman, 2012; Schwegmann, 2018). The euclidian distance measures the distance between the colour of the background and hare along a two-dimensional space, between the a and b values within the CIELAB-like colour space, with greater difference occurring when the colours are further apart (Schwegmann, 2018; Sharma, 2018).

Mismatch was calculated from the percentage of white for each hare and the percentage of snow cover for each background in increments of 5%. A hare was considered mismatched if the difference in coat colour and background colour exceeded 60%, in accordance with categorisation outlined in Mills *et al.* (2013).

Background Complexity

Background complexity was calculated using the scalar feature congestion measure of visual clutter (Rosenholtz *et al.*, 2007) Feature congestion is calculated within the CIELAB-like colour space and processes features of an

image based upon changes in the luminance, colour, and shape orientation, using the average measurement of the entire image for the feature congestion score (for full methodology see Rosenholtz *et al.*, 2007). In theory, complex scenes will contain more features that appear to be the desired target, which reduces the rate of target detection (Rosenholtz *et al.*, 2007). For an image to be deemed complex, changes in luminance, colour, and shape orientation occurring close together in space is required. The feature congestion score of the backgrounds, without hares present, was calculated in MATLAB (MATLAB, 2012). Feature congestion metrics have been shown to predict camouflage efficacy in previous studies (Xiao & Cuthill, 2016).

Hare Position

The distance from the coordinates of the hare location to the edge of the screen was calculated along the x and y axes, with the shortest distance being used. Previous research utilising similar data collection methods found target location on the screen significantly influences detectability, and therefore should be controlled for in the model (Troscianko *et al.*, 2017).

Exclusion of Data Points

A total of 1398 games were played between August 2018 and June 2019. 1190 games have been included within detection time analysis, and 1183 within hit success analysis.

Two games were excluded due to participant screen size being extreme outliers; calculated as the 3rd quartile plus the interquartile range multiplied by three (Schwertman *et al.*, 2004).

Hit data with a response time below 200ms were excluded (n = 26) as it is sufficiently unlikely that this response time would be achieved naturally, with visual reaction time alone frequently exceeding 200ms (Shelton & Kumar, 2010; Wolfe *et al.*, 2010; Jain *et al.*, 2015).

Initial linear mixed effects models found device type – computer, mobile, or tablet – had a significant impact on detection time, therefore all data collected from mobile devices and tablets were removed (n = 206), using only data collected from computers in analysis (n = 1197). This significant difference in detection times between computers and handheld devices is likely due to screen size on handheld devices being too small for efficient game play. In addition, the first slide displayed to participants had significantly longer

detection times than consecutive slides. Therefore, the first slide functioned as a practice slide and was removed from analysis.

When examining the influence on detection time, only hit data was used to enable direct comparison between successfully located hares. When examining the impact of variables on whether a participant successfully located a hare or not - hit or miss - slides where three or more consecutive misses occurred were removed from analysis (n = 79), this was to minimise the risk of including data where participants were not actively participating in the game.

Ethical Note

The experiment was approved by the University of Exeter Bioscience ethics committee (application 2018/2333) All individuals playing the game were made aware the data would be used within a scientific experiment, and data were only stored for participants who actively submitted their results at the end of the trial. Participants were informed on the initial screen (Figure 1.1, A) that submission of scores was consent for their results used within the experiment. No identifying data was stored with participants scores to ensure anonymity.

Statistical Analyses

All statistics were conducted using R version 3.5.2 (R Core Team, 2018). Analysis included participant number, hare image number, and background image number as random effects. Models were produced using the lme4 package (Bates *et al*., 2015). The marginal and conditional pseudo-R^2 values for the linear mixed effects model and the theoretical and marginal pseudo-R^2 values for the binomial generalised linear mixed effects model were calculated using the R package 'MuMIn' and the 'r.squaredGLMM' function (Bartoń, 2019).

A linear mixed effects model was used on the continuous response variable detection time in milliseconds (log normal error structure (Troscianko *et al*., 2013; Hughes *et al*., 2015)) as the model fit all the assumptions of a linear mixed effects model; e.g. absence of collinearity, homoscedasticity of residuals, normality of residuals, and the absence of highly influential data points (Baayen *et al*., 2008). A binomial generalised linear mixed effects model was used for hit success analysis. In both models, fixed effects of screen size, absolute brightness contrast, colour difference, background complexity, hare size and the hare location were standardised (scaled), by subtracting the mean and dividing by the standard deviation, to enable direct comparison of variables (Becker *et*

al., 1988; Fielding, 2004). Absolute brightness difference and colour difference were logged prior to standardisation. Results of the models are reported using the type III analysis of variance as the order of parameters has no influence on their relative importance (Smith & Cribbie, 2014).

The most parsimonious detection time model was selected using backwards elimination. The corrected Akaike Information Criterion (AICc) was used to determine the most parsimonious model (Powell & Gale, 2015). AICc was selected in place of Akaike Information Criterion (AIC) to prevent overfitting, and because sample size divided by the number of model parameters in the model with the greatest number of parameters was 30.5, which is below the score of 40 suitable for use of AIC (Burnham & Anderson, 2004; Powell & Gale, 2015). The most parsimonious hit success model was selected using forward stepwise selection, selecting the variable that most influenced the fit of the model starting with the null model. Forward stepwise selection was necessary to use within the binomial model as too many variables prevented the full model from running. Models were compared using the Akaike Information Criterion (AIC) to identify the most parsimonious model. For both detection time and hit success, a threshold of 2 AIC, or AICc, was set to determine whether one model was sufficiently parsimonious and a better fit (Burnham & Anderson, 2004).

Post-hoc analysis was conducted using the Holm-Bonferroni method to examine significant differences between the levels of categorical variables and produce holm-adjusted vales of significance using the emmeans package in R (Lenth, 2019). The emmeans package estimates marginal means of variables within a linear mixed model to enable comparisons between means. The Holm-Bonferroni method was selected to minimise the problem of multiple comparisons increasing the risk of Type I error.

Results

Detection Time

The most parsimonious model had an AICc of 20116.30, a ∆AICc of 10.56 from the next most parsimonious model, therefore all results are recorded from the most parsimonious model (Burnham & Anderson, 2004). The most parsimonious model had a marginal R^2 of 0.17 and a conditional R^2 of 0.48 (For

full list of fixed factors included in the most parsimonious model and results, see Table 1.1).

Table 1.1: Results of linear mixed effects in the most parsimonious model.
The sum of squares (Sum Sq), mean of squares (Mean Sq), numerator degrees of freedom (Num DF), denominator degrees of freedom (Den DF), the F statistics (F-value) and P values of the variables retained in the most parsimonious model. Model variables include visual system, screen size, whether a participant had played before, background type (BG), hare type (Hare), background complexity (BG Complexity), hare location, absolute brightness contrast (Brightness), colour difference (Colour), percentage difference between hare coat colour and background colour (Mismatch), and interactions between variables.

Variable	Sum Sq	Mean Sq	Num DF	Den DF	F-value	P- value
Visual System	0.302	0.302	1	888.4	1.684	0.195
Screen Size	47.980	47.980	1	1172.9	267.565	< 0.001
Played Before	7.241	7.241	1	1167.1	40.379	< 0.001
BG	1.026	0.513	2	360.6	2.861	0.059
Hare	0.760	0.513	2	186.4	2.120	0.123
BG Complexity	11.383	11.383	1	351.3	63.477	< 0.001
Hare Location	177.113	177.113	1	14028.0	987.690	< 0.001
Brightness	39.744	39.744	1	14102.5	221.635	< 0.001
Colour	15.817	15.817	1	13001.2	88.206	< 0.001
Mismatch	0.839	0.839	1	13902.7	4.679	0.031
BG * Hare	5.231	1.308	4	13812.7	7.293	< 0.001
BG * BG Complexity	1.231	0.615	2	352.9	3.432	0.033
BG * Brightness	6.627	3.314	2	14075.6	18.479	< 0.001
BG Complexity * Brightness	1.457	1.457	1	13910.4	8.127	0.004
Visual System * Brightness	1.488	1.488	1	14115.9	8.296	0.004
BG Complexity * Colour	1.590	1.590	1	13360.4	8.868	0.003

<u>Visual System</u>

514 participants played using the simulated dichromatic visual system and 676 using the trichromatic visual system. Visual system had no significant impact on detection time (F = 1.684, p = 0.195, Table 1.1).

<u>Camouflage Efficacy</u>

As the absolute brightness contrast between the background and the hare increased, detection times significantly decreased (F = 221.635, p <0.001, Table 1.1). Absolute brightness contrast showed a significant interaction with background type (F = 18.479, p < 0.001, Table 1.1). On snowy backgrounds, detection times between low and high absolute brightness contrast decreased less than on patchy and snowless backgrounds (Table 1.2, Figure 1.3). Visual system significantly interacted with brightness contrast (F = 8.296, p = 0.004), with dichromatic participants showing a steeper decrease in detection times as brightness contrast increased (dichromatic slope: -0.076 (95% CI -0.088, -0.063]); trichromatic slope: -0.053 (95% CI [-0.064, -0.042]). Whilst the snowshoe hare was well matched, dichromatic participants took longer to locate them, but as brightness contrast increased the difference between the visual systems was reduced.

Colour difference between the hare and the background significantly influenced detection time, with detection times being longer for better colour camouflaged snowshoe hares (F = 88.206, p < 0.001, Table 1.1).

Table 1.2: The pairwise comparison between background type when interacting with brightness. *The comparison estimate (Est.), standard error (SE), 95% confidence interval (CI), z-ratio and p-value of the pairwise comparison of background type when interacting with brightness contrast.*

Contrast	Est.	SE	95% CI (asymptotic)		Z-ratio	p-value
			Lower	Upper		
Patchy -Snowless	0.017	0.010	-0.006	0.040	1.754	0.185
Patchy - Snowy	-0.050	0.011	-0.075	-0.026	-4.768	< 0.001
Snowless - Snowy	-0.068	0.012	-0.094	-0.041	-5.884	< 0.001
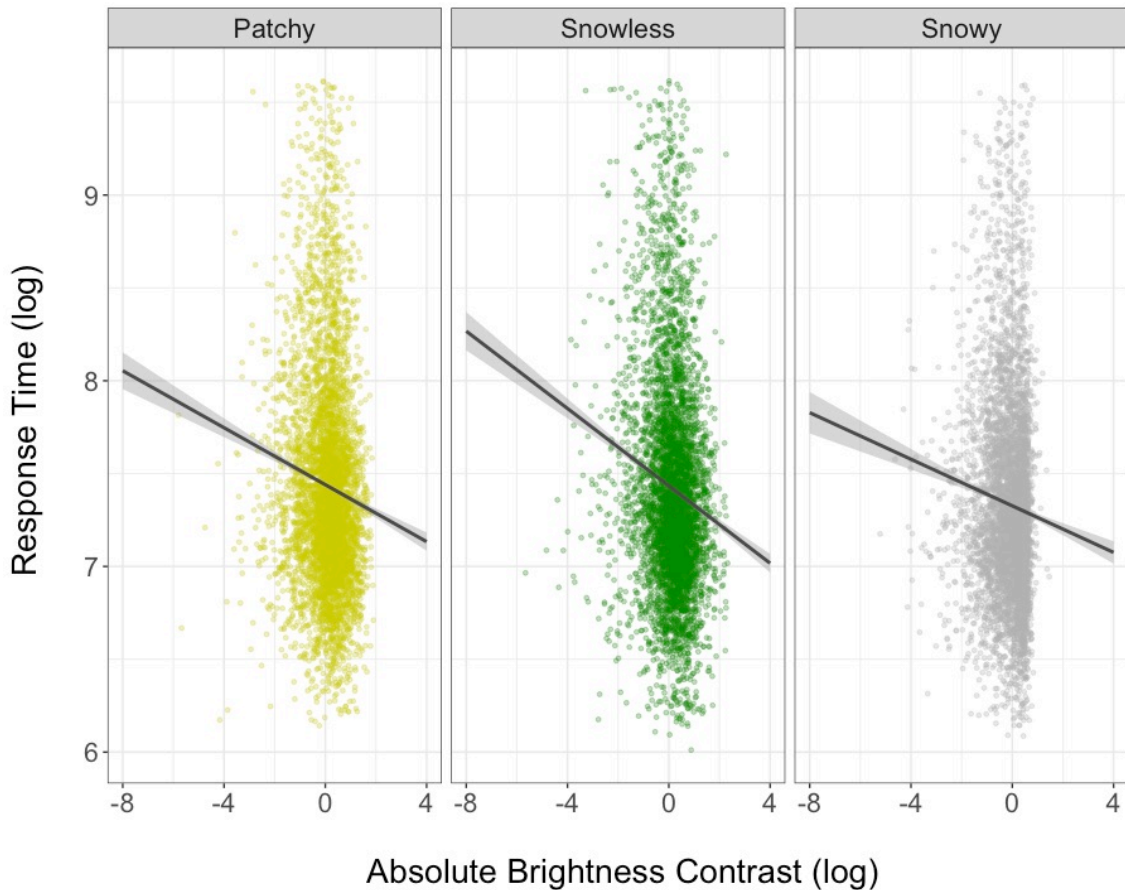
Figure 1.3: The influence of absolute brightness contrast on detection time - $\log_e$(ms) - had varying effects dependent upon background type. Detection times varied more on snowless and patchy backgrounds between high and low brightness contrast compared with snowy backgrounds. *Patchy backgrounds exhibited a trend of -0.075 (95% CI -0.088, -0.062]), and snowless backgrounds of -0.093 (95% CI -0.107, -0.078]). Snowy backgrounds significantly differed from snowless and patchy backgrounds with a trend of -0.025 (95% CI [-0.041, -0.009]).*

<u>Background Complexity</u>

As background complexity increased, detection times increased (F = 63.477, p < 0.001, Table 1.1). Colour difference interacted with background complexity to influence detection time (F = 8.868, p = 0.003, Table 1.1). On simple and complex backgrounds, detection times were longer when hares more closely matched their background chromatically (Figure 1.4A). Colour camouflage increases in importance when locating snowshoe hares on complex background, with better camouflaged hares taking much longer to locate.

A)

B)
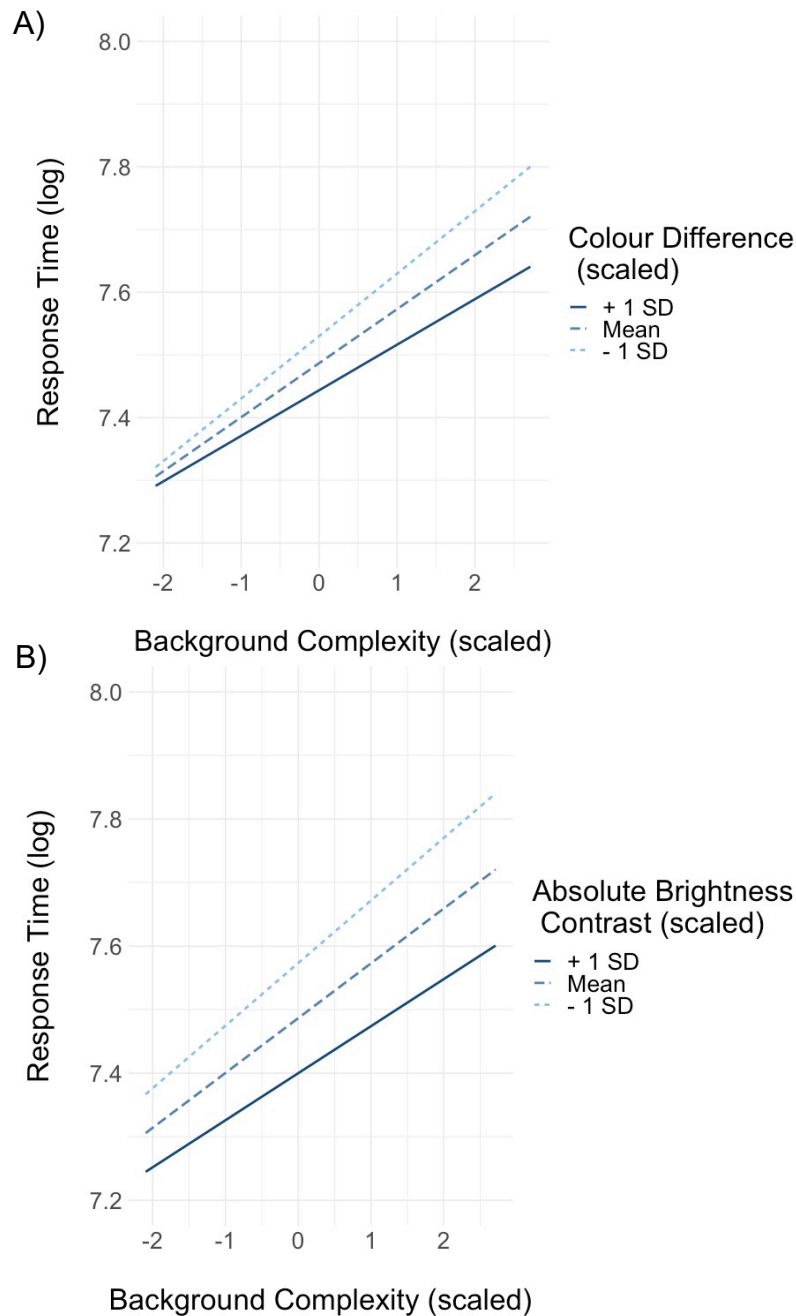
Figure 1.4: The influence of camouflage efficacy on detection time differed dependent on background complexity. *The response time - log$_e$(ms) - for high levels of* background complexity *was longer when the colour difference was less (**A**). The trend for -1 SD (more camouflaged) below the mean measurement of colour difference was 0.091 (95% CI [0.070, 0.112]), the mean of 0.078 (95% CI [0.058, 0.097]), and +1 SD (less camouflaged) above the mean of 0.064 (95% CI [0.043, 0.085]). The response time - log$_e$(ms) - for high background complexity is longer for all levels of absolute brightness contrast (**B**). The trend for -1 SD below the mean measurement of absolute brightness contrast was 0.090 (95% CI [0.069, 0.110]), the mean of 0.078 (95% CI [0.058, 0.097]), and +1 SD above the mean of 0.065 (95% CI [0.044, 0.086]).*

Background complexity significantly interacted with absolute brightness contrast to influence detection time (F = 8.127, p = 0.004, Table 1.1). Hares took longer to locate on complex backgrounds across all levels of brightness contrast, but when hares closely matched their background in brightness detection times increased more from simple to complex backgrounds (Figure 1.4B).

Background type (Patchy, Snowy, Snowless) showed a significant interaction with background complexity (Table 1.1, Table 1.3). Snowy backgrounds (trend: 0.104, 95% CI [0.071, 0.136]) had a steeper increase in detection time between simple and complex backgrounds in comparison with snowless backgrounds (trend: 0.043, 95% CI [0.009, 0.077], Table 1.3).

Table 1.3: The pairwise comparison between background type when interacting with background complexity on detection time. *The comparison estimate (Est.), standard error (SE), 95% confidence interval (CI), z-ratio and p-value of the pairwise comparison of background types when interacting with background complexity.*

Contrast	Est.	SE	95% CI (asymptotic)		Z-ratio	p-value
			Lower	Upper		
Patchy - Snowless	0.044	0.024	-0.012	0.099	1.839	0.157
Patchy - Snowy	-0.017	0.023	-0.072	0.037	-0.747	0.735
Snowless - Snowy	-0.061	0.024	-0.117	-0.005	-2.552	0.029

Coat Colour and Background Type

Hare coat colour and background type when considered alone did not significantly influence detection time (Table 1.1). Hare colour and background type interacted to significantly influence detection time (F = 7.293, p < 0.001, Table 1.1). Figure 1.5 shows how background type and hare coat colour interact. As predicted, brown hares took longest to locate on their ecologically relevant background type – snowless – and took the least time to locate when fully mismatched – snowy. However, white hares took longer to locate on patchy backgrounds in comparison with fully mismatched backgrounds, and there was no significant difference in detection time for white hares on patchy

and snowy backgrounds. There was no significant difference in the detection time of moulting hares on any background type.

On patchy backgrounds, white hares took significantly longer to locate in comparison with both moulting and brown hares. On snowless backgrounds brown hares took significantly longer to locate than moulting. Brown hares took longer to locate on snowless backgrounds in comparison with white hares but not significantly so. On snowy backgrounds white hares took significantly longer to locate than brown hares.

The percentage of mismatch between the hare and the background in colour influenced detection time ($F = 4.679$, $p = 0.031$, Table 1.1). Hares took less time to locate as their percentage of mismatch increased.

<u>Game Elements</u>

The size of the screen participants played on significantly influenced detection time, with detection time decreasing as screen size increased ($F = 267.565$, $p < 0.001$, Table 1.1). Participant naivety also influenced detection time, with experienced players taking less time to locate hares ($F = 40.379$, $p < 0.001$, Table 1.1). Hare location significantly influenced detection time, with hares located closer to the edges of the background image taking longer to locate than centralised hares ($F = 987.690$, $p < 0.001$, Table 1.1).
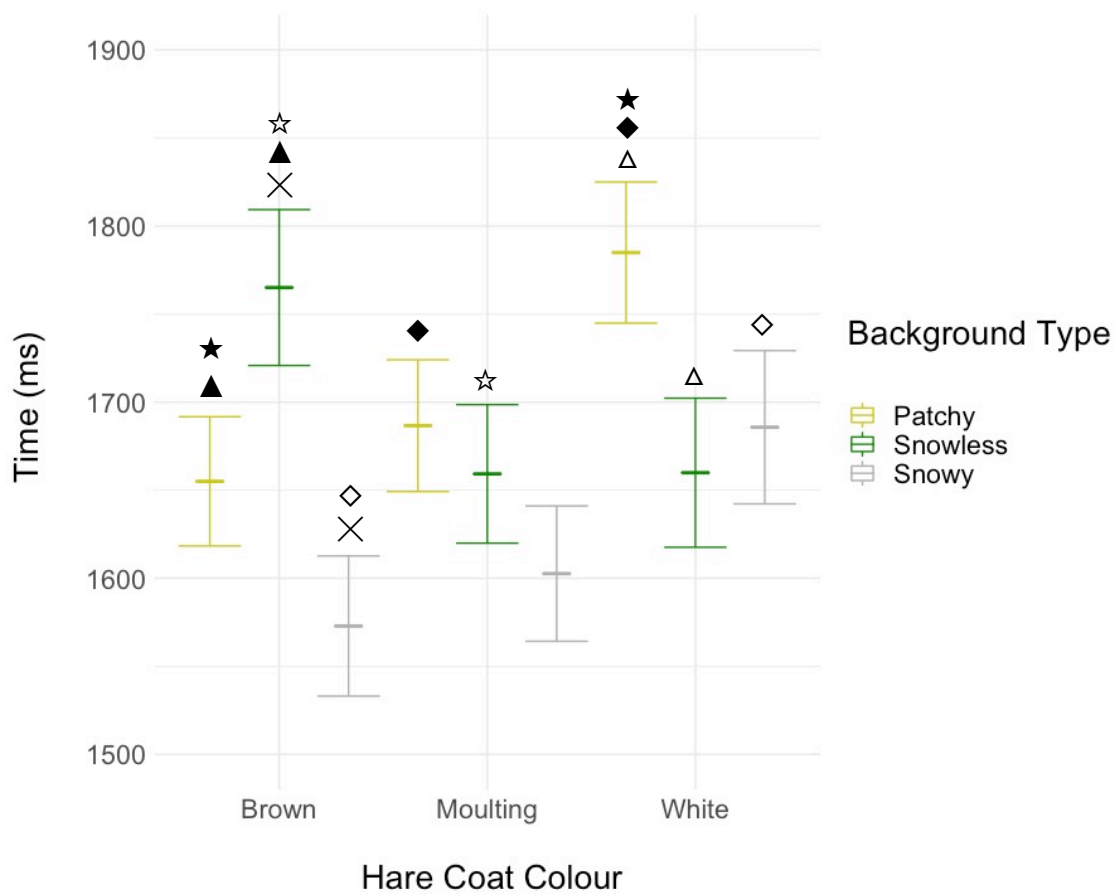
Figure 1.5: The type of background a hare was hidden on significantly influenced the length of time it took participants to locate the hare. *The estimated marginal mean and standard error for brown hares on* patchy *(1655.029±36.680, n = 1685),* snowless *(1765.091±44.262, n = 1613) and snowy background (1572.878±39.792, n = 1709), moulting hares on* patchy *(1686.665±37.412, n = 1686),* snowless *(1659.271±39.335, n = 1641) and snowy backgrounds (1602.648±38.435, n = 1728) and white hares on* patchy *(1784.954±40.068, n = 1639),* snowless *(1659.942±42.330, n = 1663) and snowy backgrounds (1685.768±44.527, n = 1632). Matching symbols indicate a significant difference.*

Hit Success

The most parsimonious hit success model had an AIC of 3197.6, a ΔAIC of 13.3 from the next most parsimonious model, therefore all results are reported from the most parsimonious model (Burnham & Anderson, 2004). The most parsimonious model had a theoretical marginal R^2 of 0.08 and conditional R^2 of 0.53, with a Δmarginal R^2 of. 0.01 and Δconditional R^2 of 0.08. The most parsimonious model included the variables absolute brightness contrast, background complexity, colour difference and screen size. 98% of the trials resulted in a hit response, with 2% resulting in a miss.

Camouflage Efficacy

Absolute brightness contrast significantly influenced hit success ($X^2_{(1)} = 30.529$, $p < 0.005$), with missed snowshoe hares matching their background more closely in brightness than hit hares (Figure 1.6A). The colour difference between the background and hare significantly influenced hit success ($X^2_{(1)} = 15.707$, $p < 0.005$), with misses occurring when the snowshoe hare more closely matched their background in colour (Figure 1.6B). Whether a hare was categorised as mismatched or not influenced hit success ($X^2_{(1)} = 4.588$, $p = 0.032$). Hares that were not considered mismatched accounted for 53% of hits and 66% of misses.

Background Complexity

The complexity of the background significantly influenced hit success ($X^2_{(1)} = 39.164$, $p < 0.005$), with missed hares being located on more complex backgrounds than hit hares (Figure 1.6C).

Screen Size

The size of screen a participant played on significantly impacted hit success ($X^2_{(1)} = 15.580$, $p < 0.005$), with hits occurring on larger screens in comparison with misses (Hit: 0.612 ± 0.001, n = *14912*; Miss: 0.575 ± 0.005, n = *383*).
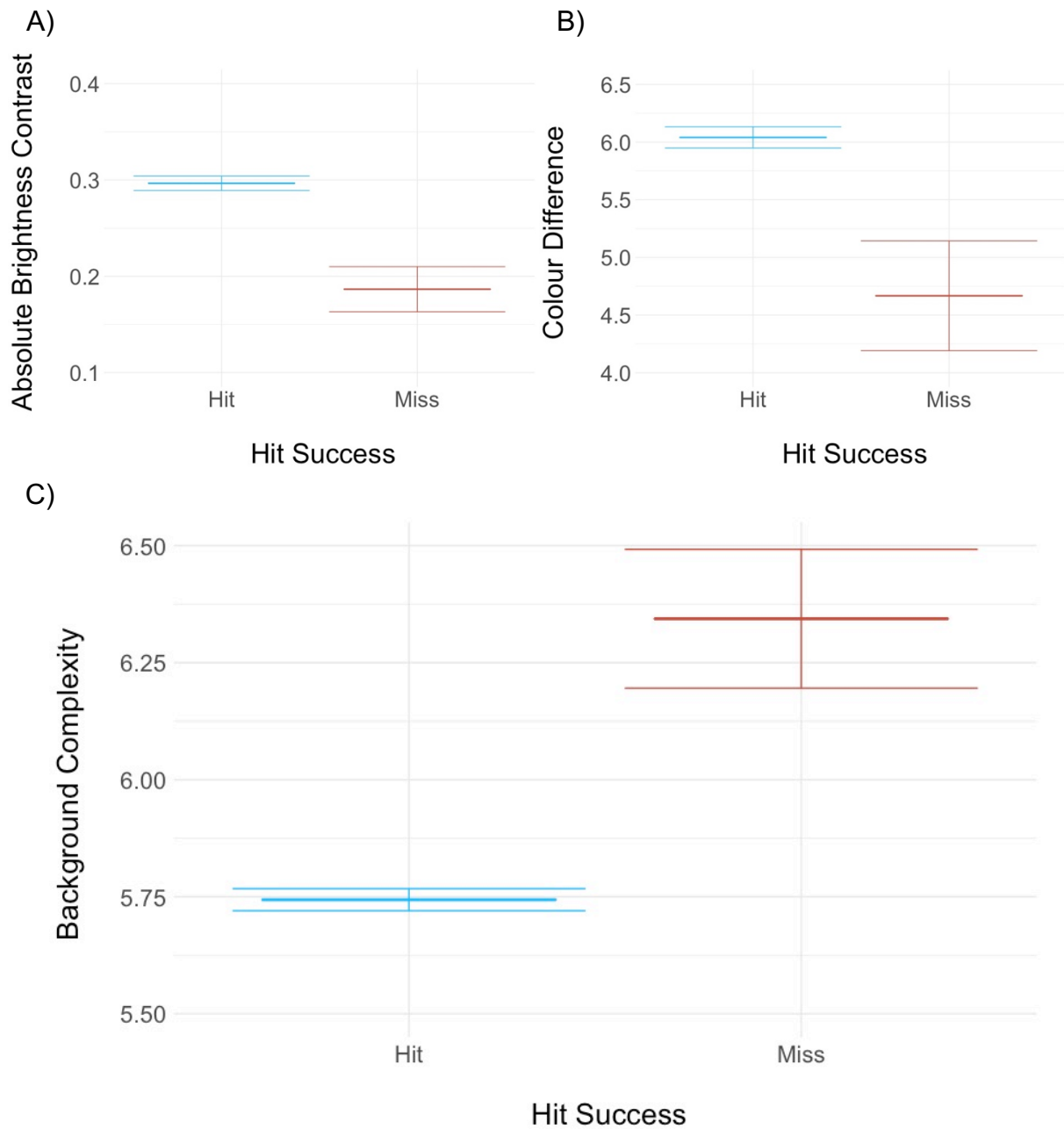
Figure 1.6: Hit success was significantly influenced by camouflage efficacy and background complexity. *The median and 95% confidence intervals of hit and miss play attempts for absolute brightness contrast (**A**), colour difference (**B**), and background complexity (**C**).*

Discussion

This research finds that snowshoe hare detectability is significantly influenced by camouflage efficacy, background complexity, snowshoe hare coat colour, and background type. Snowshoe hares that were well camouflaged, both in terms of brightness and colour, were missed most often. This suggests that the reduced survival of mismatched snowshoe hares in the wild is likely directly due to being more detectable as a result of ineffective camouflage (Zimova *et al*., 2016; Wilson *et al*., 2018). However, this study additionally demonstrates that ineffective camouflage is not the only factor that influences detection rate. This highlights the importance of not oversimplifying increased predation rates of seasonal coat colour (SCC) species to ineffective camouflage alone and indicates other aspects of environment and coat colour may impact detectability.

Previous research into seasonal coat colour mismatch has been constrained in validity by only examining mismatch from the perspective of a trichromatic visual system (e.g. Mills *et al*., 2013; Zimova *et al*., 2016; Atmeh *et al*., 2018). This study showed that predator visual system, when considered independently, did not influence either detection rate or hit success. However, differences in the ease of brightness-based camouflage breaking did occur between the visual systems. Participants playing as simulated dichromatic predators took longer to detect brightness camouflaged snowshoe hares than trichromatic participants, with detection times of brightness mismatched hares being equal between visual systems. A similar result has been found in avian predators, indicating they will detect brightness mismatched prey more quickly than camouflaged prey (Osorio *et al*., 1999a; Hiramatsu *et al*., 2008; Stobbe *et al*., 2008). Therefore, it seems likely that all potential predators will detect snowshoe hares more rapidly when brightness contrast is exacerbated by mismatch. The key differences between seasonal coat colour species and their background, and across coat colours, is in brightness. Therefore, as brightness camouflage is detected differently dependent upon visual system, a greater consideration of brightness camouflage from multiple predator visual systems should be included in future research.

Trichromats and simulated dichromats did not differ in their detection of colour camouflaged snowshoe hares. This is likely due to alpine, sub-arctic, and arctic ecosystems being primarily monochromatic (Pastilha *et al*., 2019), which

reduces the importance of colour discrimination in camouflage breaking. Previous research has classified mismatch as colour difference between the species and the environment from the perspective of a trichromat (e.g. Mills *et al.*, 2013; Zimova *et al.*, 2014; Zimova *et al.*, 2016; Zimova *et al.*, 2018). Whilst this study indicates that colour camouflage does not differ in detectability between trichromats and dichromats, thereby increasing the validity of previous research, the importance of colour matching is likely less influential than brightness matching. In future, 'mismatch' should be classified according to brightness and/or colour depending upon predator visual system.

It is important to note that snowshoe hares, and many seasonal coat colour species, are additionally predated by tetrachromatic species (Murray, 2002; Lind *et al.*, 2017). Tetrachromacy is anticipated to increase colour discrimination ability (Jones *et al.*, 2007; Stevens, 2011). Therefore, whilst dichromats and trichromats show no difference in colour camouflage breaking, tetrachromatic predators are expected to more rapidly break colour camouflage. Future research should endeavour to examine how camouflage mismatch influences tetrachromatic predators, as this will enhance our understanding on how ineffective camouflage influences detectability in a natural context.

Three aspects of camouflage efficacy were considered within this study: percentage mismatch (Mills *et al.*, 2013), brightness, and colour camouflage. All measures of camouflage influenced participant hit success, indicating that ineffective camouflage increases detectability. Hares classified as being mismatched, using the threshold of 60% or greater difference in colour between the snowshoe hare and the background outlined in Mills *et al.* (2013), were missed less frequently than camouflaged snowshoe hares. Of all the snowshoe hares that were missed by participants, 66% were classified as matching their background. Comparatively, of all the snowshoe hares that were found by participants, only 53% were classified as matching their background. As matching hares were missed more frequently than mismatched hares, this threshold of mismatch classification can explain differences in the visual detectability of snowshoe hares. Furthermore, detection times increased as the percentage of mismatch increased. This indicates that percentage mismatch utilising this methodology (Mills *et al.*, 2013; Zimova *et al.*, 2016) directly correlates with detectability.

Both brightness and colour camouflage influenced hit success, with well camouflaged snowshoe hares being missed most often. Within this study, a snowshoe hare was missed if the participant was unable to detect it within a 15 second timeframe. Therefore, well camouflaged SCC species are anticipated to be less detectable and thus have larger windows in which to locate, identify, and respond to threats in comparison with mismatched individuals. Whilst behavioural plasticity in response to predators is limited within snowshoe hares (Zimova *et al.*, 2014), behavioural differences, such as movement or habitat use, have been observed across populations due to varied predation pressures (Gigliotti & Diefenbach, 2018). Therefore, elevated predation pressures on mismatched snowshoe hares may elicit behavioural adaptations to promote more appropriate predator avoidance responses. However, the shorter window experienced by mismatched hares prior to detection may mean predation rates rise too rapidly for behavioural adaptations to occur.

Due to the monochromatic nature of alpine, sub-arctic, and arctic environments and SCC camouflage (Osorio *et al.*, 1999a; Schaefer *et al.*, 2006; Hiramatsu *et al.*, 2008; Pastilha *et al.*, 2019), as well as dichromatic predators' reliance upon brightness-based cues within prey detection (Melin *et al.*, 2007; Smith *et al.*, 2012), brightness contrast is anticipated to be greatly important in SCC species detectability. Indeed, the importance of brightness in prey detection is supported by lynxes hunting predominantly under full moons (Heurich *et al.*, 2014), when brightness contrast would be most identifiable, and by snowshoe hares reducing activity and seeking denser canopies at these times (Gigliotti & Diefenbach, 2018; Studd *et al.*, 2019). Beyond differences across visual systems, the impact of brightness contrast on detectability also differed across background type. Theoretically, patchy backgrounds should elicit the least variation in detection times as a result of brightness camouflage, due to regions of high and low brightness contrast frequently occurring within close proximity (Turatto & Galfano, 2000; White *et al.*, 2017). These fluctuations in brightness should provide multiple attentional draws prior to target detection, thereby extending detection times (Turatto & Galfano, 2000; White *et al.*, 2017). However, in this study, detection times for brightness mismatched and camouflaged snowshoe hares actually varied least on snowy backgrounds. Moreover, brightness camouflaged hares on snowy backgrounds were found more quickly than camouflaged hares on either patchy or snowless

backgrounds, with no difference in detection rate of mismatched snowshoe hares across all background types. Therefore, whilst ineffective camouflage is detrimental across all backgrounds, brightness camouflage is most effective when snowshoe hares are located on snowless or patchy backgrounds. It therefore seems likely that predation rates are highest throughout snowy periods at a full moon (Heurich *et al.*, 2014) because even camouflaged snowshoe hares are more detectable under these conditions. This might be particularly important for lynx, which stash surplus prey, and so can make the most use of a surplus in hare catches (Kossak, 1989; Heurich *et al.*, 2014).

Background complexity has consistently been shown to decrease target detectability (Merilaita, 2003; Dimitrova & Merilaita, 2010; Xiao & Cuthill, 2016; Crane *et al.*, 2020). Despite this, no previous research into SCC camouflage has examined how background complexity influences detection or predation rate. This study showed that complex backgrounds not only decrease detectability when considered independently but interact with camouflage efficacy and background type to decrease detectability. This provides the first indication that the detectability of mismatched SCC species could be minimised by altering their habitat to promote increased complexity.

Detection times were consistently higher when snowshoe hares were located on complex backgrounds, regardless of their camouflage efficacy, indicating background complexity facilitates and improves the efficacy of SCC camouflage (Merilaita, 2003; Dimitrova & Merilaita, 2010). However, complex backgrounds exhibited the greatest increase in detection time from simple backgrounds when participants were searching for brightness or colour camouflaged snowshoe hares. Therefore, whilst background complexity facilitates reduced detectability irrespective of camouflage, the benefits are greatest for well camouflaged snowshoe hares. In the wild, some snowshoe hare populations forage under denser canopy during high-risk nights (Gigliotti & Diefenbach, 2018). A high-risk night is considered one with no snow cover or high moon illumination (Gigliotti & Diefenbach, 2018). This behaviour is theorised to improve concealment from predators, but it may also increase background complexity, reducing detectability when mismatch would be most detectable by predators (Gigliotti & Diefenbach, 2018). Snowshoe hares on simple snowless backgrounds, a background type considered to be high risk (Gigliotti & Diefenbach, 2018), were less detectable than snowshoe hares on

simple snowy backgrounds. This may be because brighter, simplistic backgrounds inherently provide worse protection due to increased levels of reflected light (Merilaita & Jormalainen, 2000; Garcia & Sih, 2003; Kjernsmo & Merilaita, 2012). Therefore, whilst snowless backgrounds are considered high risk due to easier hunting conditions (Gigliotti & Diefenbach, 2018), snowshoe hares will be most at risk of visual detection on simple, snowy backgrounds.

The categorical classification of snowshoe hare coat colour and background type, although rudimentary, did provide insight into the influence of mismatch on detectability. On snowless backgrounds, brown snowshoe hares took the longest to locate, whilst on snowy backgrounds white snowshoe hares took the longest. Therefore, the hypothesis that seasonal coat colour moulting has evolved to provide background matching camouflage can be supported even in the absence of direct measures of brightness or colour matching (Zimova *et al.*, 2018). From this result alone, the recorded hybridisation of snowshoe hares with jackrabbits to produce a brown winter coat should be expected to decrease predation rates in the complete absence of winter snowfall (Jones *et al*., 2018).

Contrary to the prediction that white snowshoe hares would be least detectable on snowy backgrounds, participants took longest to locate them on patchy backgrounds. Detection times of white hares did not significantly differ between patchy and snowy backgrounds, nor snowy and snowless backgrounds. Therefore, although they were hardest to locate on snowy backgrounds in comparison with other coat colours, white hares experienced no benefit of being on a snowy background in comparison with a snowless background. In the wild, white snowshoe hares situate themselves in regions of maximum mismatch even when snowpack is present (Zimova *et al.*, 2014). This theoretically dangerous positioning is thought to provide thermoregulatory benefits, increase food access, and suggests hares are not aware of their mismatch (Smith & Litvaitis, 2000; Zimova *et al*., 2014). Positioning is therefore suggested to be a trade-off between resource availability and detectability (Smith & Litvaitis, 2000; Zimova *et al*., 2014). However, this study suggests that white hares sitting on snowless regions may not be experiencing any increased detectability. It is possible that the longer detection times on patchy backgrounds are due to the complexity of brightness (White *et al*., 2017). Increased brightness complexity, such as regions of high and low brightness

occurring close together in space, may result in longer detection times by generating multiple brightness-based attentional draws (White *et al*., 2017). Therefore, predator attention is drawn to multiple regions and they do not immediately focus on the one specific location of brightness contrast caused by white snowshoe hares. It is important to consider how the construction of the experiment may influence this result. The appearance of hares superimposed upon a uniform snowy background may 'pop out' more, be more evident to participants and promote greater attentional draw than a snowshoe hare on chromatically variable landscapes (White *et al*., 2017). In order to understand why white snowshoe hares are less detectable on patchy backgrounds, it is vital to examine how participant visual attention varies dependent upon camouflage efficacy and background type.

Brown snowshoe hares took longest to locate on their ecologically relevant background. This indicates that the detectability of brown SCC species is primarily influenced by the presence of snow. Therefore, brown hares on snowy backgrounds – termed negative mismatch – are likely to have greater reductions in survival compared to white hares on snowless backgrounds – positive mismatch. This is because brown snowshoe hares are much more detectable on snowy backgrounds than snowless, whilst the detectability of white snowshoe hares does not differ between snowless and snowy backgrounds. Overall, it can be concluded that matching the ecologically relevant background is most beneficial for brown hares, but patchy backgrounds may provide the best generalist camouflage. On patchy backgrounds, brown and moulting hares take longer to locate than on snowy backgrounds, and white hares are the least detectable. It is possible that patchy backgrounds transition the typical background matching camouflage into something resembling 'masquerade' camouflage, whereby a brown hare resembles a patch of dirt or log and a white hare resembles a snow patch whilst both are present within the immediate environment (Skelhorn & Rowe, 2016).

The impact of negative mismatch currently places certain populations, such as Colorado and Canada (Zimova *et al*., 2020), at high risk of population declines. However, as climate change progresses, the occurrences of negative mismatch will become less frequent (Zimova *et al*., 2020). Moulting snowshoe hares were equally as detectable on all background types. With snowmelt expected to occur earlier in spring due to climate change, the occurrence of

moulting on patchy or snowless backgrounds is increasing in likelihood (Zimova *et al.*, 2020). It has been previously predicted that moulting in the absence of snow will elevate detectability (Zimova *et al.*, 2020), however this study indicates that background type will not influence the detectability of moulting SCC species.

This study shows that camouflage efficacy impacts the detectability of snowshoe hares. Therefore, seasonal coat colour moulting does afford some form of adaptive, background-matching camouflage, providing empirical evidence to previously held assumptions (Mills *et* al., 2013; Zimova *et al.*, 2014), and indicating elevated predation rates of mismatched SCC species are likely due to ineffective camouflage (e.g. Mills *et al.*, 2013; Atmeh *et al.*, 2018; Zimova *et al.*, 2018). However, this study indicates that both colour and brightness matching play important roles in detectability, therefore categorising mismatch exclusively as the colour difference between the hare and the background is only explaining half of the mismatch occurring in the wild.

Although both positive and negative mismatch have the potential to increase predation pressures (Zimova *et al.*, 2020), this research indicates that white snowshoe hares on patchy landscapes may be the least influential occurrence of mismatch. Therefore, as the climate warms and snowpack density and duration decreases (Dawson *et al.*, 2011), white seasonal coat colour species will not initially be more detectable as long as some snow is present within their landscape. Overall, however, mismatch will be most detrimental to snowshoe hares when climate change results in a total absence of snow during the winter months.

Chapter 3: How does snowshoe hare (*Lepus americanus*) camouflage efficacy influence visual search behaviours?

Abstract

Camouflage is an antipredator defence often utilised to minimise detectability of an animal when in plain sight. Seasonal coat colour moulting, the moulting to or from a white winter coat and a brown or grey summer coat, is believed to have evolved to provide camouflage in the presence or absence of snow. However, climate change is reducing the duration of snow cover, meaning these species are experiencing a camouflage mismatch. Previous work shows that poorly camouflaged hares are easier to locate, particularly when backgrounds were less complex in terms of colour, luminance, and object orientation. However, the reason for these reduced search times are unclear. Here I examine how colour and brightness camouflage, background complexity, coat colour, and background type influence the visual search mechanisms used to locate snowshoe hares. Using eye-tracking equipment, human participants played an experiment searching for snowshoe hares from the perspective of a simulated dichromatic or trichromatic predator. I aimed to examine how camouflage, background complexity, coat colour, and background type influenced visual search mechanisms and efficacy, and whether differences in search efficacy can explain differences in overall detection times. Mirroring the results of my previous experiment, effective camouflage and complex backgrounds significantly increased overall detection times, whilst visual system had no impact on detection time. Participants using the simulated dichromatic visual system utilised significantly different visual search mechanisms in comparison with trichromatic participants, highlighting the importance of considering ecologically relevant visual systems when examining camouflage efficacy. Effective camouflage and complex backgrounds hindered participant visual search efficacy by reducing the detectability of the snowshoe hares. Simulated dichromacy elicited ineffective visual searches when searching for brightness camouflaged snowshoe hares. Overall, this research highlights the importance of understanding how brightness and colour camouflage efficacy influence the detectability and discriminability of snowshoe hares differently and the differences in visual search mechanisms across visual systems.

Introduction

Predation pressures influence numerous prey species life history traits, such reproductive success and investment (Fontaine & Martin, 2006; Guppy *et al*., 2017), migration (Lank *et al*., 2003), and the evolution of colouration and signalling, including camouflage (Håstad *et al*., 2005; Skelhorn & Rowe, 2016; Kang *et al*., 2017).

Camouflage is an anti-predator defence which often functions by reducing prey detectability (Stevens & Ruxton, 2019). Although camouflage can be used to defend against multiple sensory systems (Brooker *et al*., 2015; Neil & Shen, 2018), it is most commonly associated with the avoidance of visually guided predators (Schaefer & Stobbe, 2006). Despite other senses playing important roles in prey detection (Conover *et al*., 2010; Amo *et al*., 2017), many prey species focus on the visual component of detection when concealing themselves or their offspring (De Robertis *et al.,* 2000; Conover *et al*., 2010). Background matching is the best-known method of camouflage, however other methods such as disruptive colouration (Duarte *et al*., 2019; Price *et al*., 2019), and masquerade, whereby a predator misclassifies their prey as an unimportant feature of the environment (Konstantinov *et al*., 2018; Lima & Salvador, 2018), are common in nature. Background matching refers to a species matching the brightness, pattern, colour, or all, of their background (Osorio & Vorobyev, 2005; Troscianko et al., 2017). In conjunction with camouflage, the visual properties of a background play an important role in prey detection (Andersson *et al*., 2009). Background complexity, the visual complexity of an environment, reduces detectability even with less effective or absent camouflage by increasing the cognitive requirements of a visual search (Merilaita, 2003; Dimitrova & Merilaita, 2010; Dimitrova & Merilaita, 2012; Kjernsmo & Merilaita, 2012). Prey with effective camouflage benefit drastically from background complexity, being significantly less detectable than those on simplistic backgrounds (Merilaita, 2003). Understanding how camouflage and background complexity influences the visual search mechanisms of predators is important in isolating why these factors aid predator avoidance.

Background matching camouflage reduces predation by making predator visual searches more difficult, as camouflaged targets cannot be immediately identified (Troscianko *et al*., 2008). Visual search mechanisms and efficiency have been explored in other scientific fields using eye-tracking equipment, but

relatively little has been done utilising this equipment on animal camouflage (Webster *et al*., 2013). Eye movements have primarily been studied in the context of visual searches in humans, which have many parallels with search images in predators (Wolfe, 1994; Gijp *et al*., 2017; Kerr-Gaffney *et al*., 2019; Pennington *et al*., 2019). This research has shown that attentional biases are important in determining search times, with more visually salient objects being detected more quickly (Gijp *et al*., 2017; Kerr-Gaffney *et al*., 2019; Pennington *et al*., 2019). A search image is constructed over multiple encounters with a cryptic prey type and involves isolating specific features, such as edges, which can be rapidly identified (Dukas, 2002; Troscianko *et al*., 2008). Search images may be particularly relevant for snowshoe hare predators as they are a primary and abundant prey species (Krebs, 2010). Within camouflage research, eye tracking has primarily been used to examine the efficacy of military camouflage (Lin *et al*., 2014a; Lin *et al*., 2014b; Brunyé *et al*., 2019). These studies show the importance of target detectability on rapid camouflage breaking (Lin *et al*., 2014a; Lin *et al*., 2014b), and the efficacy of disruptive camouflage (Brunyé *et al*., 2019). Eye-tracking technology has been previously used to examine how disruptive camouflage reduces the detectability of moth targets (Webster *et al*., 2013). This study highlighted that reductions in target recognisability dramatically extends overall search times (Webster *et al*., 2013). However, Webster *et al*. (2013) intentionally disentangled background matching camouflage from disruptive markings. Therefore, very little research has directly explored how background-matching camouflage influences visual search behaviours within the context of predator-prey dynamics.

Variations in eye movements signify differences in the detectability or discriminability of a target from its background. Detectability refers to how rapidly a target is detected (Fitts *et al*., 1950; Spain & Perona, 2008), whilst target discriminability is explained by the cognitive requirements of discriminating the target from the background (Henderson *et al*., 2018). Eye movements typically alternate between fixations and saccades (Land, 2019). Fixations are the focus on one feature in the fovea for 200-400ms (Salthouse & Ellis, 1980; Salvucci & Goldberg, 2000; Jain *et al*., 2015). These usually occur on distinct features, such as areas of high contrast or discriminable objects (Table 2.1, Buswell, 1935; Kummerer *et al*., 2017). The duration of a fixation is associated with the cognitive processing requirements of discriminating a target

from its background (Table 2.1, Just & Carpenter, 1980; Hegarty *et al.*, 1992; Tsai *et al.*, 2012; Ahlström *et al.*, 2019). A saccade is the unidirectional movement of the eyes between fixations (Purves *et al.*, 2001). Saccades are reflex eye movements but can be voluntary movements to particular detectable stimuli (Purves *et al.*, 2001). Saccadic amplitude refers to the angular distance the eye travels during a saccade (Baloh *et al.*, 1975). Saccadic velocity is this amplitude over time (Table 2.1, Raab, 1985). Saccades and fixations are useful parameters to examine when exploring the efficacy of camouflage (Lin *et al.*, 2014a; Lin *et al.*, 2014b).

Snowshoe hares (*Lepus americanus*) are a seasonal coat colour (SCC) species, which moult from a white, winter coat to a brown, summer coat (Zimova *et al.,* 2018). Seasonal moulting is believed to be an evolutionary adaptation to provide effective camouflage in seasonally variable habitats (Zimova *et al.,* 2018). In recent years, research has indicated the occurrence and consequences of 'camouflage mismatch' whereby, as a result of climate change reducing snow-pack duration, SCC species differ in colour from their background by 60% or more (Mills *et al.*, 2013; Atmeh *et al.*, 2018; Zimova *et al.*, 2018). Snowshoe hare predators, such as coyotes, wolves, and raptors, are largely visual hunters (Krebs *et al.*, 1995; Murray, 2002; Zimova *et al.*, 2019). Coyotes (*Canis latrans*) require visual cues for predation success (Wells, 1978; Windberg, 1996; Lawson *et al.*, 2019), and have a generalist dependence on visual signals (Jacobs *et al.*, 1993). Felid snowshoe hare predators, such as lynxes, have poorer vision and are less dependent upon visual cues than canid predators (Maffei *et al.*, 1990). However, within ambush predation, the predation method favoured by lynxes, visual cues remain important in the processes of prey detection and capture (Kelber *et al.*, 2003; Stevens, 2006; Rockhill *et al.*, 2013; Lone *et al.*, 2014). Due to dichromatic snowshoe hare predators primarily utilising vision in predation, examining visual search mechanisms will help to explain whether ineffective camouflage increases detectability and therefore predation rates (Zimova *et al.*, 2018).

In the previous chapter, using a detection experiment I found that ineffective camouflage increased detection rates. However, it did not explain why snowshoe hares became more detectable. Here, I examine the visual mechanisms behind the variation in detection rate, and examine how visual search mechanisms vary when predators locate well verses poorly camouflaged

hares, and hares on complex verses simplistic backgrounds. I ask whether visual search parameters differ as a result of target camouflage efficacy and background complexity. To do this, I use human participants and eye-tracking equipment to record eye movements as participants play a detection experiment.

I predict that well camouflaged hares and hares located on more complex backgrounds will result in a greater number of fixations and longer search times due to being more difficult to detect (Table 2.1). Well camouflaged hares and hares located on complex backgrounds will be less discriminable from the background and harder to detect as the salient feature of the background, resulting in longer mean fixation durations, more fixations within the search rectangle (*see* Figure 2.1), more time spent searching within the search rectangle, and longer times between the first fixation on the target and slide completion (Table 2.1). Poorly camouflaged hares and hares on simple backgrounds will have faster average saccade velocities and less time until the first fixation in the target area (*see* Figure 2.1) due to these hares being more detectable and thus more easily identified in participant peripheral vision (Table 2.1). On patchy backgrounds, there will be more fixations in the search rectangle and longer delays between fixating on the target and slide completion due to participants misidentifying snowshoe hares as an unimportant feature within the image. I predict there will be no significant differences in the visual mechanisms used within the simulated dichromatic condition and the trichromatic condition.

Table 2.1: Visual Search mechanisms, explanations, and predictions. *An explanation of the visual search mechanisms tested and how these mechanisms explain snowshoe hare detectability.*

Visual Mechanism	Explanation	Prediction
Fixation Count	More fixations indicate an ineffective visual search.	More fixations will occur when snowshoe hares are difficult to locate.
Fixation Duration	Longer fixations indicate more information is processed or increased cognitive requirements.	Longer fixations will arise when snowshoe hares are difficult to discriminate from their background.
Fixation Count in the Search Rectangle	Fixations in close proximity to the target indicate reduced target distinguishability (Figure 2.1).	More fixations will occur in the search rectangle when snowshoe hares are difficult to discriminate from the background.
Saccade Velocity	Faster saccade velocities indicate peripheral attentional draw.	Fast saccades will occur when snowshoe hares are immediately detectable.
Mean Time in the Search Rectangle	Longer search times in the search rectangle indicate the target has not been located in peripheral vision (Figure 2.1).	Participants will spend longer in the search rectangle when snowshoe hares are difficult to discriminate from the background.
Time until the First Fixation on the Target	Time between the slide starting and the first fixation on the target (Figure 2.1).	The length of time until the first fixation on the target will be shorter if snowshoe hares are easily detectable.
Slide Duration	Time between the slide start and target identification.	Hares which are more difficult to locate will result in longer overall slide durations.
Time between the First Fixation on the Target and Slide Completion	The difference in time between the participant fixating on the target (Figure 2.1) and slide completion.	Snowshoe hares that are difficult to discriminate from the background or are misidentified will have longer times between the first fixation on target and slide completion.

Methodology

Experimental Overview

This experiment was a detection experiment to be played by participants whilst their eye movements were tracked. Participants were required to locate different coat colours of hares on different seasonal background types. The detection experiment was produced using OGAMA (Open Gaze and Mouse Analyser) software (Voßkühler *et al*., 2008) and eye movements were tracked using an EyeTribe eye-tracker (The EyeTribe, 2014). Eye movement data was recorded from the EyeTribe after each trial within OGAMA (Popelka *et al*., 2016). The participants for the experiment were acquired from within the University population and a total of 30 participants were tested. All participants tested were not aware of having colour blindness. Each participant was shown a total of 30 image slides, the slide would change once the participant clicked on the hare or would time out after 15 seconds. These 30 images were split into three distinct trials containing 10 images, with re-calibration occurring between each trial. The experiment was playable as a simulated dichromatic predator, or a trichromatic predator. A total of 15 participants played for each visual system.

Experiment Set Up

Image Collection

The images used within this experiment were collected from images produced by the detection experiment used in chapter two. All photographs were provided by the University of Montana having been collected during previous research. Images were collected from the online detection experiment to ensure random generation of coordinates, hare, and background images. 63 images were used for both the dichromatic and trichromatic conditions. These 63 images included 7 images for each coat colour and background type combination. No hare or background image was repeated within each visual system.

In OGAMA (Voßkühler *et al*., 2008), the experiment was produced using the inbuilt design slideshow option. These 63 images were split into three folders, each folder therefore contained 21 unique images, for the three distinct trials to be played by each participant. Each folder contained two unrepeated images of each coat colour and background type combination, plus an additional three images selected at random to ensure an even distribution of

camouflaged, mismatched, and partially mismatched scenarios within each folder. Of the 21 images available for each trial, 10 were selected randomly by OGAMA for the trial and shown to each participant.

The 'target' area of the hare was defined as an 8100-pixel area centred on the hare, either as 90x90-pixel square, 101.25x80 or 80x101.25-pixel rectangle (Figure 2.1). The use of a square or rectangular target area was selected dependent upon the pose of the snowshoe hare (Figure 2.1). The shape used for the target area was the shape that best explained the snowshoe hare outline, for example, if the snowshoe hare image was longer than it was tall, a rectangle would be used, however if height and width were roughly equivalent a square would be used. The area of interest was defined as being twice the size of the target area (16,200px area; Figure 2.1), and the search rectangle was defined as being twice the size of the area of interest (32,400px area; Figure 2.1).

Apparatus

Eye movements were sampled using an EyeTribe eye-tracker. This is a non-invasive eye-tracker which sits below the monitor. The EyeTribe samples at a rate of 60Hz (Ooms *et al.*, 2015), with an average accuracy of 0.5°-1.0° (Dalmaijer, 2014). The eye-tracker was raised 110mm above the table to improve alignment with participant viewing angle. The angle of the device was set individually for each participant to ensure accurate pupil tracking (Ooms *et al.*, 2015). A personal computer (Intel Core i7-4850HQ, 2.3GHz) was connected to the eye-tracker via a USB 3 cable and used to display images to participants, via an external monitor, and record eye movement data. Participants sat at a desk, using a chinrest to maintain a consistent viewing angle and minimise head movements (Dalmaijer, 2014; Titz *et al.*, 2018). The chin rest sat at 225mm above the table and 640mm from the display monitor.

The experiment was displayed to participants using a 27" ACER T272HUL Widescreen LCD monitor, with a maximum resolution of 2560x1440. Participants used a mouse to identify the location of the hares to minimise head movements. The screen display was placed on a pre-set mode with brightness of 77 and contrast of 56 for each participant, and room brightness was controlled for by the absence of windows and lights were turned off during the

experiment. The screen was raised 75mm above the table to compensate for the raising of the eye-tracker.
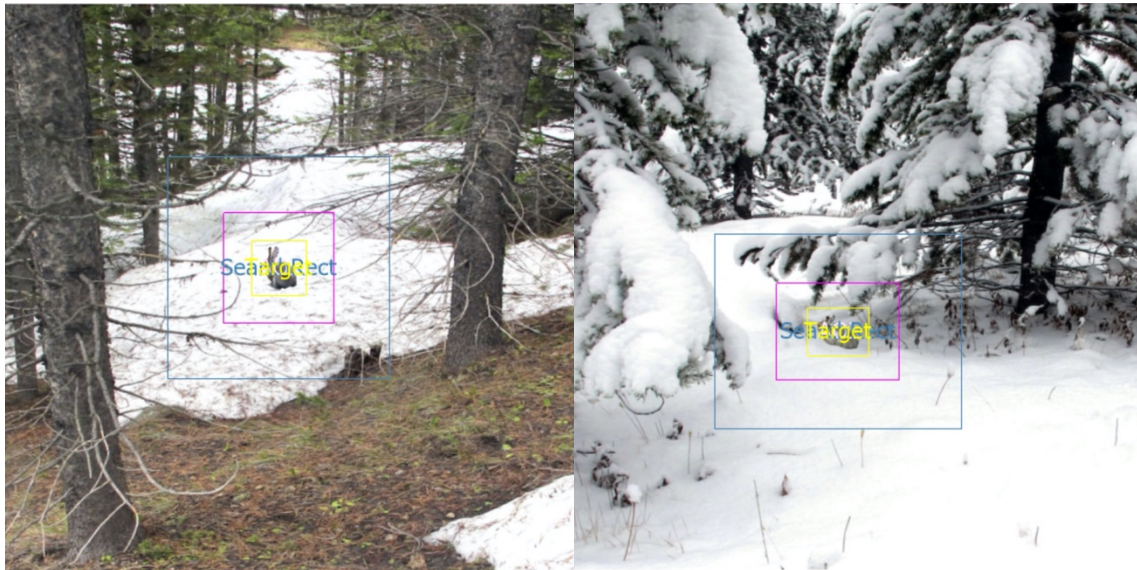
Figure 2.1: Examples of the size of the target, area of interest, and search rectangle. *The target area is indicated by the yellow box, area of interest by the pink box, and search rectangle by the blue box, compared with the true size of the snowshoe hare image.*

Procedure

Upon entering the experimental room, participants were given an explanation of the experiment and how the data collected would be used, to ensure informed consent to participation. Participants were informed they were free to withdraw at any point during the experiment, their play data would be stored anonymously and would be used within a scientific experiment in accordance with the ethical approval. Participants rested their chin on the chin rest to minimise movement and begin initial calibration (Titz *et al*., 2018).

Successful detection of the eyes was determined using the EyeTribe user interface prior to calibration (Venugopal *et al*., 2016). Calibration of the eye-tracker was conducted using OGAMA's inbuilt 16-point calibration. Calibrations were accepted if they achieved a score of 'Good' or better (Popelka *et al*., 2016). Participants were shown ten image slides, in-between each slide was a further calibration screen consisting of a 'Look here' command and a dot at which participants were required to look, this was used to manually eliminate drift between slides (Kikuchi *et al*., 2017b). After 10 slides were completed, the

data was saved and the folder changed for the second trial, this was repeated until all 30 images had been shown to the participant.

Ethical Note

This experiment was approved by the University of Exeter Bioscience ethics committee (application eCORN001788 v3.3). All individuals participating within the experiment were made aware their data would be used within a scientific experiment, that they could withdraw at any time throughout the experiment and that their detection data would be stored anonymously.

Camouflage Efficacy

Camouflage efficacy was measured based upon the difference between the snowshoe hare and the background in terms of both brightness and colour (Osorio & Vorobyev, 2005). Brightness contrast and colour difference between the snowshoe hare and the background was calculated using the methodology used in chapter two. The value of the hare and a 200x200 pixel square surrounding the hare was taken using a CIELAB-like colour space (Sharma, 2018); the CIELAB colour space most accurately represents human colour perception (Westland, 2003; Wübbeler et al., 2017).

Brightness contrast was calculated using Weber contrast and the absolute value was used (Peli, 1990). Absolute brightness contrast produces a positive result irrespective of whether the target or the background is more luminous. Colour contrast was calculated using the euclidian distance between the a* and b* values of the hare and the background. Both colour and brightness matching are frequently used together or independently within background matching camouflage (Osorio & Vorobyev, 2005). Therefore, to understand the efficacy of camouflage it is important to explore how these elements of camouflage independently influence detection.

Mismatch was calculated using the 60% threshold outlined in Mills et al. (2013). The percentage of white for each hare and the percentage of snow cover for each background was recorded in increments of 5%. The total percentage difference was then calculated to produce an absolute value. A hare was reported as being mismatched if the difference between the background and hare was greater than 60%. Using the >60% threshold from previous

research enables us to examine whether use of this classification explains visual search mechanisms differently to colour or brightness matching.

Background Complexity

Background complexity was calculated using the methodology used in chapter 2; Rosenholtz *et al*. (2007) measure of visual clutter. The scalar feature congestion of each background was calculated, based upon changes in luminance, colour, and object orientation.

Hare Position

The distance between the hare location and the edge of the screen was calculated along the x and y axes. The nearest distance was then used in analysis to examine the influence of hare location. Fixations occurring central to the screen occur more often than at the peripherals, therefore this is controlled for within analysis (Holmqvist *et al*., 2011).

Removal of Drift

The EyeTribe has been reported as having more upward drift in comparison with more expensive eye-trackers (Dalmaijer, 2014). Therefore, the raw data was manually modified to centralise data points and minimise drift based upon the calibration screen coordinates between each slide. The data for the calibration screen was modified so that the closest coordinates to the dot were aligned with the actual coordinates of the dot, and the following slide eye coordinates modified by an equal number of pixels (Kikuchi *et al*., 2017b). This method was repeated for each individual slide to minimise the influence of drift throughout each trial. These new raw data sheets were reimported into OGAMA, using the statistics module to calculate the measures used within the experiment.

Visual Mechanisms

The visual mechanisms studied within this experiment are split into three distinct categories: fixations, time, and saccade velocity.

Fixations

The mean fixation duration in milliseconds, the number of fixations within the search rectangle, and the total fixation count have been used as response variables within analysis.

The mean fixation duration indicates the average length of time, in milliseconds, spent fixating within each individual slide. The number of fixations within the search rectangle examines the number of times a participant overlooked the target prior to identifying it (Holmqvist *et al*., 2011). The use of the search rectangle within this analysis, as opposed to area of interest or target area, was selected as these models best explained the data. Finally, fixation count examines the total number of fixations within an image.

A fixation has been defined as 5 or more samples taken in one location. A fixation was counted as remaining in the same location if the participant looked within 20 pixels of the average fixation point, and consecutive fixations within this distance were merged to make one fixation.

Time

Slide duration, mean time within the search rectangle, length of time until the first fixation on the target, and the difference in time between the first fixation on the target and slide duration have been used as response variables within analysis.

Slide duration refers to the length of time it took a participant to find the hare. Participants had a time limit of 15 seconds to locate the snowshoe hare within each slide, if a hare was not located the slide would time out and load the following slide. The mean time within the search rectangle is the mean length of time in milliseconds a participant spent looking within the search rectangle surrounding the hare. The search rectangle was used, as opposed to the area of interest or target area, because these models best explained the data. The length of time before the first fixation on the target examines how long in milliseconds it took a participant to look directly at the target snowshoe hare after the trial began. Examining the difference in time between the first fixation in the target area and slide duration allows the exploration of whether participants fixated on the target and immediately identified it and completed the slide, or whether they continued to search beyond this initial fixation. If a participant fixates on the target but fails to identify it as the salient feature it indicates effective cryptic camouflage, or misclassification of the target (Stevens & Ruxton, 2019).

Saccade Velocity

The average saccade velocity, calculated as the number of pixels participants moved their pupils per millisecond, examines the speed of eye movements throughout the duration of the trial.

Exclusion of Data Points

One trial was removed for three participants (n = 30) due to errors in the communication between the EyeTribe and OGAMA resulting in improper recording of data points.

Within each model, extreme outliers were removed (fixation count n = 50; mean fixation duration n = 8; fixations in the search rectangle n = 11; average saccade velocity n = 60; mean time in the search rectangle n = 49; time until the first fixation on the target n = 238; time between the first fixation on the target and completion n = 39). A data point was defined as an extreme outlier if it was greater than the 3rd quartile plus the interquartile range multiplied by three, or smaller than the 1st quartile minus the interquartile range multiplied by three (Schwertman *et al*., 2004).

Statistical Analyses

All statistical analysis was conducted using R version 3.5.2 (R Core Team, 2018). Analyses of continuous response variables – fixation duration, slide duration, mean time in the search rectangle, length of time until the first fixation on the target, difference in time between the first fixation on the target and slide duration, and average saccade velocity – were conducted using linear mixed effects models, with participant number and image number included as random effects, using the lme4 extension (Bates *et al*., 2015). Linear mixed models were used as the models fit the assumptions of a linear mixed effects model (Baayen *et al*., 2008). Within these models - where applicable - the log normal error structure of time (ms) was used and model parsimony was calculated using backward stepwise selection (Troscianko *et al*., 2013; Hughes *et al*., 2015). Analyses of discrete response variables – total fixation count, and number of fixations in the search rectangle – were conducted using poisson distribution generalised linear mixed effects models, with participant number and image number included as random effects using the lme4 extension (Bates *et al*., 2015). Overdispersion was calculated using the R package 'Performance' and the 'check_overdispersion' function (Lüdecke *et al*., 2019). This function

returns an approximate estimate of overdispersion in generalised linear mixed effects models, calculating overdispersion by dividing the sum of squared standardized residuals by the expected value of *n-k (*Gelman & Hill, 2007). The chi-square goodness-of-fit compares whether the predicted frequency of the dependent variables deviate from the observed frequency (Manjón & Martínez, 2014; Lüdecke *et al*., 2019). Within the 'Performance' package, a p-value smaller than 0.05 indicates overdispersion (Lüdecke *et al*., 2019). The models showed no overdispersion; fixation count model average: $X^2 = 460.52$, p = 1.00; number of fixations in the search rectangle: $X^2 = 452.40$, p = 1.00. The most parsimonious model was selected using forward stepwise selection from the null model. Forward stepwise selection was necessary as a model containing all variables could not run.

Models were compared using Akaike Information Criterion with a threshold of 2 AIC set to determine the most parsimonious model (Burnham & Anderson, 2004). When multiple models fell within this threshold, the relative weight of each variable retained within the best model subset, the mean estimate coefficient, and parameter variance was calculated across all models. The marginal and conditional pseudo-R2 values for the models were calculated using the R package 'MuMIn' and the 'r.squaredGLMM' function (Bartoń, 2019).

Results

Fixations

Fixation Count

Simulated dichromatic participants fixated fewer times overall (Dichromatic – 2.86±0.08 (n = 417); Trichromatic - 4.52±0.13 (n = 403); Table 2.2). Camouflage efficacy and background complexity did not influence participant fixation count, suggesting the number of fixations required to locate snowshoe hares does not differ on complex verses simple backgrounds, or for camouflaged verses mismatched snowshoe hares (Table 2.2). However, colour difference between the hare and the background influenced fixation count when interacting with visual system (Table 2.2). Specifically, dichromatic participants exhibited no difference in fixation count when searching for colour camouflaged or mismatched hares, whereas trichromatic participants had more fixations

when searching for well camouflaged hares (Figure 2.2). Therefore, trichromats exhibited less effective visual searches.

Hares positioned centrally on the screen required fewer fixations to locate compared with peripheral hares (Table 2.2).
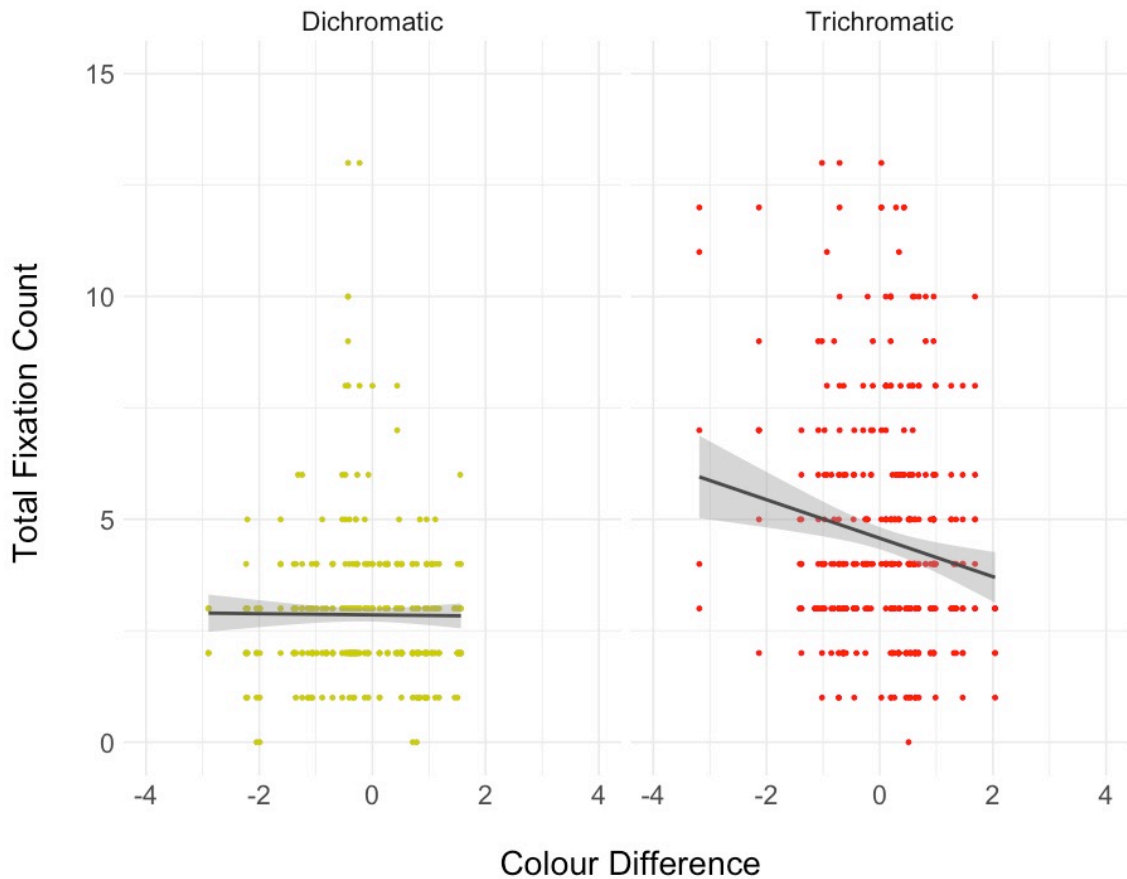
Figure 2.2: The influence of colour difference on fixation count dependent upon visual system. *Fixation count for trichromatic participants decreased as colour difference increased, whilst dichromatic participants displayed no change in fixation count.*

Table 2.2: The mean estimate coefficient, variance and relative weight of the parameters included within the best model subset for total fixation count. *The mean estimate coefficient calculated as the mean of the estimate across all models, variance calculated as the square of the mean standard error across all models and multiplied by sample size, and relative weight of each variable included in the best model subset.*

Parameter	Estimate of Coefficient	Variance	Relative Weight
Intercept	1.058	0.098	-
Visual System Trichromatic	0.441	0.190	1.00
Background Complexity	0.063	0.022	0.01
Nearest Distance	-0.139	0.024	0.43
Brightness Contrast	-0.052	0.021	0.13
Colour Difference	-0.042	0.030	0.05
Visual System Trichromatic * Colour Difference	-0.100	0.089	0.00

<u>*Mean Fixation Duration*</u>

The mean fixation duration was longer for simulated dichromatic players than trichromatic players (Dichromatic - 364±6ms (n = 426); Trichromatic - 319±6ms (n = 436); Table 2.3), indicating dichromatic participants were less effective at target discrimination. Background complexity had no significant effect on mean fixation duration (Table 2.3). This suggests that more complex backgrounds do not influence participants ability to process fixation information.

Hare coat colour did not influence participant mean fixation duration, therefore no one coat colour was more difficult to discriminate from the background (Brown - 351±8ms (n = 280); White - 342±8ms (n = 286); Moulting - 331±7ms (n = 296); Table 2.3). Slide number and trial number did not influence mean fixation duration (Table 2.3).

Table 2.3: The mean estimate coefficient, variance and relative weight of the parameters included within the best model subset for mean fixation duration. *The mean estimate coefficient calculated as the mean of the estimate across all models, the variance calculated as the mean standard error across all models squared and multiplied by sample size, and relative weight of each variable included within the best model subset.*

Parameter	Estimate of Coefficient	Variance	Relative Weight
Intercept	5.969	0.140	-
Visual System Trichromatic	-0.073	0.169	1.00
Slide 2	-0.071	0.069	
Slide 3	-0.066	0.064	
Slide 4	-0.160	0.069	
Slide 5	-0.016	0.067	
Slide 6	-0.151	0.069	1.00
Slide 7	-0.051	0.070	
Slide 8	-0.164	0.069	
Slide 9	-0.121	0.068	
Slide 10	-0.082	0.069	
Trial 2	-0.048	0.030	0.32
Trial 3	-0.038	0.028	
Coat Colour Moulting	-0.085	0.056	1.00
Coat Colour White	-0.040	0.061	
Background Complexity	-0.029	0.024	0.64

Number of Fixations in the Search Rectangle

The most parsimonious model for the number of fixations in the search rectangle had an AIC of 2633.1, with a ΔAIC of 10.1 from the next most parsimonious model.

Trichromatic participants fixated in the search rectangle significantly more often than simulated dichromatic participants ($X^2_{(1)} = 22.044$, $p < 0.001$). These increased fixations in close proximity to the target indicate that trichromats found peripheral discrimination of snowshoe hares from the background more difficult than dichromats.

Trial number significantly influenced the number of fixations within the search rectangle ($X^2_{(2)}$ = 16.101, p < 0.001). More fixations occurred within the search rectangle in the 3rd trial than in the 1st and 2nd trial (Table 2.4). More fixations occurred within the search rectangle when the hare was central on the background image ($X^2_{(1)}$ = 12.790, p < 0.001).

Table 2.4: The pairwise comparison of trial number. *The comparison estimate, standard error (SE), 95% confidence interval (CI), z-ratio and p-value of the pairwise comparison of trial number.*

Contrast	Est.	SE	95% CI (asymptotic)		t-ratio	p-value
			Lower	Upper		
1 - 2	-0.053	0.0617	-0.201	0.095	-0.854	0.393
1 - 3	-0.226	0.060	-0.371	-0.082	-3.747	< 0.001
2 - 3	-0.173	0.058	-0.312	-0.035	-2.989	0.006

Saccade Velocity

Simulated dichromatic players had slower average saccade velocities (Dichromatic - 2.10±0.07°/ms (n = 388); Trichromatic - 3.14±0.08°/ms (n = 422); Table 2.5). Average saccade velocity was influenced by absolute brightness contrast (Table 2.5), with faster saccade velocities occurring when searching for more contrasting hares. This indicates that brightness contrasting hares were located in participant peripheral vision. Visual system interacted with coat colour to influence participant average saccade velocity. Average saccade velocities were faster for participants using the trichromatic visual system when searching for all coat colours (Figure 2.3). Visual system also influenced the impact of brightness contrast on saccade velocity, with trichromatic participants exhibiting faster velocities when searching for contrasting hares and dichromatic participants experiencing no difference in velocity (Table 2.5). Therefore, trichromatic participants were able to peripherally identify all coat colours and brightness contrasting snowshoe hares more easily than the simulated dichromatic participants.

The position of the hare on the screen did not influence average saccade velocity (Table 2.5). Participants had faster saccade velocities in trial one than trial three.
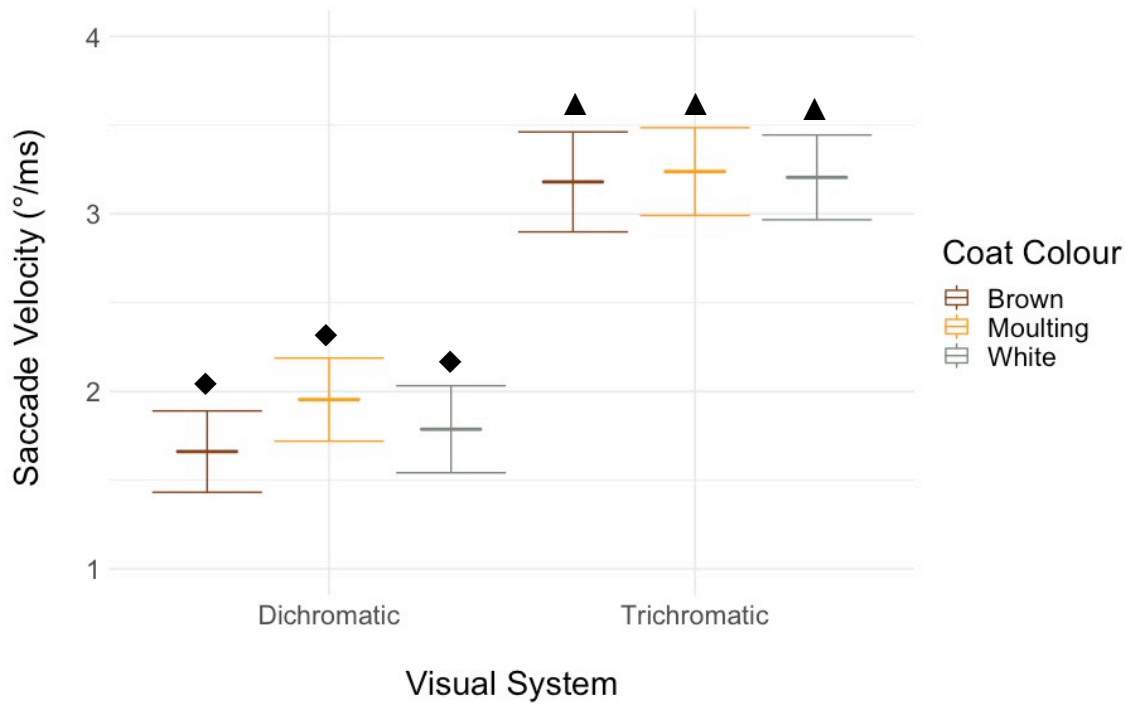
Figure 2.3: The impact of visual system on average saccade velocity.

Trichromatic participants had faster average saccade velocities when searching for all coat colours. This means that trichromatic participants identified all coat colours more rapidly in their peripheral vision than simulated dichromatic participants. Matching symbols indicate not significant differences.

Table 2.5: The mean estimate coefficient, variance and relative weight of the parameters included in the best model subset for average saccade velocity. *The mean estimate coefficient calculated as the mean of the estimate across all models, the variance calculated as the mean standard error across all models squared and multiplied by sample size, and relative weight of each variable included within the best model subset.*

Parameter	Estimate of Coefficient	Variance	Relative Weight
Intercept	0.425	0.451	-
Visual System Trichromatic	0.427	0.597	1.00
Trial 2	0.052	0.112	0.43
Trial 3	0.128	0.100	
Background Snowless	-0.073	0.320	1.00
Background Snowy	0.105	0.351	
Coat Colour Moulting	0.012	0.403	0.61
Coat Colour White	0.017	0.412	
Hare Position	0.024	-0.174	1.00
Brightness Contrast	-0.075	0.084	1.00
Visual System Trichromatic * Coat Colour Moulting	-0.185	0.544	0.55
Visual System Trichromatic * Coat Colour White	0.110	0.534	
Brightness Contrast * Background Type Snowless	0.181	0.131	1.00
Brightness Contrast * Background Type Snowy	0.120	0.226	
Visual System Trichromatic * Brightness Contrast	-0.135	0.109	1.00

Time

Slide Duration

The most parsimonious model for slide duration had an AIC of 986.93; with a ΔAIC of 5.54 from the next most parsimonious model. The most parsimonious model had a marginal R^2 of 0.15 and a conditional R^2 of 0.56.

Table 2.6: Results of linear mixed effects in the most parsimonious model for slide duration. *The sum of squares (Sum Sq), mean of squares (Mean Sq), numerator degrees of freedom (Num DF), denominator degrees of freedom (Den DF), the F statistics (F-value) and P values of the variables retained in the most parsimonious model. Model variables include visual system, trial number, background complexity, hare position, brightness contrast, and colour difference.*

Variable	Sum Sq	Mean Sq	Num DF	Den DF	F-value	P- value
Visual System	0.504	0.504	1	76.68	3.856	0.053
Trial Number	0.710	0.355	2	721.26	2.715	0.067
Background Complexity	0.568	0.568	1	121.00	4.349	0.039
Hare Position	2.150	2.150	1	121.05	16.452	< 0.005
Brightness Contrast	0.930	0.930	1	119.87	7.115	0.009
Colour Difference	0.931	0.931	1	118.30	7.124	0.009

Simulated dichromatic and trichromatic participants did not differ in the length of time it took them to complete each slide (Table 2.6). Background complexity, brightness contrast between the hare and the background, and colour difference between the hare and the background all significantly influenced the length of time a participant spent on each slide (Table 2.6). Detection times were longer when participants were searching for hares on complex backgrounds, and when searching for well brightness and colour camouflaged snowshoe hares.

Centrally located hares took significantly less time to locate in comparison with peripheral hares (Table 2.6). The trial number had no significant impact on slide duration.

<u>*Mean Time in the Search Rectangle*</u>

There was no significant difference in search time between coat colours (Moulting - 421±13ms (n = 280); Brown - 460±13ms (n = 269); White - 477±15ms (n = 272); Table 2.7), or mismatch categorisation (Mismatched -

439±12ms (n = 371); Matched - 463±11ms (n = 450); Table 2.7). Therefore, no one coat colour was easier to discriminate from the background, nor did the 60% or greater classification of mismatch (Mills *et al*., 2013) influence discriminability.

Participants spent longer searching the search rectangle when hares were located on the screen periphery (Table 2.7). Neither slide number nor trial number significantly influenced the time spent searching within the search rectangle (Table 2.7).

Table 2.7: The mean estimate coefficient, variance and relative weight of the parameters included in the best model subset for mean time in the search rectangle. *The mean estimate coefficient calculated as the mean of the estimate across all models, the variance calculated as the mean standard error across all models squared and multiplied by sample size, and relative weight of each variable included in the best model subset.*

Parameter	Estimate of Coefficient	Variance	Relative Weight
Intercept	6.125	0.261	-
Slide 2	-0.013	0.150	1.00
Slide 3	0.019	0.150	
Slide 4	-0.104	0.147	
Slide 5	-0.003	0.144	
Slide 6	-0.199	0.146	
Slide 7	-0.104	0.147	
Slide 8	-0.170	0.143	
Slide 9	-0.116	0.144	
Slide 10	-0.105	0.145	
Trial 2	-0.075	0.059	1.00
Trial 3	-0.043	0.055	
Coat Colour Moulting	-0.093	0.126	1.00
Coat Colour White	-0.052	0.172	
Hare Position	-0.070	0.014	1.00
Mismatch Yes	-0.030	0.157	0.48

Mean Time Until the First Fixation in the Target Area

Participants took longer to first fixate in the target area when searching for snowshoe hares on complex backgrounds (Table 2.8). Visual system had no significant impact on the average time to fixate in the target area (Dichromatic - 676 ± 16ms (n = 304); Trichromatic - 832 ± 27ms (n = 328); Table 2.8). There was no significant impact of hare coat colour on the length of time until the first fixation on the target (White - 814 ± 30ms (n = 192); Moulting - 731 ± 26ms (n = 223); Brown - 732 ± 28ms (n = 217); Table 2.8). Absolute brightness difference did not influence the length of time until the first fixation in the target area.

The impact of background complexity was significantly different dependent upon the hare being located. Brown and moulting hares took longer to locate when on complex backgrounds in comparison with simple backgrounds, whereas white hares did not differ in the length of time until the first fixation in the target area regardless of background complexity (Figure 2.4A). The length of time until the first fixation in the target area was longer for trichromatic participants when searching for white hares in comparison with simulated dichromatic participants (Figure 2.4B). Participants locating centralised hares took less time to fixate within the target area (Table 2.8).

Table 2.8: The mean estimate coefficient, variance and relative weight of the parameters included within the best model subset for mean time until the first fixation in the target area. *The mean estimate coefficient calculated as the mean of the estimate across all models, the variance calculated as the mean standard error across all models squared and multiplied by sample size, and relative weight of each variable included within the best model subset.*

Parameter	Estimate of Coefficient	Variance	Relative Weight
Intercept	6.581	0.407	-
Visual System Trichromatic (Tri)	-0.139	0.491	1.00
Trial 2	-0.021	0.080	0.395
Trial 3	-0.076	0.068	
Coat Colour Moulting	0.069	0.551	1.00
Coat Colour White	-0.222	0.707	
Background Complexity	0.097	0.232	1.00
Hare Position	-0.208	0.033	1.00
Brightness Contrast	-0.041	0.081	1.00
Coat Colour Moulting * Background Complexity	0.014	0.288	1.00
Coat Colour White * Background Complexity	-0.153	0.254	
Visual System Tri * Coat Colour Moulting	0.076	0.791	1.00
Visual System Tri * Coat Colour White	0.578	0.733	

A.

B.
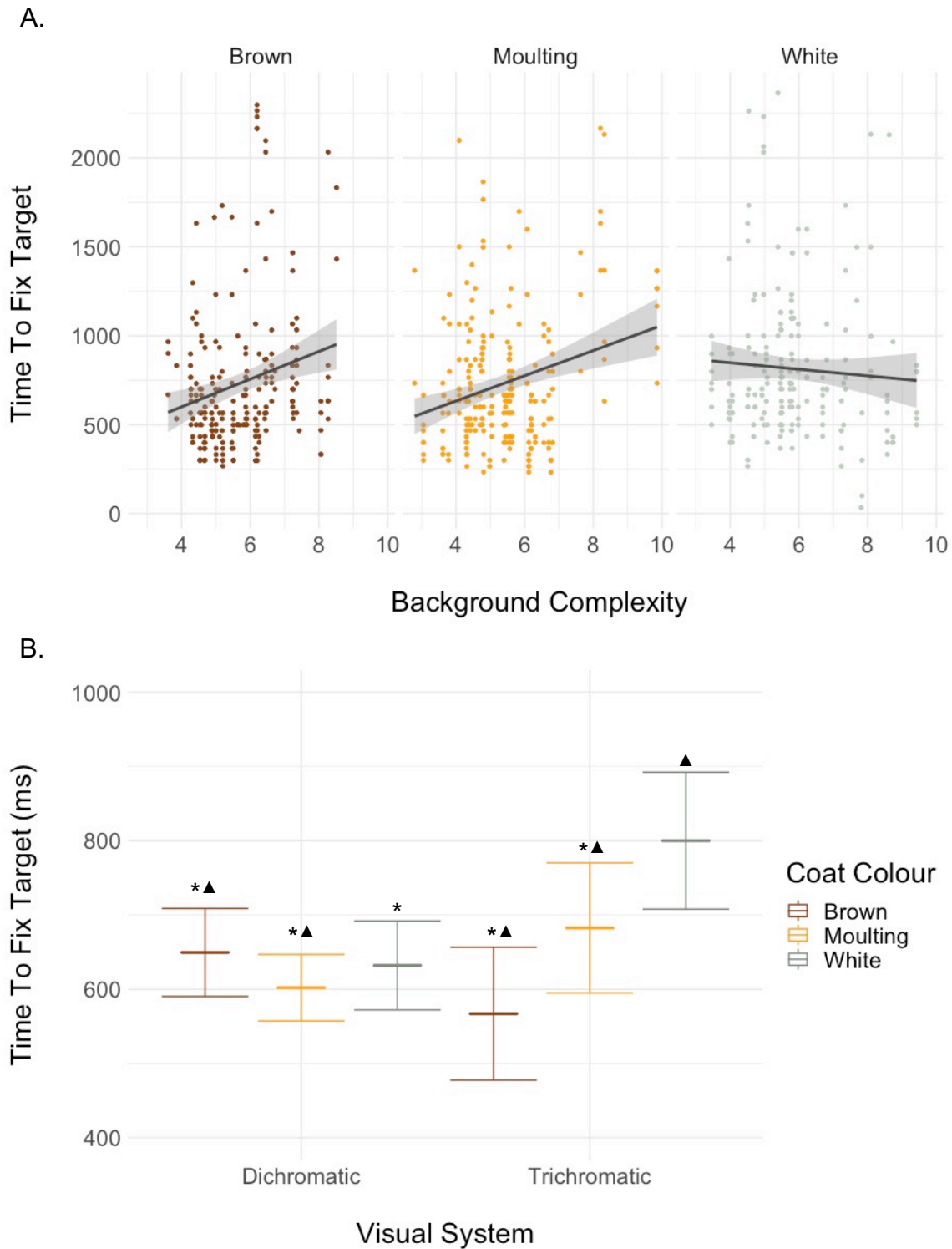
Figure 2.4: Hare coat colour influenced the length of time it took until the first fixation in the target area differently dependent upon background complexity and visual system. *Time until the first fixation in the target area was longer when searching for brown and moulting hares on complex backgrounds in comparison with simple backgrounds (**A**). Trichromatic participants took longer to first fixate in the target area when searching for white hares in comparison with dichromatic participants (**B**). Matching symbols indicate not significant differences.*

Time between the First Fixation in the Target Area and Slide Completion

Trichromatic participants had longer delays between the first fixation on the target area and clicking on the snowshoe hare than simulated dichromatic participants (Dichromatic – 939±22ms (n = 299); Trichromatic - 1214±34ms (n = 330); Table 2.9). Trichromats took longer to locate white and moulting hares after fixating on the target area in comparison with dichromatic participants (Dichromatic: Brown - 974±41ms (n = 97); Moulting - 870±33ms (n = 107); White - 981±41ms (n = 95); Trichromatic: Brown - 1051±54ms (n = 117); Moulting - 1204±55ms (n = 111); White - 1413±65ms (n = 102); Table 2.9). In addition, trichromatic participants had longer times between fixating on white snowshoe hares and clicking on them in comparison with brown hares (Table 2.9). Therefore, trichromatic participants were less effective at recognising a snowshoe hares as the salient feature, in particular white and moulting hares. White snowshoe hares were most frequently missed or misidentified by trichromats, being overlooked significantly longer than brown snowshoe hares.

Independently, hare coat colour did not significantly influence the time between fixation and completion (Brown - 1016±35ms (n = 214); Moulting - 1040±34ms (n = 218); White - 1205±42ms (n = 197); Table 2.9). Therefore, there was no coat colour that was significantly more likely to be misidentified or overlooked.

Colour camouflage efficacy had no impact on the length of time between the first fixation on the target and slide completion (Table 2.9). However, brightness camouflage efficacy did (Table 2.9). Participants searching for brightness contrasting snowshoe hares took less time to click on the hare after fixating on it in comparison with camouflaged hares. Therefore, brightness camouflaged snowshoe hares were more likely to be overlooked. Snowshoe hares located on complex backgrounds required participants to spend longer searching between the first fixation on the target and slide competition, indicating more complex backgrounds decreased snowshoe hare detectability (Table 2.9).

Hares located centrally on the screen took less time to click on after fixating compared with peripheral snowshoe hares (Table 2.9). Slide number and trial number had no impact on the length of time between the first fixation on the target and slide completion (Table 2.9).

Table 2.9: The mean estimate coefficient, variance and relative weight of the parameters included within the best model subset for the length of time between the first fixation in the target area and slide completion. *The mean estimate coefficient calculated as the mean of the estimate across all models, the variance calculated as the mean standard error across all models squared and multiplied by sample size, and relative weight of each variable included within the best model subset.*

Parameter	Estimate of Coefficient	Variance	Relative Weight
Intercept	6.950	0.333	-
Visual System Trichromatic	0.034	0.410	1.00
Slide 2	-0.076	0.111	1.00
Slide 3	-0.101	0.113	
Slide 4	-0.118	0.107	
Slide 5	-0.139	0.106	
Slide 6	-0.095	0.107	
Slide 7	-0.056	0.115	
Slide 8	-0.163	0.114	
Slide 9	-0.235	0.106	
Slide 10	-0.160	0.106	
Trial 2	-0.128	0.062	1.00
Trial 3	-0.125	0.051	
Coat Colour Moulting	-0.024	0.352	0.90
Coat Colour White	-0.035	0.454	
Background Complexity	0.085	0.102	1.00
Hare Position	-0.154	0.022	1.00
Brightness Contrast	-0.050	0.052	1.00
Colour Difference	0.017	0.125	1.00
Visual System Trichromatic * Coat Colour Moulting	0.089	0.517	0.78
Visual System Trichromatic * Coat Colour White	0.321	0.469	

Table 2.10: Summary of the Key Findings *for each variable retained in the most parsimonious model or model subset.*

Response Variable	Influenced by:	Not Influenced by:
Fixation Count	Dichromatic participants exhibited more efficient visual searches through the use of fewer fixations, in particular when searching for colour camouflaged snowshoe hares.	• Background complexity • Camouflage
Mean Fixation Duration	Dichromatic participants fixated for longer, indicating less effective visual searches or more cognitive processing within each fixation.	• Background complexity • Coat colour
Number of Fixations in the Search Rectangle	Trichromatic participants fixated more in the search rectangle suggesting they were less effective at peripherally detecting the target.	
Saccade Velocity	Trichromatic participants utilised faster saccades when searching for all coat colours, indicating they detected snowshoe hares in their peripheral vision more frequently than dichromatic participants. Trichromatic search efficacy was also more influenced by brightness contrast than dichromats, with contrasting hares being rapidly detected in their peripheral vision.	• Background type • Coat colour • Brightness contrast and background type
Slide Duration	Participants took longer to located snowshoe hares if hares were well camouflaged, both based on brightness and colour, or located on complex backgrounds.	• Visual system
Mean Time in Search Rectangle		• Coat colour • >60% Mismatch
Mean Time Until the First Fixation in the Target Area	The first fixation on the target took longer on complex backgrounds, in particular for brown and moulting snowshoe hares. Indicating complex backgrounds reduced snowshoe hare detectability. White coats were more difficult for trichromatic participants to detect compared with dichromats.	• Visual system • Coat colour • Brightness contrast
Time between the First Fixation in the Target Area and Slide Completion	Trichromats more frequently overlooked white and moulting hares in comparison with dichromats. In addition, they overlooked white hares more frequently than brown hares. Snowshoe hares were overlooked for longer if they were brightness camouflaged or were located on complex backgrounds	• Coat Colour • Colour difference

Discussion

This study has shown that camouflage efficacy and background complexity play an important role in the visual detectability of snowshoe hares, whilst the visual system utilised within the search impacts both detectability – attentional draw – and target discriminability – cognitive load of separating the target from the background. Overall, I found that seasonal coat colour camouflage functions primarily in avoiding detection from potential predators, but is limited in its impact on target discriminability. Although both dichromats and trichromats experienced limitations in the efficacy of target discrimination, dichromats most frequently used efficient visual searches. Ineffective camouflage is therefore likely to dramatically impact the detectability of all seasonal coat colour (SCC) species predated by dichromats, and the implications of this research are not limited to snowshoe hare survival.

As predicted, detection times were longer when participants were searching for well camouflaged snowshoe hares and hares located on visually complex backgrounds. This supports previous research into camouflage efficacy, which has indicated that camouflaged targets and those located on complex backgrounds will be more difficult to locate due to inefficient visual searches (e.g. Merilaita, 2003; Andersson *et al*., 2009; Stevens *et al*., 2013; Toh & Todd, 2017; Nokelainen *et al*., 2019). These longer detection times when camouflaged suggest that SCC moulting has evolved to provide background matching camouflage. However, using detection times alone to examine the efficacy of camouflage has been found to be insufficient in explaining visual search difficulty (Lin *et al*., 2014a). Therefore, although camouflage and background complexity influence detection times, this study aimed to examine whether variations in search time and predation risk can be directly explained by camouflage mismatch increasing visual search efficacy.

Contrary to prediction, simulated dichromatic and trichromatic participants significantly differed in search mechanisms. In previous research, trichromacy has been found to elicit fewer fixations; with fewer fixations being associated with efficient visual searches (Frey *et al*., 2011; Holmqvist *et al*., 2011; Bompas *et al*., 2013). However, in this task simulated dichromatic participants fixated fewer times overall. Most of the research in which trichromacy produces fewer fixations focuses upon environments and scenarios where red-green colour discrimination is important in target detection (Frey *et al*., 2011; Bompas *et al*.,

2013). Within predator-prey dynamics, and in particular within alpine, sub-arctic, and arctic ecosystems, red and green are rarely salient for prey detection. Thus, the more effective visual searches for simulated dichromats are likely due to reduced chromatic variance, and absence of red-green stimuli, within these ecosystems. The fixation count differences between visual systems were particularly apparent when interacting with chromatic camouflage efficacy. Trichromatic participants fixated more often when searching for colour camouflaged snowshoe hares, whilst dichromatic participants did not. This indicates that colour-based background matching camouflage is detrimental to trichromatic search efficacy, but is likely to have minimal impact on a dichromatic predator's ability to detect prey (Saito *et al*., 2006). Therefore, chromatic camouflage is unlikely to influence dichromatic predator success in the wild (Zimova *et al*., 2016). It is possible that the reduced chromatic variance from the dichromatic perspective promotes faster cognitive processing of stimuli, thus reducing the fixations required to detect the target (Ben-Tov *et al*., 2018). Within the context of SCC species, and other alpine, sub-arctic, and arctic camouflaged species, my results suggest that predator ability to distinguish between chromatic cues will be less important than brightness cues as the environment is primarily monochromatic. Therefore, the reduced dependency upon chromatic cues for dichromats confers a search efficacy advantage, in line with previous research (Ben-Tov *et al*., 2018). Overall, dichromacy is likely beneficial in the efficacy of predator visual searches even within more chromatically variable ecosystems, as the inability to distinguish between red and green is unlikely to impact target detection when searching for prey (Pastilha *et al*., 2019).

In regard to average saccade velocities, simulated dichromats utilised less effective visual searches. Dichromatic participants exhibited slower saccade velocities than trichromats across all coat colours. Variations in saccade velocity may arise as a result of differing search methods or search difficulty. Visual searches are generally considered to be top-down or bottom-up processes (Itti & Koch, 2000). Top-down processing of an image requires participants have prior knowledge of the task, whereas bottom-up processing is the unconscious draw to sensory inputs (Itti & Koch, 2000). Due to dichromacy being novel to participants within this study (i.e. prior knowledge of the task was limited), this visual system could have promoted the use of bottom-up searching. Therefore,

dichromats would be expected to display rapid saccades between fixations. However, the novel visual system resulted in slower saccade velocities. It is possible that these slower saccades arose from reduced chromatic variance within the dichromatic condition minimising the salience of the target, thereby resulting in slower saccades in even in the presence of bottom-up processing (Itti & Koch, 2000; Saito *et al*., 2006). Differences in saccade velocity can also arise due to search difficulty. There was, however, no difference in overall detection times between simulated dichromatic and trichromatic participants, therefore it is unlikely dichromats altered their search mechanisms due to task difficulty (Over *et al*., 2007). Previous research has indicated that canids and felids use slower saccades than humans in visual searches (Moeller *et al*., 2004; Park *et al*., 2020). Therefore, snowshoe hare predators – such as wolves, coyotes, or lynxes – are likely to naturally exhibit slower saccade velocities (Moeller *et al*., 2004; Park *et al*., 2020). It is possible that these slower saccades in dichromatic predators are due to dichromacy as a visual system promoting slower saccades and less efficient visual searches (Voraphani, 2007), with simulated dichromatic participants responding in a similar way. However, if canid and felid species use slower saccades than humans regardless of visual system, a comparison not yet made in the literature, the slow saccades exhibited within the simulated dichromatic condition here could be even slower in mammalian predators. Therefore, snowshoe hare predators may experience significantly less effective visual searches in comparison with trichromatic experimenters. Therefore, despite red-green cues not being important in alpine, sub-arctic, and arctic ecosystems, slower saccades could reduce dichromatic predators' ability to detect snowshoe hares as rapidly as trichromatic experimenters. This may be due to the reduced chromatic variance perceived by dichromats decreasing peripheral detection rate (Holmqvist *et al*., 2011; Ben-Tov *et al*., 2018).

The reduced chromatic variance observed from the perspective of a dichromatic predator is anticipated to increase their dependence upon brightness cues in prey detection (Hiramatsu *et al*., 2008; Ben-Tov *et al*., 2019). Therefore, it would be anticipated that the simulated dichromatic condition would promote more efficient detection of brightness-based background matching camouflage. Trichromatic participants showed faster saccade velocities when searching for brightness mismatched snowshoe hares, in

comparison with camouflaged hares. It is likely this is due to brightness contrast eliciting an attentional draw (Perron & Hallet,1995; Turatto & Galfano, 2000; Horwitz & Albright, 2003; Martinovic *et al.*, 2011). However, this effect was not observed in the simulated dichromats. Therefore, brightness contrast is likely more peripherally detectable for trichromats (Goldberg & Wichansky, 2003; Holmqvist *et al.*, 2011), whilst brightness camouflage requires a slower visual search. Dichromatic participants showed no variation in saccade velocities, regardless of brightness camouflage efficacy. This suggests that brightness-based camouflage impacts visual detection by trichromats more than dichromatic predators. From this, it can be theorised that the elevated predation rates of mismatched snowshoe hares by dichromatic predators (Zimova *et al.*, 2016; Atmeh *et al.*, 2018; Wilson *et al.*, 2018) are not due to brightness contrast increasing their detectability.

Trichromatic participants took longer to first fixate on white hares in comparison with dichromatic participants. Brown and moulting hares were equally as detectable for both visual systems. Therefore, positively mismatched (Zimova *et al.*, 2020) – white coat on snowless backgrounds – and white camouflaged SCC species are likely to be more easily detected by dichromats than trichromats. Negative-mismatched (Zimova *et al.*, 2020) – brown hares on snowy backgrounds – and brown camouflaged SCC species will be detected equally by dichromats and trichromats. This may be because simulated dichromatic participants depended primarily upon brightness cues in target detection (Ben-Tov *et al.*, 2018). Therefore, a white coat is more readily detected by dichromats as they are naturally brighter. As the climate continues to change, the length of time that snowshoe hares are positively mismatched is likely to increase (Zimova *et al.*, 2020). Therefore, it is important to account for trichromatic visual systems reduced ability to detect white coats when considering the impact of camouflage mismatch on detectability.

In line with previous research, participant search efficacy was reduced when searching complex backgrounds (e.g. Merilaita, 2003; Dimitrova & Merilaita, 2010; Xiao & Cuthill, 2016). Visual search is generally biased towards discontinuities and distinctive features within an image (Neider & Zelinksy, 2006; Boot *et al.*, 2009), therefore visually complex environments result in participants searching more discontinuities, which delays target detection (Neider & Zelinksy, 2006). The increased variation of luminance, colour, and

object orientation within complex backgrounds function as distractors, requiring participant's attention to be drawn to these regions, whilst on less complex backgrounds the target outline is more likely to be the most distinctive object requiring inspection (Neider & Zelinksy, 2006; Boot *et al.*, 2009). Within SCC species, the impact of background complexity on detectability has yet to be properly explored in the wild. This result indicates that increased complexity will facilitate camouflage efficacy by decreasing snowshoe hare detectability. Visual system had no impact on the length of time it took a participant to first fixate on the target on complex backgrounds. Therefore, as has been indicated in previous research (Xiao & Cuthill, 2016), target detectability is reduced by background complexity when perceived by all predator visual systems.

The ability of a participant to discriminate the target from the background was influenced by visual system and brightness contrast. Brightness camouflage slowed participant response rate between fixating on the target and completing the slide. This indicates participants either misidentified or took longer to cognitively process brightness camouflaged hares as being the desired target, in comparison with brightness mismatched snowshoe hares. Despite visual system influencing discriminability, there was no one visual system that was consistently better at target discrimination. Simulated dichromatic participants had longer mean fixation durations, suggesting that dichromatic participants took longer to discriminate snowshoe hares from the background. However, as dichromats had fewer fixations than trichromats, these longer fixations may be due to dichromatic participants processing more information during each fixation (Greene, 1999). Trichromats fixated more frequently in the search rectangle than dichromats. More fixations in close proximity to the target indicates that trichromats struggle to discriminate the target from the background, either due to ineffective use of peripheral information or reduced inhibition of return (Greene, 1999; Itti & Koch, 2001). Inhibition of return prevents visual attention repeatedly returning to stimuli of high attentional draw, so returning to previously searched locations indicates inefficient visual searches (Itti & Koch, 2001). Therefore, dichromacy and trichromacy may not necessarily differ in ability to discriminate a target from its background, but rather in search mechanisms, with dichromats using fewer and longer fixations whilst trichromats use frequent and short fixations. It is important to note that canid predators are expected to fixate for longer periods

of time than human participants, therefore the influence of these longer fixations on overall target detection rate will be even greater in dichromatic, canid snowshoe hare predators, such as coyotes or wolves (Park *et al.*, 2020).

Within this research, mismatch classification, using the 60% threshold outlined in previous literature (e.g. Mills *et al.*, 2013), did not explain differences in target discriminability. Therefore, the observed increased predation rates of mismatched snowshoe hares (Mills *et al.*, 2013; Atmeh *et al.*, 2018; Wilson *et al.*, 2018) are unlikely to be due to being more discriminable from their background. These elevated predation rates may instead be attributed to other factors, such as differences in avoidance behaviours between seasonal morphs (Zimova *et al.*, 2014), differences in the persistence of olfactory cues (Kitchener et al., 2010), or differences in detectability. However, mismatch classification was not retained in any models examining snowshoe hare detectability. Consequently, this study found colour and brightness contrast were no better than the 60% or greater threshold in predicting snowshoe hare discriminability, but they are better predictors of detectability in SCC species.

With climate change clearly influencing the efficacy of SCC background-matching camouflage, and limited phenotypic plasticity being observed – snowshoe hares only exhibit plasticity in the rate and initiation of their spring moult (Mills *et al.*, 2013; Zimova *et al.*, 2014; Zimova *et al.*, 2020) – it is possible that detection rates may only be reduced if mismatched camouflage transitions into masquerade camouflage. Masquerade camouflage would enable snowshoe hares to remain difficult to detect even in the absence of crypsis (Skelhorn *et al.*, 2010). For example, a white snowshoe hare on a patchy landscape may appear to be a patch of snow, whilst a brown hare may be misidentified as a tree stump or branch. Although accurately proving the presence of masquerade camouflage is difficult (Skelhorn *et al.*, 2010; Font, 2019), this study makes some indication that misidentification is occurring. Trichromats had longer delays between their first fixation on the target and slide completion in comparison with dichromats. In particular, white snowshoe hares were most frequently misidentified by trichromatic participants, both in comparison with dichromatic participants, and brown snowshoe hares. Whilst this indicates that trichromats are more susceptible to misclassifying snowshoe hares as an unimportant feature of their environment (Skelhorn *et al.*, 2010), it may simply reiterate that trichromats do not detect white snowshoe hares as

rapidly as dichromats. In addition, even if this is indicates misidentification of snowshoe hares by participants, it did not influence dichromats in the same way. Therefore, it is unlikely that misidentification would influence SCC species' detectability from mammalian predators.

By the nature of visual search tasks, some aspects of participant behaviours and experiment production may have influenced search efficacy, such as task naivety (Gijp *et al*., 2017), participant fatigue (Duffy & Chan, 2002; Neider *et al*., 2010), or target positioning (Troscianko *et al*., 2017). Trial and slide number did not influence target detectability or discriminability, indicating that participants did not develop a search image to aid with camouflaged prey detection (Troscianko *et al*., 2018), nor experience the effects of training (Boot *et al*., 2010; Neider *et al*., 2010). As expected, target positioning significantly influenced detectability and was controlled for in analyses (Troscianko *et al*., 2017). Future research should endeavour to minimise the presence of centralised targets to reduce the impact of target positioning on search mechanisms (Goldberg & Wichansky, 2003; Irwin, 2004).

Although this research indicates differences in search efficacy between visual systems, the absence of tetrachromacy minimises the application of this research in the wild. Although avian predators account for a minority of predation events (Krebs *et al*., 1995; Murray, 2002), their increased discrimination of colours is expected to improve their camouflage breaking abilities (Stevens *et al*., 2017; Tedore & Nilsson, 2019). Therefore, the full image of how camouflage mismatch will impact mortality is incomplete without including a tetrachromatic perspective.

This research displays the importance of considering visual search methods when examining differences in camouflage efficacy (Lin *et al*., 2014a), especially when examining camouflage efficacy across multiple visual systems. The differences in search mechanisms between simulated dichromats and trichromats is surprising considering that overall detection times do not differ. Therefore, understanding what aspects of background-matching camouflage influence detection rate will be fundamental in SCC species conservation and mismatch minimisation. Whilst this research utilised human participants, a simulation of dichromacy, and a novel visual system, thereby reducing the task relevancy and ecological validity of the results (Kawai & He, 2016), it is clear

that inefficient background matching camouflage increases the detectability of SCC species from a trichromatic and dichromatic perspective.

The impact of camouflage mismatch on the mortality rate of seasonal coat colour species has been well documented in the wild (e.g. Mills *et al*., 2013; Atmeh *et al.*, 2018; Wilson *et al.*, 2018). Here, I have demonstrated that ineffective background matching camouflage not only influences the overall detection rate of snowshoe hares but improves predator search efficacy. This research indicates that the elevated predation rates are likely due to camouflage mismatch making SCC species more detectable. With snowshoe hares being a primary prey species within the alpine, sub-arctic, and arctic food webs (Krebs, 2010), the influence of declining numbers due to increased detectability is expected to have dramatic impacts on the survival of many predators. Therefore, understanding how to minimise the impact of camouflage mismatch on survival will not only maintain the population sizes of snowshoe hares and other SCC species, but the numbers of the predators that depend upon them for survival.

Chapter 4: General Discussion

Overall Findings and Implications

This thesis explored whether seasonal coat colour camouflage influenced the detectability or discriminability of snowshoe hares, dependent upon environmental conditions. Specifically, the aims of this study were to examine whether seasonal coat colour moulting provides background matching camouflage, and whether ineffective camouflage increases the detectability of snowshoe hares. Utilising measurements of brightness and colour matching, background complexity, coat colour and background type, I aimed to examine whether the observed elevated predation rates on mismatched snowshoe hares in the wild can be explained by ineffective background-matching camouflage. This thesis provides support that camouflage mismatch is influencing snowshoe hare survival by increasing their detectability to visual predators. Therefore, as climate change continues to progress and seasonal coat colour species mismatch increases in duration, the survival of these species is at risk. Additionally, I show that the use of the 60% or greater threshold of camouflage mismatch classification does explain some variation in snowshoe hare detectability, but this measure is not as reliable as brightness and colour matching in predicting detectability. Finally, predator colour vision influences visual search mechanisms used in prey detection. Despite overall detection times being equal across visual systems, simulated dichromacy reduced the efficacy of brightness-based camouflage breaking. Therefore, future research should endeavour to utilise ecologically relevant visual systems when reporting on the efficacy of camouflage and camouflage mismatch.

Anti-Predator Defences

Colour and Brightness Background-Matching Camouflage

This thesis found that the efficacy of snowshoe hare camouflage significantly influenced detectability. Overall, effective camouflage resulted in participants taking longer to locate snowshoe hares in comparison with poorly camouflaged snowshoe hares. This effect was found for both brightness-based and colour-based camouflage, indicating that both aspects of background matching camouflage independently influence target detectability within seasonal coat colour (SCC) species. Ineffective brightness camouflage primarily influenced snowshoe hare detectability by being identified in participant peripheral vision, as displayed by faster saccade velocities (Xu-Wilson et al., 2009; Di Stasi et al.,

2013). Despite this, participants did not fixate more frequently when locating brightness or colour camouflaged snowshoe hares in comparison with poorly camouflaged snowshoe hares. With the longer detection times observed for camouflaged hares both within chapter two and three, it would be expected that increased fixation count would explain these differences in overall detection time. In previous research, an increased number of fixations is indicative of a more difficult visual search (Over *et al.*, 2007). Therefore, despite camouflaged hares taking longer for participants to locate, their visual search mechanisms do not indicate that camouflaged targets elicited more difficult searches.

However, the results of specific measures of visual search efficacy, such as average saccade velocity, fixation count, and overall detection time, are likely skewed by cross-visual system comparison. Trichromatic participants utilised faster average saccade velocities when locating brightness mismatched snowshoe hares and fixated more frequently when searching for colour camouflaged snowshoe hares, in comparison with dichromatic participants. Therefore, despite the general trend of more effective camouflage resulting in longer search times and more misses, brightness camouflage most significantly impacts dichromatic search efficacy, whilst colour camouflage most influences trichromatic search efficacy. With previous research primarily being conducted from the perspective of a trichromat (e.g. Mills *et al.*, 2013; Atmeh *et al.*, 2018), this finding indicates the potential of this research underpredicting the differences in detectability between brightness-camouflaged and mismatched snowshoe hares. Whilst this finding supports some previous research, in as much as it shows trichromacy is less effective at breaking colour camouflage due to increased levels of perceived chromatic variance (Anon, 1940; Saito *et al.*, 2006), it indicates that dichromats are less effective at breaking brightness-based camouflage. This finding contradicts previous research, which suggests dichromat camouflage breaking is less affected by environmental luminance (Anon, 1940; Troscianko *et al.*, 2017). With snowshoe hares and other seasonal coat colour species primarily inhabiting monochromatic environments, it would be expected that a predator's ability to break brightness-based background matching would be most important in prey detection. However, this thesis indicates that, for seasonal coat colour species, matching the environment in brightness is more important than in colour when avoiding detection by dichromatic predators. Therefore, consideration of brightness camouflage

efficacy should be of primary importance in future research, and it should be anticipated and accounted for that brightness camouflage is more difficult to break from the perspective of a dichromatic predator than recorded by human experimenters.

<u>Camouflage Mismatch Classification</u>

Previous research into seasonal coat colour species' camouflage mismatch has primarily utilised percentage mismatch; either on a scale from 0-100%, or classifying an organism differing in colour from its background by 60% or more as a threshold for mismatch (e.g. Mills *et al*., 2013; Zimova *et al.,* 2014). In this thesis, I found that percentage mismatch explains differences in detection time, whilst mismatch classification explains differences in hit success. These results indicate that the 60% or greater threshold for mismatch is adequate to explain differences in detectability (Mills *et al*., 2013).

Nevertheless, within the eye-tracking experiment, mismatch classification did not influence target discriminability nor detectability. Therefore, mismatch classification, both percentage difference and the >60% threshold (Mills *et al*., 2013; Zimova *et al*., 2014), are not as repeatable or reliable as directly measuring colour or brightness matching in explaining camouflage efficacy. However, as few variables explained differences in discriminability within the visual search task, seasonal coat colour moulting can be assumed to primarily function as background-matching camouflage to reduce detection by predators. As mismatch classification explains differences in detection rates, and with previous research indicating it explains differences in predation rates (Zimova *et al*., 2016), these guidelines for mismatch classification are not to be entirely dismissed. Although direct measurements of camouflage have been shown to be more reliable in predicting detectability differences, taking accurate measurements of chromatic or achromatic matching prior to a predation event is not always possible. Therefore, this thesis indicates that the 60% or greater classification of mismatch is functional in explaining differences in camouflage efficacy in the field. In future research, using measures of chromatic and achromatic differences to compliment mismatch classification will yield the most reliable and achievable measurements of camouflage efficacy.

Coat Colour and Background Type

Coat colour and background type, when considered independently, did not explain any differences in detection time or search efficacy. Therefore, it can be assumed that all detectability differences observed are not as a result of one coat colour being more detectable, or one background type being easier to locate snowshoe hares on.

On snowy backgrounds brightness camouflaged snowshoe hares were located more quickly than on patchy or snowless backgrounds. Whilst brightness mismatched snowshoe hares were located equally across all background types. Therefore, brightness-based camouflage is least effective within snowy environments. Snowshoe hare predation primarily occurs in the winter, with coyotes hunting in winter or autumn, and lynxes and avian predators in the winter or spring (Feierabend & Kielland, 2015). Although predation pressures are reduced in the spring and autumn, this thesis suggests that these patchy periods are likely the most beneficial time for white snowshoe hares to match their background in brightness, as brightness camouflage delays detection in these conditions (Feierabend & Kielland, 2015). In addition, as snowpack duration decreases, the likelihood of a white coat residing on a patchy background similarly increases. Therefore, it can be theorised that white snowshoe hare detectability will not immediately be negatively influenced by climate change.

Although brightness camouflage is less effective on snowy backgrounds, matching the background in both brightness and colour is the evolutionary norm, indicating snowshoe hares do compensate for their increased detectability at this time. However, it is important to consider snowpack composition when examining ineffective camouflage throughout snowy periods. Coyotes hunt most efficiently on dense and shallow snow, whilst lynxes are prolific hunters even within deep snow (Murray *et al*., 1994). Therefore, even if camouflage is ineffective on deep snow, predation pressures will be reduced because coyotes are less successful (Murray *et al*., 1994). However, as the climate is changing and snowpack density is reducing (Klein *et al*., 2016; Marty *et al*., 2017), the presence of fully camouflaged snowshoe hares during these snowy months may still result in increased predation rates due to coyotes being able to predate more freely when brightness camouflage is least effective (Murray *et al*., 1995). Snowshoe hare predation pressures are higher

surrounding a full moon when there is snow, in comparison to no snow (Griffin et al., 2005). This may be due to snowshoe hares being more visible even when fully camouflaged under snowy conditions, therefore resulting in greater predation success. Alternatively, brightness mismatch may be even more detrimental in snowy periods due to predation pressures being naturally higher at these times (Griffin et al., 2005). Therefore, despite brightness mismatched snowshoe hares being equally detectable on all background types, the increased predation during snowy conditions suggests that this increased detectability will be most detrimental when snow is present.

Despite this, background type did not influence the average saccade velocities of participants searching for brightness camouflaged or mismatched snowshoe hares. Therefore, fully camouflaged white snowshoe hares are not necessarily more detectable due to being noticed in the peripheral vision, but other visual search mechanisms are influencing detection rate. From the findings of this thesis, the reasons for brightness camouflaged white snowshoe hares being easiest to detect cannot be explained. Overall, the most detrimental conditions to snowshoe hare survival is unlikely to be the total absence of snow in the winter but rather reduced snowpack density. Therefore, taking action to minimise predation pressures should be imperative prior to mismatch occurring.

The interaction between coat colour – white, brown, or moulting – and background type – snowy, snowless, or patchy – was only sufficient in explaining differences in detection rate within the online target detection experiment. Brown hares took the longest to locate on their evolutionarily relevant – snowless – background type, whilst white hares took the longest to locate on patchy backgrounds. Overall, this thesis indicates that remaining white during snowmelt in the spring, or becoming white during snowfall in the autumn, may not severely impact snowshoe hare survival. This is particularly important for the spring, as this correlates with snowshoe hare breeding, a time in which snowshoe hares are most active (Feierabend & Kielland, 2015). Although snowpack in the spring is expected to become less common as the climate changes, white snowshoe hares did not significantly differ with brown snowshoe hares in their detectability on snowless backgrounds. This further indicates that predation during the breeding period, if white coats are retained, would not be severely elevated beyond their evolutionary norm. In addition, with white snowshoe hares being less detectable on patchy backgrounds than snow

covered backgrounds, the negative consequences of reduced snow cover during the winter, specifically the potential for increased coyote predation (Murray *et al*., 1994), may be minimised due to snowshoe hares being less detectable.

In alpine, sub-alpine, and arctic regions the density of shrubbery is reduced in the spring, autumn, and winter. Sparser shrubbery minimises the degree of cover available for snowshoe hares to hide in, therefore increasing their detectability (Feierabend & Kielland, 2015). From the results of this thesis, it can be predicted that predation rates will increase most in the autumn and the spring as mismatch becomes more frequent. The primary reason for this is because these time periods indicate the transitional moult between seasonal coat colours, and moulting hares are more detectable on patchy backgrounds than white hares, and on snowless backgrounds than brown snowshoe hares. Despite this, hare type and background type combination did not influence participant visual search mechanisms or overall detection times in chapter three. This invokes questions surrounding the repeatability of these findings and indicates that, although differences in detection time did arise, these differences are less reliable than measuring colour and brightness contrast. Additionally, it is important to note that the eye-tracking experiment indicated differences in visual system for detecting white snowshoe hares, with trichromatic participants taking longer to first fixate on the target when searching for white hares in comparison with dichromatic participants. Therefore, it is likely that explaining camouflage through a human perceived classification of coat colour will result in white coats being considered more camouflaged than is perceived by a dichromatic predator. This result reiterates that brightness cues are more influential for target detection in dichromats than they are for trichromatic human experimenters.

Background Complexity

Background complexity is important to consider when examining camouflage mismatch, as previous research has indicated that more complex backgrounds improve the efficacy of otherwise ineffective camouflage (e.g. Merilaita, 2003; Dimitrova & Merilaita, 2012; Xiao & Cuthill, 2016). No prior research into seasonal coat colour camouflage has considered the impact of complex backgrounds on detectability, only considering undergrowth to function for

behavioural concealment from predators (Hodges & Sinclair, 2005). Across both experiments, background complexity influenced detection time, with hares located on more complex backgrounds taking longer for participants to locate. In addition, background complexity interacted with camouflage efficacy to influence detection time. Irrespective of the efficacy of camouflage, snowshoe hares took longer to locate on complex backgrounds, but well camouflaged hares on complex backgrounds benefited most. This indicates that, as has been displayed in prior research, seasonal coat colour camouflage will benefit from complex backgrounds by making the organism more difficult to locate (Dimitrova & Merilaita, 2010; Dimitrova & Merilaita, 2012; Xiao & Cuthill, 2016). However, contrary to previous research (Wolfe *et al.*, 2002; Uetz *et al.*, 2011), this thesis showed that, in regard to seasonal coat colour species, background complexity primarily functions in minimising detectability but does not influence the predator's ability to discriminate the target from the background.

In the wild, predation rates throughout the summer are much lower than in the winter (Feierabend & Kielland, 2015). This is thought to be primarily driven by denser canopies being used for concealment (Feierabend & Kielland, 2015). However, the results of this thesis indicate that the detectability of snowshoe hares may be limited by the background complexity, even when snowshoe hares are not fully obscured by the canopy or understory. However, whilst background complexity does appear to improve camouflage efficacy in snowshoe hares, these more complex backgrounds may additionally improve predator hunting success. Both lynxes and coyotes, two primary snowshoe hare predators, use dense canopy to avoid detection whilst hunting (Murray *et al.*, 1995). Whilst lynxes are equally as successful irrespective of canopy density, coyotes are at an advantage when the canopy is dense (Murray *et al.*, 1995). Therefore, whilst snowshoe hares may avoid detection for longer when located in denser, more complex woodland, many snowshoe hare predators can similarly use these complex backgrounds to avoid detection. Additionally, denser canopy and understories promote more efficient predation strategies in lynxes and coyotes, with lynxes using their more successful ambush predation, and coyotes using stalking (Murray *et al.*, 1995; Thomas *et al.*, 2019).

Independently, these previous results indicate that increasing background complexity via the introduction of denser understories may not positively influence snowshoe hare survival. However, in conjunction with aforementioned

findings, increasing canopy density in the winter months could facilitate survival, but only if snowpack is deep. Coyotes use chasing and pouncing as a predation method irrespective of canopy density, but deeper snow restricts overall chase duration (Murray *et al.*, 1995; Thibault & Ouellet, 2005). Therefore, one prolific snowshoe hare predator would be limited in their hunting success despite additional canopy cover, and snowshoe hares would be less detectable due to complex backgrounds. Despite this, these winter conditions are becoming less common, as climate change is minimising snowpack density and duration (Dawson *et al.*, 2011; Zimova *et al.*, 2020). Additionally, white snowshoe hares were detected more quickly by participants when located on complex backgrounds in comparison with brown snowshoe hares. Therefore, with the most likely scenario of camouflage mismatch being white snowshoe hares on snowless backgrounds (Zimova *et al.*, 2020), minimising detectability and mortality via more complex backgrounds will not be achievable.

Predator Visual System

Previous research into snowshoe hare camouflage efficacy has exclusively considered camouflage from the perspective of a human experimenter. Humans use trichromatic colour vision, whereas the majority of snowshoe hare mammalian predators are expected to be dichromatic (Rowe, 2002), and avian predators would be tetrachromatic (Lind *et al.*, 2017). Therefore, the question remained as to whether snowshoe hare predators perceive mismatch to the same degree as reported in previous research.

I have previously highlighted the first difference in snowshoe hare detectability between the visual systems: dichromatic predators are less efficient at locating brightness camouflaged snowshoe hares in comparison with trichromats. However, despite brightness camouflaged snowshoe hares being harder to detect, dichromatic participants' average saccade velocities did not differ when searching for brightness camouflaged or mismatched snowshoe hares. Contrastingly, trichromatic participants utilised faster average saccade velocities when searching for brightness mismatched hares. There are two primary explanations for these differences. Firstly, trichromatic participants may detect brightness mismatched snowshoe hares in their peripheral vision and, as a result of this, their attention is drawn to these high contrast regions (Xu-Wilson et al., 2009). However, trichromatic participants did not detect brightness

mismatched snowshoe hares more quickly than dichromats, indicating this doesn't explain the observed differences in saccade velocities. Alternatively, simulated dichromacy could promote the use of short saccades within all visual searches. Therefore, whilst brightness mismatched hares are located on the initial scan, brightness camouflaged snowshoe hares are initially overlooked. Longer detection times due to not identifying brightness camouflaged snowshoe hares immediately could be explained through inhibition of return (Itti & Koch, 2001). This would mean dichromatic participants exhibit inefficient searches when locating brightness camouflaged snowshoe hares due to needing to re-search areas.

In general, simulated dichromats exhibited more indicators of efficient visual searches than trichromats. The fewer but longer fixations of dichromatic participants indicate more information is being processed within each fixation (Greene, 1999), and are typical in experienced searchers (Savelsbergh *et al.*, 2002; Uchida *et al.*, 2014). Therefore, whilst trichromatic researchers would be expected to exhibit more efficient searches than untrained participants, this trend should similarly be mirrored by experienced dichromatic predators (Oca & Black, 2013). Snowshoe hare dichromatic predators frequently utilise cooperative hunting, with wolves, coyotes, and lynxes all exhibiting some degree of cooperation in hunts (Bailey *et al.*, 2013). When considering cooperative hunting, multiple individuals are visually searching for potential prey. Multiple individuals with effective search mechanisms are likely to detect a snowshoe hare more rapidly than a single individual. This may mean that, if it is dichromacy promoting more efficient visual searches, cooperative hunting would dramatically reduce overall detection times in comparison to individual trichromatic experimenters, or even cooperative trichromats.

Within the task of camouflage breaking, there has been much debate in the literature as to whether dichromats or trichromats are more efficient (Galloway *et al.*, 2020). In recent years, research has indicated that trichromacy is superior to dichromacy, primarily due to the ability to distinguish fine variations in colour between the target and its background (Frey *et al.*, 2011; Bompas *et al.*, 2013; Troscianko *et al.*, 2017). However, when considering the efficacy of a visual system in camouflage breaking, the context of the task is of the utmost importance. Many scenarios in which trichromacy confers the advantage focus upon red-green colour discrimination, which is often not

achievable by dichromats (Frey *et al*., 2011; Bompas *et al*., 2013). Instead, when colour is not relevant, dichromatic subjects are better at camouflage breaking (Melin *et al*., 2007; Smith *et al*., 2012). This thesis showed that, despite differences in visual search behaviours, neither simulated dichromacy nor trichromacy were faster at camouflage breaking within an alpine ecosystem. This supports that, in the absence of red-green stimuli, trichromacy is not superior for camouflage breaking (Hiramatsu *et al*., 2008). However, dichromats showed the benchmarks of more efficient visual searches, despite detection times being equal. Dichromacy in humans has been associated with inefficient visual searches (Voraphani, 2007; Frey *et al*., 2011). However, these tasks required red-green discrimination. Within predator-prey dynamics, red-green cues are rarely salient in target detection, therefore these results, which focus primarily upon foraging species or humans, cannot easily be extrapolated onto these systems. In addition, the importance of luminance, or brightness, in the detection of prey by dichromatic predators is supported by this thesis (Hiramatsu *et al*., 2008; Troscianko *et al*., 2017). In the absence of three cone cells, luminance perception becomes increasingly important in prey detection (Hiramatsu *et al*., 2008). Therefore, examining camouflage within ecosystems containing dichromatic predators should consider luminance, or brightness, matching prior to colour camouflage.

Limitations of this Research

Both the experiments within this thesis were conducted using human participants and artificially generated dichromatic colour images, therefore extrapolating these results to wild, naturally dichromatic snowshoe hare predators should be done with care. The primary issue with using human participants to simulate animal behaviours is the importance of the stimuli. Evolutionarily important stimuli result in shorter detection rates (Jackson & Calvillo, 2013; Simpson *et al*., 2014), with motivationally relevant stimuli being detected more quickly than a neutral stimulus (Oca & Black, 2013). Natural snowshoe hare predators depend upon prey detection for survival; therefore, the motivational relevance of a snowshoe hare is far greater in a predator than it would be for a human participant. This effect is further exacerbated when considering the pool of participants. Both experiments used a primarily English participant pool, although the online detection experiment did achieve a wider

reach. Many of these participants were unlikely to be familiar with detecting snowshoe hares, therefore the novelty of the task likely slowed detection rates (Gijp *et al.*, 2017). Whilst these effects could be minimised if these experiments were repeated using participants that frequently searched for snowshoe hares, such as hunters or researchers, the evolutionary relevance of locating a snowshoe hare would remain less for these humans than for predators, which depend almost entirely upon snowshoe hares for survival (Krebs, 2010).

The coat colour and background type displayed to each participant changed with each observed slide. In the wild, varying coat colour and environmental conditions would never occur so close together in time, and no effort was made to simulate a natural cycle of seasons or coat colours. The reason for this was to maximise the number of combinations of camouflaged and mismatched hares observed by each participant to maximise data collection. Changing the colour of the stimuli between each slide is expected to slow detection rates in human participants by preventing learning of the stimuli (Shiffrin & Schneider, 1977). It is possible this changing of stimuli colour prevented participants within this experiment to develop a search image of the snowshoe hare (Troscianko *et al.*, 2018). Therefore, these detection times may be longer than should be expected in the wild, where coat colour and environmental transitions are slower, enabling predators to learn prey appearance and develop effective search images. However, participants were exclusively looking for snowshoe hares within these experiments, whilst in the wild snowshoe hare predators may utilise a more generalist search. By examining only one type of stimulus, participants would prioritise the importance of detecting a snowshoe hare (Wade & Vickery, 2018). Prioritising one target as being the most important decreases overall detection times. Therefore, it is possible that, by participants 'self-associating' with snowshoe hare images (Wade & Vickery, 2018), the overall search times mimicked the shorter detection rates expected through the formation of a search image.

Although snowshoe hares utilise immobility to avoid detection by predators, it is unlikely that a snowshoe hare would remain entirely stationary for the duration of a visual search (Zimova *et al.*, 2014). Across both experiments, participants were searching for immobile snowshoe hare images. Target movement is hugely important in influencing the speed with which they are detected, with movement promoting faster detection rates (Jackson &

Calvillo, 2013). Therefore, the total absence of movement within these search tasks reduces the ecological validity of the findings as movement, even if minor, is expected to increase target detectability (Jackson & Calvillo, 2013). Despite this, the absence of movement allows for the measuring of camouflage efficacy on detectability, and direct comparison of results across both experiments. However, introducing how movement influences detectability in seasonal coat colour species would be particularly interesting to examine in future research. Understanding how different types of movements influence detectability would improve our understanding of when mismatch would be most detrimental based upon currently occurring anti-predator behaviours (Zimova *et al.*, 2014), and what avoidance behaviours would be necessary to minimise predation risk even in the occurrence of mismatch.

Finally, the results of this thesis were constrained by the inability to use human participants to examine tetrachromatic colour vision. Whilst avian predators predate snowshoe hares less frequently in comparison with mammalian predators, they still account for up to 40% of predation events (Krebs *et al.*, 1995; Murray, 2002). With tetrachromatic predators being prevalent in the snowshoe hare, and other seasonal coat colour species, food webs, it is fundamental to understand how these predators perceive snowshoe hares to develop a full image of the consequences of mismatch.

Future Research

This thesis highlights some of the shortcomings of previous research into seasonal coat colour species and camouflage efficacy. Primarily, I have shown that examining coat colour mismatch from the perspective of dichromatic mammalian predators is important in understanding what aspects of camouflage mismatch are influencing elevated predation rates. Although overall detection times remained consistent between trichromatic and dichromatic participants, the differences in the perception of colour and brightness matching, as well as the visual search mechanisms, indicate vast differences in the processing of seasonal coat colour species camouflage and mismatch. At present, examining coat colour and background colour from the perspective of the dichromat introduces minimal additional workload, yet it will provide dramatic improvements to the validity of experiments. This thesis also highlights the importance of considering brightness matching when examining the

detectability and predation rates of seasonal coat colour species. Overall, brightness cues are more important in prey detection for dichromats than they are for trichromats. Therefore, explaining seasonal coat colour species' camouflage mismatch as colour difference or from the perspective of a trichromat is inaccurate in its relevancy to mammalian predators. Future research into seasonal coat colour species' camouflage should endeavour to focus upon the brightness or luminance aspects of background matching.

Furthermore, the limitations of this thesis provide additional aspects requiring future research, primarily the perception of seasonal coat colour camouflage from the perspective of a tetrachromatic predator and in the presence of movement. Accurately exploring tetrachromacy is not possible using human participants, however the presence of tetrachromatic predators in the snowshoe hare food web indicates this visual system is important to explore (Murray, 2002; Mitkus *et al*., 2018; Höglund *et al*., 2019). To successfully build upon the findings of this thesis, detection experiments using tetrachromatic species will be vital to improve our understanding on how camouflage mismatch will influence seasonal coat colour species' survival in the wild. Target movement would likely reduce overall search times (Jackson & Calvillo, 2013), therefore understanding how movement interacts with camouflage efficacy is important to put these findings in an ecologically relevant context. In particular, understanding how movement dependent upon coat colour (Zimova *et al*., 2014) and time of year, such as the breeding period (Feierabend & Kielland, 2015), influences detectability will be vital in understanding how these detection time differences accurately come into play in the wild.

One simple, but important, step that could be introduced into all future research would be the use of photographs to simultaneously classify mismatch, via the previously used percentage difference measurements (e.g. Mills *et al*., 2013), and to measure chromatic and achromatic differences from the perspective of a dichromat and a trichromat. Utilising both of these measurements will enable us to examine whether predation rates can be best explained by the current threshold, chromatic matching, or achromatic matching, and whether visual system influences these overall results. Direct comparison of these measurements in the field could provide support for the percentage classification of mismatch, highlight the shortcomings of this

system, or expose aspects of predator vision or camouflage that are most important in survival for seasonal coat colour species.

Snowshoe Hare Conservation

Throughout this thesis, many limitations on potential conservation options for seasonal coat colour species and snowshoe hares have been highlighted. With snowshoe hare detectability being associated with ineffective camouflage, the most important and effective method to minimise predation pressure would be phenotypic and behavioural adaptation. However, previous research has highlighted that plasticity in these aspects are constrained (Zimova *et al*., 2014). Despite evidence that changes can, and do, occur within snowshoe hares, specifically across geographical regions (Gigliotti *et al*., 2017; Jones *et al*., 2018), it is the rate of climate change that is of primary concern. It is unlikely that, if the climate continues to change at the projected rate, snowshoe hares will be able to adapt to these changes as quickly as required (Zimova *et al*., 2016). Therefore, future conservation efforts should focus upon reducing predation risks during the winter and transitional months (Feierabend & Kielland, 2015), and restricting population declines at present to provide adequate time for snowshoe hares to adapt to the changing climate.

Principally, it is important to note that, within the snowshoe hare ten-year cycle, predator numbers decline approximately two years after snowshoe hare numbers decline (O'Donoghue *et al*., 1997). It can be theorised that a similar trend will occur if snowshoe hare populations experience a decline due to over predation as a consequence of camouflage mismatch. This delayed response in predators may result in snowshoe hare populations declining beyond a genetically viable population for resurgence once adaptations do arise. Therefore, ensuring predator numbers decline simultaneously with snowshoe hare numbers will be important to ensure an unsustainable decrease in population size does not occur. Reducing coyote population size is particularly important, as a shallower snowpack due to climate change will enable coyotes to inhabit and predate in regions and time periods they previously could not (Murray *et al*., 1995). Minimising these predation pressures will not only benefit snowshoe hare survival, it will also improve reproductive success (Sheriff *et al*., 2009), therefore increasing overall population sizes.

Additionally, minimising prescribed burning and actively preventing forest fires during periods of high risk could potentially support snowshoe hare population size. Snowshoe hares depend upon dense understories in predator avoidance (Thomas *et al*., 2019). Prescribed burning limits the presence of snowshoe hares due to the absence of this important understory (Gigliotti *et al*., 2017). Therefore, restricting fires within snowshoe hare ecosystems, particularly when the ten-year cycle is on the decline and camouflage mismatch is prevalent, could buffer the negative impacts of mismatch long enough for adaptations to arise. Once snowshoe hares have exhibited adaptations, either behaviourally or phenotypically, in a way that minimises detectability, prescribed burning could be reinstated in a manner that provides adequate habitat for snowshoe hares to inhabit prior to these regions being re-inhabited.

Concluding Remarks

This thesis shows that ineffective camouflage increases the detectability of snowshoe hares, therefore the elevated predation rates of snowshoe hares and other seasonal coat colour species are likely directly due to the impact of camouflage mismatch as a result of climate change. However, considering camouflage efficacy as the only explanation for elevated predation rates is an oversimplification. The interactions between hare coat colour, environmental conditions, season, camouflage efficacy, and background complexity are all likely to play important roles in the risk of predation in seasonal coat colour species. With the lowest snowshoe hare population sizes in the current ten-year cycle expected to occur in 2023-2025 (Reynolds *et al*., 2017; Krebs *et al*., 2018), it is more important than ever to understand how to buffer the negative consequences of camouflage mismatch so they can recover from this decline. The impact of snowshoe hare increased visibility due to climate change and the threat of over predation is likely to have dramatic impacts on these alpine, subalpine, and arctic food webs that rely so strongly on the presence of snowshoe hares. Therefore, limiting population declines long enough to allow for adaptations within snowshoe hares is a vital step in protecting all the species that inhabit these particularly vulnerable ecosystems.

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