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**Exploring the mechanisms of iridescence as camouflage**

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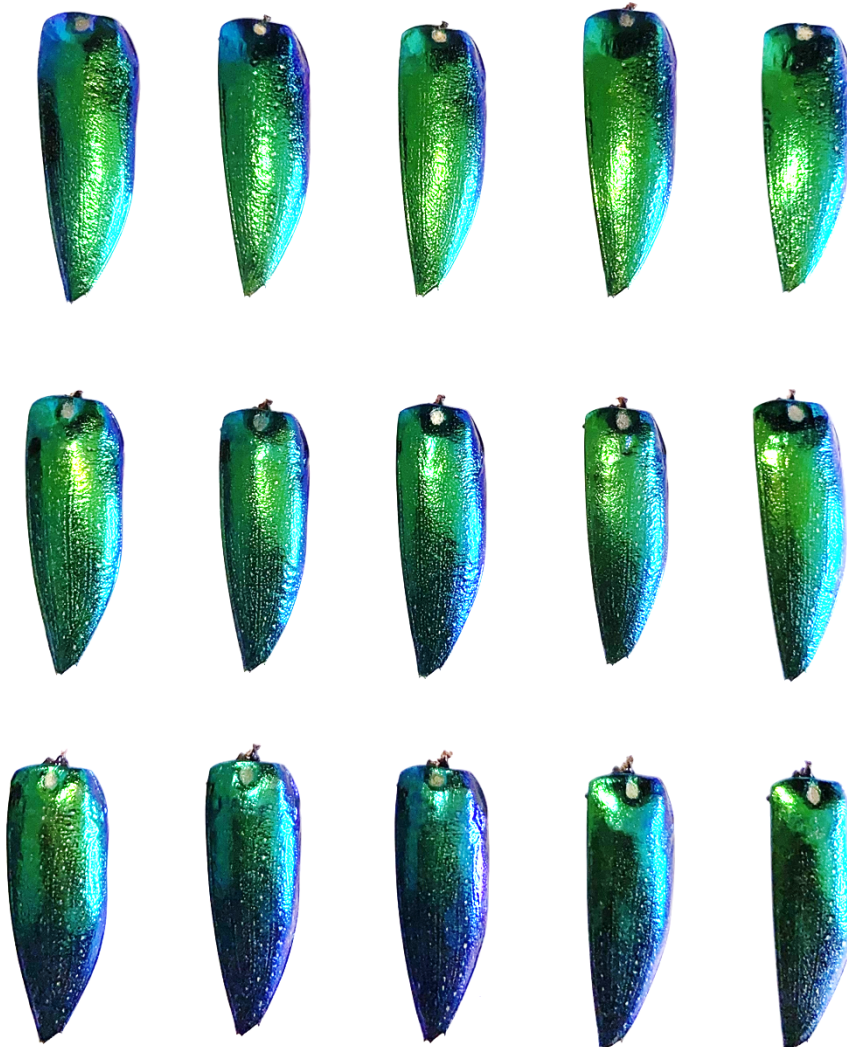
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## COVID Statement

Under 'normal' circumstances, my MSc project would have involved two experimental parts: an avian predation experiment and a human search experiment, both of which would have been performed in the field. In typical human search experiments, volunteers search for targets while carrying a laser range finder, which is used to measure detection distance. I had planned for eye-tracking technology to accompany methods for measuring detection distance. This relatively novel approach would have allowed the collection of data that would have enabled a much more detailed analysis of the mechanisms of iridescence as camouflage. However, due to social distancing, restrictions on social meetings and the continual risk of COVID-19 transmission, I have been unable to complete any human search experiments. Nevertheless, the avian predation experiments alone generated sufficient data to advance our understanding of iridescence as camouflage, especially when considered in the context of previous research.

# Exploring the mechanisms of iridescence as camouflage

*by Dylan Harvey Nolton Thomas*



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

*Word count: 17,967*

# Abstract

Iridescence is a taxonomically widespread form of structural colouration that produces striking rainbow-like hues. It has a wide range of hypothesised biological functions, including species recognition, mate choice, thermoregulation, and – rather counter-intuitively – camouflage. Empirical evidence for iridescence as camouflage is relatively recent and, as such, exactly how iridescence provides effective concealment has remained unknown. Here, the functional mechanisms of iridescence as camouflage are explored, with a particular focus on separating the relative contributions of target colour and target gloss. Using field experiments with natural avian predators, the survival of iridescent and non-iridescent beetle-like targets was investigated. Consistent with previous research, iridescent colouration was found to have strong protective benefits. Target colour was found to be the most important factor in enabling this camouflaging effect. Target gloss and the gloss of the leaves on which targets were placed were both found to significantly affect survival, but they were less important in providing effective concealment. The roles of each factor in iridescence as camouflage are discussed, and it is concluded that changeable iridescent colours likely provide camouflage by reducing the signal-to-noise ratio.

**Keywords:** camouflage; defensive colouration; iridescence; specular reflectance; gloss.

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## Author's Declaration

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

SIGNED: ..... DATE: .....

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# **1 | What is iridescence and what are its functions? A review of iridescent colouration, concealing strategies and visual perception.**

## **1.0 | Summary**

This thesis considers one possible, and rather counter-intuitive, function of iridescent colouration: camouflage. To make sense of the experimental work presented in the second chapter, the reader must understand three things: the nature of iridescent colouration and its hypothesised functions, how colours can be used in defence against predation, and how that defensive colouration is perceived by the animals it has evolved to influence. These areas of background literature are discussed in the three sections that comprise the first chapter.

## **1.1 | Iridescence**

There are two main mechanisms of colour production in animals: pigmentary and structural (Sun, Bhushan & Tong, 2013; Shawkey & D’Alba, 2017). Iridescence is perhaps the most common type of structural colouration (White, 2018), and it – like other structural colours – occurs due to the way light wavelengths interact with structural order in biological materials (Housecroft, 2019). Although its specific mechanisms and properties can vary, iridescence – in a broad and general sense – describes the phenomenon in which surfaces exhibit angle-dependent changes in colour (Kinoshita, Yoshioka & Miyazaki, 2008). Typically, iridescent colouration is characterised by bright, vibrant and rainbow-like hues (Doucet & Meadows, 2009). Indeed, the term ‘iridescence’ actually derives from the Ancient Greek word for rainbow (Barnhart & Steinmetz, 1988). Iridescence may serve several purposes, including species recognition, age identification, mate attraction, group communication, and possibly – as will be discussed in this thesis – various mechanisms of defence against predation (Doucet & Meadows, 2009).

### **1.1.1 | TAXONOMIC DISTRIBUTION**

Iridescence is taxonomically widespread (Doucet & Meadows, 2009). Since invertebrates account for the majority of animal life on Earth (May, 1988), it is no surprise that iridescence has been particularly well-documented in invertebrate taxa. It is particularly common in arthropods and molluscs (Doucet & Meadows, 2009). In insects, iridescent colouration is

found in bees and wasps (Sarrazin et al., 2008), beetles (Seago et al., 2009), butterflies and moths (Mouchet & Vukusic, 2018), dragonflies and damselflies (Vukusic, Wootton & Sambles, 2004; Guillermo-Ferreira et al., 2015), flies (Braet, Downes & Simonis, 2016), and some bugs and grasshoppers (Doucet & Meadows, 2009). Jumping spiders provide good examples of iridescence in arachnids (Ingram et al., 2011), while various copepods and decapods provide examples of iridescent colouration in crustaceans (Chae & Nishida, 1994; Parker, McKenzie & Ah Yong, 1998; Takahashi, Ichikawa & Tadokoro, 2015). Iridescence is also associated with cephalopod iridophores (Mäthger & Denton, 2001; Mäthger et al., 2009), as well as the surfaces of some gastropod and bivalve shells (Williams, 2016). Iridescent colouration is comparatively rare in vertebrates, but there are still examples. Among the vertebrates, birds are particularly well-known for their iridescent colouration. Feather iridescence is widely distributed throughout the birds, with notable examples including birds-of-paradise (Stavenga et al., 2011a), ducks (Eliason & Shawkey, 2012), hummingbirds (Eliason et al., 2020), kingfishers (Stavenga et al., 2011b), peacocks (Zi et al., 2003) and starlings (Maia, Rubenstein & Shawkey, 2016). Other iridescent vertebrates include several fishes (Gur et al., 2013), lizards (Pérez i de Lanuza & Font, 2014) and snakes (Gans & Baic, 1977). Iridescence is also observed in the eyes of many vertebrates, where it is produced by the reflective tapetum lucidum (Doucet & Meadows, 2009). Iridescent colouration is not restricted to animals; it is also found in some plants (Graham, Lee & Norstog, 1993; Glover & Whitney, 2010; Whitney et al., 2016). However, plant iridescence is neither well-studied nor relevant, so it will receive no further discussion.

### 1.1.2 | PHYSICAL PROPERTIES

Iridescence can arise from three different structural mechanisms: multilayer reflectors, photonic crystals and diffraction gratings (Kinoshita, 2008; Seago et al., 2009). Multilayer reflectors are the most common, and these are often considered to be the oldest form of iridescent colouration in animals (Seago et al., 2009). In a multilayer reflector, iridescence is created through the interaction of light with layers differing in their refractive indices (Johnsen, 2011). The concept of multilayer reflection is simple: colour is produced as white light passes through multiple layers of reflectors. The light reflected from the different layers interact constructively or destructively at wavelengths dependent upon the spacing of the multilayers. The resulting wavelengths are visible at different angles of observation, resulting in a surface that appears to shift colour. Since a multilayer reflector will usually reflect wavelengths within a specific portion of the electromagnetic (EM) spectrum, the surface will show a consistent shift in colour with viewing deviation. However, the reflected portion is not consistent across species: this will depend, perhaps unsurprisingly, on the refractive properties of the reflective

surfaces within the structure. But, there will always be a 'blueshift', whereby colours become increasingly short-wave with greater deviation from the 'normal' viewing angle (Vigneron et al., 2006). Blueshift highlights one of the advantages of iridescent colouration: it allows short-wave colours to be produced. Since there are few animal pigments that are able to produce colours at this end of the EM spectrum (Bagnara, Fernandez & Fujii, 2007), short-wave iridescence could have implications for signalling, perhaps enabling visual signals to appear more conspicuous. Multilayer reflectors are particularly common in insects, and they have been relatively well-studied in beetles and butterflies. Beetle multilayer reflectors are produced by layers of chitin that become hardened during sclerotization (Seago et al., 2009; Yoshioka et al., 2012); butterfly multilayer reflectors are produced by overlapping wing scales (Vukusic et al., 2001). Photonic crystals produce iridescence through the interference of light reflecting from nanoscale particles, which are arranged in a lattice structure (Barrows & Bartl, 2014). Photonic crystals can be one-dimensional, two-dimensional or three-dimensional (Seago, Oberprieler & Saranathan, 2019). Photonic crystal iridescence may not be as consistent as multilayer iridescence in that the reflected wavelengths are not necessarily continuous (Poladian et al., 2009). Instead, reflected wavelengths represent a wider portion of the EM spectrum, resulting in surfaces with less fluidity in colour changes. Although not as common as multilayer reflectors, photonic crystals are still found in many species and are responsible for iridescence in peacock feathers and the wings of various butterfly species (Corkery & Tyrode, 2017). Finally, diffraction gratings, which are made up of nanoscale arrangements of slits and grooves, produce iridescence by separating white light into its component wavelengths, resulting in a rainbow-like pattern of reflectance. Unlike multilayer reflectors and photonic crystals, diffraction gratings have received relatively little attention, and as such the subsequent discussion of iridescent colouration will refer to non-diffraction-grating iridescence. Indeed, since multilayer reflectors are so common, iridescence tends to be predominantly associated with the colours produced by this structural mechanism.

Iridescence tends to be conceptualised in terms of human vision, in which the brilliant and bright colours are considered key components. However, this interpretation is flawed as it fails to consider how iridescence is perceived by other taxa. Despite some overlapping similarities, most species do not share the same spectral sensitivities as humans (Osorio & Vorobyev, 2005). Even relatively closely related species can have rather different vision – among mammals, for example, there is surprising variation in long-wave spectral sensitivities (Osorio & Vorobyev, 2005; Peichl, 2005). Many species – perhaps even most (Cronin & Bok, 2016) – are sensitive to ultraviolet (UV) wavelengths (Kevan, Chittka & Dyer, 2001; Douglas & Jeffery, 2014; Elphick, 2014). This is an important consideration because structural colouration is not limited to the visible spectrum; UV iridescence occurs (Doucet & Meadows, 2009). Indeed,

several studies have shown that UV reflectance patterns are important in certain birds and insects (e.g., Silberglied & Taylor, 1978; Bennett et al., 1997; Hunt et al., 1998). In addition to UV reflectance, iridescence can involve polarised light (Stavenga et al., 2011c). Considering the way different species perceive iridescence is crucially important because this will have implications for the possible functions of iridescent colouration within those species.

### 1.1.3 | BIOLOGICAL FUNCTIONS

The range of species that display iridescent colouration is extensive, and so too is the range of hypothesised functions (Meadows et al., 2009). Iridescence is mostly involved in visual communication, though it does have some non-communicative roles (Doucet & Meadows, 2009). This includes cases where the observed colour is an incidental by-product of a structural function of the layers generating the reflections – no-one would argue that iridescence in beef has a visual function, for instance (Swatland, 2012). Given the breadth of iridescent species, not all functional aspects of iridescence have been investigated, and thus it is important to note that some ideas remain somewhat speculative. In addition, it should be noted that much of the empirical work has focused on the UV reflectance patterns of iridescent structures.

#### 1.1.3.1 | Social Identity, Mate Choice and Sexual Selection

Iridescence can convey information about an individual's social identity. In some taxa, iridescence might be used as an indicator of species (Rutowski, 1977; Kinoshita, Yoshioka & Kawagoe, 2002). Ultimately, this aspect of iridescent signalling is under-researched, and evidence is thus lacking. Indeed, Rutowski (1977) more convincingly demonstrated UV iridescence as a method of sex identification. Sex identification seems to be an important function of iridescence in copepods (Chae & Nishida, 1994), butterflies (Sweeney, Jiggins & Johnsen, 2003) and jumping spiders (Lim & Li, 2006a; Lim, Land & Li, 2007). In some species, iridescence can indicate the age of an individual – there are reports of age-related changes in iridescent signals in satin bowerbirds (*Ptilonorhynchus violaceus*) and various butterflies (Komdeur et al., 2005; Doucet et al., 2006; Doucet & Meadows, 2009). Papke, Kemp & Rutowski (2007) suggested that these age-related changes in iridescent colouration may be correlated with mating preferences.

Many species use iridescence in mate choice, and most studies agree that females tend to prefer males with brighter iridescent colouration (Omland, 1996; Kodric-Brown & Johnson, 2002; Bitton, O'Brien & Dawson, 2007; Kemp, 2007, 2008; Loyau et al., 2007; Papke, Kemp

& Rutowski, 2007; Dakin & Montgomerie, 2013). Female preferences for bright iridescence suggest a potential association between iridescence and male quality. Since sexually selected iridescent traits are likely to be conspicuous and thus costly, the 'Handicap Principle' might apply. Zahavi (1975) hypothesised that sexually selected traits are honest signals of quality because only high-quality males can pay the cost of producing the handicap. Females thus gain by selecting attractive males because they will have access to high-quality resources (Kodric-Brown & Brown, 1984). For sexually selected iridescence to be involved in honest signalling, it must be dependent on male quality. Correlational evidence suggests that this is true for many birds (Doucet, 2002; Møller & Petrie, 2002; Doucet & Montgomerie, 2003a, 2003b; Bitton, Dawson & Ochs, 2008) and some insects (Fitzstephens & Getty, 2000; Papke, Kemp & Rutowski, 2007). More convincing evidence comes from experimental manipulations, which have shown that developmental stress (including food deprivation, temperature fluctuations and parasite infection) can significantly affect iridescence in birds (McGraw et al., 2002; Hill, Doucet & Buchholz, 2005), butterflies (Kemp, Vukusic & Rutowski, 2006; Kemp & Rutowski, 2007) and spiders (Lim & Li, 2006b). In most cases, increased stress results in decreased brightness.

The environment poses a potential problem to iridescence as an honest signal. Since patterns of iridescent reflectance depend on lighting, environmental variation might influence perception of quality and mate selection. Bennett et al. (1997) demonstrated this in European starlings (*Sturnus vulgaris*) – females ranked males differently under UV-visible and UV-non-visible conditions. Perhaps iridescent signals alone are not always suitable in mate assessments. There are certainly examples where iridescence, although involved in mate choice, is not exclusively assessed (e.g., Omland, 1996). In such cases, iridescence could have an alternative role: it might function as an amplifier trait. Hasson (1989) proposed the concept of amplifier traits, explaining that evolutionary constraints on display traits themselves sometimes creates a requirement for additional signals of quality (Hasson, 1990). These amplifier traits enhance existing display signals and help in female assessment by more clearly signalling male quality (Bogaardt & Johnstone, 2016). Dakin et al. (2016) describe a possible example of iridescence as an amplifier trait in peacocks, whereby iridescent train feathers are vibrated to create a dynamic background against which the iridescent eyespots remain stationary. Alternatively, some species may modify their behaviour to maximise the conspicuousness of their iridescent colouration. Recent evidence has shown that male cursorial flies (*Lispe cana*) do just this, preferentially displaying courting behaviour against backgrounds that enhance iridescent signal salience and efficacy (White, Vogel-Ghibely & Butterworth, 2019). Despite strong evidence that iridescence is involved in mate choice in

some species, not all studies are supportive of the importance of iridescent signals in mate choice (Mateos & Carranza, 1995; Perrier et al., 2002; Kemp, 2006).

### **1.1.3.2 | Physiology**

Various studies have suggested that iridescence has a role in thermoregulation, though they are contradictory in their conclusions: some suggest a role in cooling (Kobelt & Linsenmair, 1992; Koon & Crawford, 2000; Biró et al., 2003); others suggest a role in warming (Heilman & Miaoulis, 1994; Miaoulis & Heilman, 1998; Tada et al., 1998; Bosi et al., 2008); and some have found little evidence either way (Schultz & Hadley, 1987). Since there are different types of iridescent microstructure (Seago et al., 2009; Krishna et al., 2020), it may indeed be that iridescence has different thermoregulatory effects in different species. However, there are studies that report opposing patterns of thermoregulation even in closely related species (Davis et al., 2008), and since one might expect closely related species to be similar, this casts some doubts. In some cases, though, there may be a simple explanation for the apparent disparity: in butterflies, for example, iridescence seems to have evolved independently several times (Wickham et al., 2006). In addition – as Davis et al. (2008) explained – there may be polymorphism and local adaptation. Other physiology-related roles of iridescence include friction reduction (Gans & Baic, 1977; Vulinec, 1997; Gower, 2003) and photoprotection (Stavenga, 2002; Mäthger et al., 2009), though these are under-researched.

### **1.1.3.3 | Defensive Colouration**

Many species are sexually monomorphic, in which both the males and females are iridescent. In these species, iridescence is unlikely to be involved in sexual signalling (though mutual sexual selection is possible, e.g., Komdeur et al., 2005). Instead, it may be involved in defensive colouration. This is particularly true for smaller animals, such as insects. Since iridescence has numerous optical properties, multiple defensive colour strategies have been hypothesised.

#### *1.1.3.3.1 | Distraction, Deimatism and Misdirection*

Although not iridescent, many pelagic fish appear metallic silver due to structural colouration in their scales. Denton (1970) described how ‘flashes’ produced by the movements of these silver fish seem to distract and startle predators. Perhaps iridescence can play a similar role, though contemporary accounts of defensive colouration would treat distraction of attention and startle (or deimatism) as distinct mechanisms (see Section 1.2.2). Schultz (2001)

described how *Pseudoxyscheila tarsalis* tiger beetles reveal iridescent colours when they move their cryptic elytra. Although Schultz suggested that the iridescence has an aposematic effect, it seems more likely to function as a startle display given that it is revealed from under cryptic coverings (Umbers, Lehtonen & Mappes, 2015). In addition to startling predators, iridescence has been speculated to impair predators' abilities to track moving prey (Schultz, 1985). Recent evidence suggests that iridescence can indeed interfere with motion signals, protecting moving prey from predator attacks (Pike, 2015; see Section 1.2.3.1).

#### 1.1.3.3.2 | Aposematism

Aposematism involves conspicuous signals that warn predators of prey defences (Caro & Ruxton, 2019). Prey unprofitability is often advertised visually through bright colour patterns (Summers, 2003), though some species use auditory, olfactory or behavioural signals, and some species combine signals to enhance their aposematic effect (Rowe & Guilford, 1999; Cuthill et al., 2017). Since iridescence produces bright colours, it is perhaps easy to see how it could have an aposematic function. Indeed, many authors have suggested that aposematism might be the primary function of iridescent colouration in some insect groups (Hinton & Gibbs, 1971; Pearson et al., 1988; Bowers & Larin, 1989; Schultz, 2001), particularly tiger beetles, many of which are known to possess defensive compounds (Pearson et al., 1988). However, a major problem with these studies is that they only correlate iridescence and unpalatability; there is actually little empirical evidence that iridescence has an aposematic effect. For instance, although Bowers & Larin (1989) identified the defensive compound cycasun in lycaenid butterflies, their suggested link between this and iridescent colouration on the wings is undermined by the fact that the abdomen of the species studied is bright red, which is a typical aposematic colour (Stevens & Ruxton, 2012). This raises questions about their conclusion that iridescence is aposematic in lycaenid butterflies. Perhaps it is, and its salience is enhanced by the red abdominal colouration (or vice versa), but without experimental manipulations, these ideas are simply speculative. Given that a consistent conditional stimulus would seem to be important for associative learning, colours that change with viewing angle might be, *a priori*, poor candidates for aposematic signals, unless of course the changeability itself can be learned. However, the fact that there are many cases of iridescence in non-toxic species is further evidence that aposematism might be an unlikely function of iridescent colouration.

#### 1.1.3.3.3 | *Camouflage*

Iridescence as camouflage might seem counter-intuitive, but there is growing evidence that camouflage is an important function of iridescent colouration. The idea was first proposed by Abbott Thayer, who stated that iridescence is “one of the prime factors of disguise” (Thayer, 1909). Until recently, Thayer’s hypothesis lacked empirical support, and the idea of camouflaging iridescence was largely ignored, with any references to it remaining speculative. Although the specific functional mechanism of iridescent camouflage remains unclear, it has been shown that iridescence can interfere with motion signals (Pike, 2015) and object recognition (Kjernsmo et al., 2018). The most significant evidence of iridescence as camouflage is very recent indeed. Using artificial beetle targets, Kjernsmo et al. (2020) showed that iridescent-coloured prey have a survival advantage under both avian and human predation. Since the results of the avian-predation and human-search experiments were aligned, the often-hypothesised aposematic effect of iridescence could be ruled unlikely. Despite still failing to fully address the mechanisms, this study provided two clues: iridescent targets were significantly less detectable than identically coloured non-iridescent targets, and there was no significant difference between the iridescent and black targets. This shows that changeability of the colour is a key component of the effects, and, since the only feature shared by the iridescent and black targets was their glossy surface appearance, specular reflectance might have an important role in camouflaging iridescence.

## 1.2 | Defensive Colouration

### 1.2.1 | CAMOUFLAGE STRATEGIES

Camouflage is widespread in animals. It describes the strategies that animals use to avoid being detected or recognised by other animals (Endler, 1991; Stevens & Merilaita, 2009a; Ruxton et al., 2018; Cuthill, 2019). Camouflage is often studied in a predator-prey context, where each animal in the interaction benefits from gaining concealment from the other. Although camouflage is also used by predators, much of the camouflage research in this context is biased towards studying prey colouration, perhaps because the survival costs of failed camouflage are greater for prey than the failed capture costs to predators (Dawkins & Krebs, 1979). Generally, three main camouflage strategies are considered: background matching, disruptive colouration and masquerade (Endler, 2006). Both background matching and disruptive colouration may be particularly important when considering the role of iridescence as camouflage.



### 1.2.1.1 | Background Matching

Background matching could be considered the most archetypal and universally understood form of camouflage – after all, the classic, text-book example of the peppered moth (*Biston betularia*) illustrates the strategy perfectly (Cook & Saccheri, 2013; Walton & Stevens, 2018). Originally termed ‘background picturing’ by Thayer (1909), background matching in its simplest sense describes how animals often have colours and patterns that match those seen in their background environments (Cuthill, 2019); their colour patterns represent “samples of the visual background” (Endler, 2006). Perhaps unsurprisingly, animal colouration is often correlated with the background colour patterns of the habitats in which they live. Allen et al. (2011) illustrated this in felids, demonstrating that coat patterns are correlated with habitat, and showing that cat species tend to have plain coats in open environments, such as mountains, and spotted coats in closed habitats, such as forests. Such animal-background colour correlations point to background matching as a widespread camouflage strategy. Indeed, background matching is rather taxonomically widespread (Merilaita & Stevens, 2011), and experimental evidence has shown that it can be a highly effective and adaptive strategy, promoting increased survival (Merilaita & Stevens, 2011).

Much of the research on background matching has sought to identify the optimal background sample upon which an animal’s colours and patterns should be based. Endler (1978, 1981, 1984, 2006) has repeatedly suggested that a random sample is best, though many argue that – because they can include rare samples – random samples are not equally cryptic and that some provide poor matching (Merilaita, Tuomi & Jormalainen, 1999; Merilaita & Lind, 2005). Indeed, given that many animals choose both their backgrounds and body orientations against those backgrounds to maximise concealment (Kang et al., 2012, 2014; Kang et al., 2015; Kjernsmo & Merilaita, 2012; Lovell et al., 2013; Marshall, Philpot & Stevens, 2016), it is easy to see how a random sample could be deleterious. Merilaita, Tuomi & Jormalainen (1999) proposed the idea of compromise crypsis, suggesting that the optimal sample contains pattern features from two microhabitats. This may be particularly true for species that regularly move across different backgrounds (Cuthill, 2019). Empirical evidence suggests that compromise crypsis is effective (Merilaita, Lyytinen & Mappes, 2001), though it is not always the best strategy (Houston, Stevens & Cuthill, 2007). Recently, it has been shown that common samples are indeed best (Michalis et al., 2017), presumably because they match more areas of a given background. But this is only true in the absence of predator learning (Michalis et al., 2017) – if predators are capable of learning prey colour patterns, there will be frequency-dependent selection, and polymorphism in prey appearance will develop (Bond & Kamil, 2002, 2006; Troscianko et al., 2018). Search image formation is a classic example of predator

learning. Search images are short-term perceptual filters that predators develop through frequent prey encounters and subsequent learning that enable fast identification of specific prey features (Tinbergen, 1960; Pietrewicz & Kamil, 1979; Langley, 1996). Under search-image-influenced apostatic predation (negative frequency-dependent selection), rare forms are favoured (Plaisted & Mackintosh, 1995; Bond & Kamil, 1999, 2002; Karpestam, Merilaita & Forsman, 2014), until there is stability in prey polymorphism (Bond & Kamil, 1998). In some cases, resembling a specific background sample might be irrelevant. Some species, including various cephalopods, can actively change colour, using pigment-containing chromatophores, to allow rapid physical alteration to match new backgrounds (Mäthger & Hanlon, 2012; Gilmore, Crook & Krans, 2016). Finally, there is one type of ‘colouration’ that could theoretically produce perfect background matching against all possible backgrounds: transparency. However, there is a fundamental constraint: for transparency to provide effective invisibility camouflage, the refractive indices of the animal’s tissues and the surrounding environment must be the same (Johnsen, 2001; Arias et al., 2020). This is achievable in water, and there are examples of transparent pelagic species (Cronin, 2016), though these tend to be small in size (Mäthger & Hanlon, 2012). In terrestrial environments, true transparency is virtually impossible, though some Lepidopterans have semi-transparent wing scales that enhance cryptic colouration (Arias et al., 2020). Imperfect transparency (or translucency) may be the best compromise in terrestrial habitats, and it has been shown to provide more effective camouflage in glass frogs through reducing the distinctiveness of the body’s edge (Barnett et al., 2020).

Despite a tendency to associate iridescence with particularly bright and vibrant colours (Doucet & Meadows, 2009), there are instances where it could provide species with background-matching camouflage. Although iridescent structures often produce short-wave colours, they can produce medium-wave colours, including various greens (Sun, Bhushan & Tong, 2013), which are typical woodland and forest background hues (Endler, 1993). When there is sufficient similarity between the primary iridescent hue and the main background hues, iridescence could conceivably enable at least some degree of background matching. While there is no direct evidence, observational conclusions have suggested that this may indeed be true for some species. For instance, the iridescent manuka beetle (*Pyronota festiva*), which – despite exhibiting angle-dependent purple, blue, orange and red hues – is mostly green in appearance, spends much of the summer resting on the green leaves of manuka plants (*Leptospermum scoparium*; De Silva et al., 2005). Of course, the colour-changing properties of an iridescent surface must be acknowledged in any consideration of background-matching iridescence – if the hue deviates quickly away from green (or the primary background-matching colour) with changes in viewing angle, background matching could be challenged.

That said, there might be a simple solution: selective body position and orientation. Many animals choose their body orientations against different backgrounds to maximise concealment (Kang et al., 2012, 2014; Kang et al., 2015). Perhaps iridescent prey are able to take advantage of the colour-shifting nature of their iridescence to achieve both improved background matching and concealment in different locations.

### **1.2.1.2 | Disruptive Colouration**

Disruptive colouration could be thought of as an enhanced version of background matching as it typically combines background colours with features that interfere with edge detection (Cuthill, 2019). Outline-disrupting features are a key aspect of disruptive colouration, with Thayer (1909) originally describing the concept as raptive patterning for this reason, arguing that camouflage can be easily achieved if an animal's patterning breaks up its appearance. Such edge-disrupting patterns have indeed been observed and documented in animals for many years – for example, Merilaita (1998) showed that the marine isopod *Isopada baltica* has colour patches that intersect the body outline more often than expected by chance. Hugh B. Cott (1940) expanded Thayer's concept, provided a more robust definition and described a series of fundamental, defining features. These ideas were revisited, revised and reorganised into a new framework by Stevens & Merilaita (2009b), who outlined five key characteristics of disruptive colouration. Firstly, there is differential blending of colour patches, such that some provide background matching. In Cott's original definition of differential blending, he proposed that other colours would stand out from the background; hence the "differential". Empirical evidence suggests that this may not be the case. Numerous studies have highlighted the importance of possessing some background-matching colour patches in maximising the survival of disruptively coloured prey (Cuthill et al., 2005; Stevens et al., 2006; Fraser et al., 2007). In fact, Fraser et al. (2007) demonstrated that disruptively coloured artificial moths only avoided detection (by humans on a computer screen) if their disruptive patterns had been combined with background matching. Secondly, there is high contrast between adjacent colour patches, providing maximum disruptive contrast. Although possessing colours that match different components of the background maximises the survival of disruptively coloured prey, some degree of concealment can still be achieved by targets with non-background-matching colour patches, provided these patches contrast with the surrounding colours (Stevens et al., 2006; Schaefer & Stobbe, 2006). Thirdly, both false edges contained within the body and – fourthly – edge-intersecting disruptive marginal patterns help to conceal the true body outline (Stevens et al., 2009). Since outline detection is a key aspect of identification (Troscianko et al., 2009), it is perhaps unsurprising that edge disruption through the presence of false edges and/or disruptive marginal patterns promotes

concealment (Cuthill et al., 2005; Schaefer & Stobbe, 2006; Stevens et al., 2006; Webster, Godin & Sherratt, 2015; Egan et al., 2016). Finally, there is coincident disruptive colouration, where colour patches on different parts of the body are aligned (Cott, 1940). Coincident disruptive colouration helps to reduce three-dimensional (3D) body cues, as well as disguise conspicuous body features that could otherwise be targeted by predators (Cuthill, 2019). Experimental evidence has suggested that coincident disruptive colouration is highly effective at providing concealment – for example, Cuthill & Székely (2009) demonstrated that artificial moths with patterns of contrasting colours that were aligned across their wings and bodies survived significantly better than treatment targets both under avian predation and in human search experiments.

There is no doubt that disruptive colouration is a particularly effective camouflage strategy, especially in comparison to background matching (Cuthill et al., 2005), and it is thought to work in two main ways: by interfering with edge detection (Stevens & Cuthill, 2006; Sharman, Moncrieff & Lovell, 2018), and by interfering with perceptual grouping such that different parts of the animal are perceived as matching different background objects, effectively providing camouflage at different spatial scales (Espinosa & Cuthill, 2014). Although iridescence may not conform to typical expectations of disruptive colouration (in that iridescent surfaces appear continuous in terms of colour, with colour patches that lack boundaries), it could provide camouflage through disruptive-like mechanisms, and iridescence could very feasibly interfere with edge detection. Since iridescent surfaces exhibit angle-dependent changes in colour (Kinoshita, Yoshioka & Miyazaki, 2008), iridescence might produce instability and unpredictability in body outline and edge signals, preventing successful recognition (or promoting delayed recognition) in a similar way to false edges and edge disruption. While there is no definitive evidence that iridescence provides camouflage through disruptive colouration, it has been shown to impair object recognition in bumblebees (Kjernsmo et al., 2018), so it remains highly plausible that iridescent colouration can have a disruptive-like camouflaging function. Iridescence is often associated with specular reflectance (Stuart-Fox et al., 2021), and Kjernsmo et al. (2020) suggested that this could be associated with iridescence as camouflage. Glossy surfaces are often characterised by regions of high reflectance that are perceived as bright, white highlights (Franklin & Ospina-Rozo, 2021). These highlights differ sufficiently from the surrounding area such that gloss creates high-contrast patches, false edges and – depending on the angles of incident light and viewing – edge disruption. Perhaps iridescence can achieve concealment if components of the iridescent colouration itself provide some degree of background matching, which is then enhanced by the disruptive patterns of surface gloss.

### 1.2.1.3 | Masquerade

Masquerade describes the resemblance of an animal to an inedible object in their visual background (Endler, 1981). Unlike background matching and disruptive colouration, masquerade does not involve avoiding detection; instead, masquerading animals *are* detected, but are misclassified by the receiver and so are ignored (Skelhorn et al., 2010; Cuthill, 2019). Masquerade is a relatively widespread and effective method of concealment (Skelhorn, 2015). In fact, masquerade is so effective in the orb-weaving spider *Cyclosa ginnaga* that both it and its web are indistinguishable from bird droppings when calibrating for the vision of hymenopteran predators (Liu et al., 2014). In many species, active behavioural choices can enhance the success of masquerade. Suzuki & Sakurai (2015) found that many caterpillars adopt a bent posture when resting on leaves to exaggerate their resemblance to bird droppings beyond simply colour similarity. Background choice and subtle movements can also enhance resemblance (Skelhorn, 2015; Stevens & Ruxton, 2019). Masquerade has advantages over background matching and disruptive colouration in that it is effective independent of the background (Skelhorn & Ruxton, 2010; Skelhorn et al., 2010). But there are downsides: for masquerade to be maximally effective, there has to have been previous exposure to the object being mimicked and learning by the receiver (Skelhorn & Ruxton, 2011). Although it is an important and successful form of camouflage, masquerade is not really relevant to iridescence, since iridescence has never been proposed to involve mimesis of inedible objects.

### 1.2.2 | OTHER PROTECTIVE COLOURS

Aposematism involves conspicuous signals that warn predators of prey defences (Poulton, 1890; Rojas, Nokelainen & Valkonen, 2017; Caro & Ruxton, 2019). It was first described by Alfred Russel Wallace, who noticed a link between conspicuous colouration and the possession of secondary defences (Wallace, 1867). Unlike camouflage, which seeks to prevent detection and recognition, aposematic colouration actually promotes recognition. Indeed, recognition is key in the success of aposematism: predators must recognise that an animal is defended, and, unless aversion is innate, this requires learnt avoidance. Using field experiments with artificial caterpillar targets, Mappes et al. (2014) showed that aposematic prey survival is lowest when there are naïve predators (fledglings) because learning is yet to occur; when adult birds are common, survival is high because learnt avoidance has been achieved. Although one-trial learning can occur (Roper & Redston, 1987), frequent encounters between predators and defended prey are usually necessary for reinforcement of learnt avoidance (Gittleman & Harvey, 1980). This can be achieved through gregarious behaviour.

Using a comparative phylogenetic analysis, Tullberg & Hunter (1996) found an association between larval gregariousness and unpalatability in Lepidoptera, concluding that gregariousness provides the conditions necessary for frequent encounters between predators and defended prey. If reinforcement of learnt avoidance is not possible (perhaps because the behaviour of either predator or prey prevents frequent encounters), advertising unpalatability might not be entirely sensible. After all, for learning to be facilitated in the first place, warning signals need to be distinctive and salient, but the latter will usually make the animal conspicuous. Some species may have evolved a solution: distance-dependent colouration. This involves combining different colours and patterns to produce colouration that has a different effect at different spatial scales; namely, aposematism when viewed at close range, and crypsis when viewed from a distance. Distance-dependent colouration is effective (Barnett & Cuthill, 2014; Barnett, Scott-Samuel & Cuthill, 2016), and it has been documented in caterpillars (Tullberg, Merilaita & Wiklund, 2005; Barnett, Cuthill & Scott-Samuel, 2018) and frogs (Barnett et al., 2018).

Since aposematism is an effective anti-predator strategy, it has facilitated the evolution of mimesis in both other aposematic and non-aposematic species (Quicke, 2017). In Batesian mimicry, a palatable species gains protection by resembling a defended, aposematic species (Bates, 1862). Since predators have already learned to avoid the defended models, the Batesian mimics are mistakenly identified and thus avoided. Batesian mimicry can be a highly effective strategy, especially if there is close resemblance between mimics and models (França, Braz & de Araújo, 2017). But, perhaps surprisingly, mimicry need not be perfect (at least to our eyes) to promote mistaken identification and avoidance – França, Braz & de Araújo (2017) showed that just sharing colours with the model was enough to provide coral snake mimics with some degree of protection. Perhaps imperfect mimicry can persist because of features that go beyond simple colour resemblance, such as behavioural mimicry, which is well-documented (Pereira et al., 2013; Alif, Sparkman & Pfennig, 2020; Pekár, García & Bulbert, 2020) and has been shown to enhance mimesis (Pereira et al., 2013). Generally, wherever there are defended, aposematic species, there will be Batesian mimicry. Davis Rabosky et al. (2016) illustrated this using a phylogenetic analysis, which revealed a correlation between the colouration of non-toxic snakes and the colouration of venomous coral snakes in both space and time. Most evidence suggests that Batesian mimicry can only evolve in populations where there is a high abundance of models (Kikuchi & Pfennig, 2010); in populations where the model is absent, mimicry cannot be sustained and mimesis will be eroded (Alif, Sparkman & Pfennig, 2020). Müllerian mimicry – in which two or more aposematic species resemble one another, to their mutual benefit (Müller, 1879) – is not constrained by this abundance-dependent limitation. Müllerian mimicry could be viewed as an evolutionary

shortcut to achieving effective warning colouration, because, through prey convergence on similar morphological features, predators need only have a few encounters with any one of the prey species to learn avoidance of all. Simply put, Müllerian mimicry enhances aposematism when both species live in sympatry (Rowland et al., 2010). Once a pair of species has established Müllerian mimicry, they may be joined by other species through convergent evolution (Bocak & Yagi, 2010), forming mimicry rings. While most are relatively small, some mimicry rings can be surprisingly large and complex – Wilson et al. (2012) identified a velvet ant mimicry ring found throughout western North America that contains 18 different species. Such Müllerian mimicry rings can have implications for Batesian mimicry (Franks & Noble, 2004).

It has been suggested that some instances of insect iridescence could represent examples of Batesian or Müllerian mimicry (Acorn, 1988; Schultz, 2001), though this would require iridescence to be involved in aposematism. Correlational evidence suggests that some iridescent species might indeed be aposematic (Hinton & Gibbs, 1971; Pearson et al., 1988; Bowers & Larin, 1989; Schultz, 2001). However, experimental evidence is non-existent. In addition, iridescence threatens a key ingredient of successful aposematism: learning. Since learnt avoidance to unpalatable prey is facilitated primarily by bright, conspicuous and distinctive colours (Summers, 2003; Skelhorn, Halpin & Rowe, 2016; Rojas, Nokelainen & Valkonen, 2017), it is easy to see how iridescence could be involved in aposematism. However, for a colour signal to be maximally effective, it should be stable; iridescent signals are characteristically unstable and unpredictable (Stuart-Fox et al., 2021), and as such, it might not be possible to develop learnt avoidance of iridescent signals. If iridescence cannot be learned (and this remains to be investigated), it would be highly costly for prey to use it as a warning colour. Of course, a counterargument could be made that iridescence is so distinctively unique that it actually facilitates learning, though this seems unlikely, especially given recent experimental evidence in which iridescent targets survived significantly well under both avian and human predation (Kjernsmo et al., 2020).

Some colour patterns provide protection through distraction and deimatism. Distraction involves conspicuous colour patches that draw attention away from cues of body form, preventing – or at least slowing – the processes of detection and recognition (Thayer, 1909). Because distraction works by attracting attention, there are many doubts over whether it can be an effective strategy, and experimental evidence suggests that distraction marks can indeed be costly (Stevens et al., 2008; Troscianko et al., 2013; Troscianko, Skelhorn & Stevens, 2018). That said, this is a somewhat under-researched aspect of protective colouration, and there is also evidence that distraction can reduce predation (e.g., Dimitrova

et al., 2009; Olofsson, Dimitrova & Wiklund, 2013). Deimatism describes the unexpected defences (often visual) that prey reveal suddenly to deter attacking predators (Umbers, Lehtonen & Mappes, 2015). Examples of deimatic – or startle – displays include the spreading of wings in the praying mantis *Stagmatoptera biocellata* (Maldonado, 1970), and the exposing of bright colour patches in the European swallowtail (*Papilio machaon*; Olofsson et al., 2012) and the mountain katydid (*Acripeza reticulata*; Umbers & Mappes, 2015). Since iridescence involves bright, vibrant and changeable colours, it could potentially provide protection through distractive or deimatic mechanisms (or perhaps even both). However, iridescent colours tend not to occur as discrete patches, instead often covering the entire body surface, so, in the case of distraction, iridescence might have the opposite effect of attracting attention to the entire animal rather than a small, conspicuous distractive colour patch. In the case of deimatism, unless it is hidden and can be revealed suddenly (which has been documented (e.g., Schultz, 2001), but may be rare), iridescence is unlikely to be able to function as a deimatic display, because these are deployed only at the point of attack (Umbers, Lehtonen & Mappes, 2015).

### 1.2.3 | WHEN CAMOUFLAGE FAILS

#### 1.2.3.1 | Motion

Most camouflage research has focused on stationary targets, yet almost all animals need to move to some degree, and motion breaks camouflage. Indirect evidence of the camouflage-breaking costs of movement comes from age-related colour changes in caterpillars. Both early instar *Acrionicta alni* and *Saucrobotys futilalis* larvae are camouflaged, while later instar larvae are brightly coloured and aposematic. In each species, the colour change is correlated with the need to move, and it seems to be a direct response to the constraints imposed by camouflage (Grant, 2007; Valkonen et al., 2014). Hall et al. (2013) demonstrated the costs of motion experimentally, showing that when presented alone, moving camouflaged targets cannot avoid being detected. As a target moves across a background, the contrast between it and the background increases; this movement makes target edges more defined (Regan & Beverley, 1984), and the target becomes more perceptible. It seems that the brain is highly sensitive to these motion cues (Rushton, Bradshaw & Warren, 2007). Indeed, movement signals (from both slow-moving and fast-moving camouflaged targets) elicit fast neural processing in primates (Yin et al., 2015). Despite the camouflage-breaking costs associated with movement, there are solutions. If moving targets are presented alongside other similar-looking targets, camouflage is beneficial as it slows identification (Hall et al., 2013). Some insects, including dragonflies, use motion camouflage to disguise their aerial movements. This



involves using movements that mimic the appearance of a fixed object in the observer's visual field (Srinivasan & Davey, 1995; Mizutani, Chahl & Srinivasan, 2003). Mathematical simulations suggest that this can be an effective strategy (Glendinning, 2004). Another solution is to use a motion-signal-interfering colour pattern. Pike (2015) suggested that this is one of the mechanisms by which iridescence can conceal prey. Using virtual prey, Pike demonstrated that moving iridescent targets are less accurately and less successfully attacked by Japanese quail (*Coturnix japonica*).

#### **1.2.3.2 | Symmetry**

Developmental constraints mean that many animals show some degree of symmetry in the arrangement of their colours and patterns. This poses a problem, because the brain can process and detect symmetry in visual scenes with relative ease (Barlow & Reeves, 1979). So, perhaps unsurprisingly, symmetry increases the detectability of prey, reducing the effectiveness of camouflage (Cuthill, Hiby & Lloyd, 2006; Cuthill et al., 2006; Merilaita & Lind, 2006). The camouflage-breaking costs of symmetry are particularly high for background matching and disruptive colouration (Cuthill et al., 2006); with masquerade, as long as the model is symmetrical, mimicking prey are not affected by symmetry (Cuthill, 2019). The positioning of symmetrical patterning is important in determining detectability – Wainwright, Scott-Samuel & Cuthill (2020) showed that by positioning symmetrical patterns away from the midline of artificial moths, the costs of symmetry can be overcome. It might also be possible to overcome the costs of symmetry through iridescence – the angle-dependent colour-changing nature of iridescence might make the symmetry of iridescent surfaces harder to detect. This has never been investigated (or, to my knowledge, suggested).

### **1.3 | Visual Systems, Perception & Receiver Psychology**

Understanding the visual systems of receivers is vitally important when studying animal camouflage. Since no form of camouflage (aside from that created by humans, such as military camouflage) has evolved to deceive humans, approaching animal camouflage with no consideration of the visual systems of the evolutionary relevant receiver(s) is flawed.

### 1.3.1 | VISUAL SYSTEMS

#### 1.3.1.1 | Perception

There are ten different types of visual organ (Warrant, 2017). Eye spots and pit eyes are the simplest, detecting nothing more than differences in light intensity; camera eyes are the most advanced, providing high resolution and high sensitivity. While vertebrates have only one type of visual organ (camera eyes), all ten types can be found among the invertebrates. Despite this, invertebrate visual systems tend to be relatively simple compared to the human eye (Land & Nilsson, 2012a), though there are of course exceptions – mantis shrimps, for instance, have the most complex and sophisticated known eyes (Land & Nilsson, 2012a), capable of detecting visible, UV and polarised light (Cronin et al., 2014). In fact, their spectral sensitivity is so fine-tuned that they have been shown to be as good at discriminating different UV wavelengths as they are at discriminating different human-visible wavelengths (Bok, Roberts & Cronin, 2018). That is not to say that the mantis shrimp eye is comparable to the human eye in terms of spatial resolution or even, within the human-visible spectrum, wavelength discrimination *per se* (Thoen et al., 2014). Generally, vertebrate eyes are comparatively more complex and more advanced than invertebrate eyes, and, since they are larger, provide higher resolution and sensitivity (Land & Nilsson, 2012b).

Vertebrates generally have particularly good colour vision, especially in comparison to the majority of invertebrates (Jacobs, 1983), though there is substantial inter-species variation in spectral sensitivities (Kelber, Vorobyev & Osorio, 2003; Allen, 2009). These differences are the result of variation in the types and numbers of cone photoreceptors, each of which contain opsins that are sensitive to a specific range of wavelengths (Kelber, Vorobyev & Osorio, 2003). In terms of phylogeny, there are four distinct classes of cone photoreceptor (Bowmaker, 2008). Three of these respond to human-visible light, allowing detection of short-wave (blue; 410–490 nm), medium-wave (green; 480–535 nm) and long-wave (red; 490–570 nm) visible light (Baylor, Nunn & Schnapf, 1987; Bowmaker, 2008). A fourth cone type found in many species – perhaps even most (Cronin & Bok, 2016) – contains opsins that absorb UV photons, enabling the detection of near-UV wavelengths (355–440 nm; Kevan, Chittka & Dyer, 2001; Shi & Yokoyama, 2003; Bowmaker, 2008; Douglas & Jeffery, 2014). Such UV vision seems to be important in birds (Elphick, 2014) and many insects (Chittka & Briscoe, 2001; Kevan, Chittka & Dyer, 2001; Land & Nilsson, 2012a), though Kevan, Chittka & Dyer (2001) argue that most UV signals are not particularly salient and are simply detectable. Throughout evolution, opsin gene duplications occurred in some animal groups, promoting differences and further divergence in species-specific spectral sensitivities (Owens & Rennison, 2017; Fleming

et al., 2018). Evidence based on the diversity and distribution of different photoreceptor classes would seem to suggest that the ability to perceive short-wave colours is particularly widespread (Osorio & Vorobyev, 2008). Since iridescence predominantly involves short-length wavelengths, with colours often shifting towards the blue/UV end of the spectrum (Vigneron et al., 2006), it is reasonable to assume that most species should be able to detect iridescent colouration to some degree.

Most species – both vertebrates and invertebrates – tend to have either dichromatic or trichromatic vision (Land & Nilsson, 2012b). The advantage of such multiple, spectrally distinct photoreceptors is that it enables colour discrimination. The more types of photoreceptors a species has, one would normally expect, the better their ability to discriminate different colours (with mantis shrimps, as in so many aspects of visual ecology, perhaps being the exception; Thoen et al., 2014). This is important when considering iridescence, because the wavelengths reflected by iridescent surfaces often require different photoreceptor classes for detection. Thus, multichromatic vision and the ability to discriminate between different colours is ultimately a prerequisite for full detectability of the colour-changing aspect of iridescence. Species-related differences in colour discrimination also have implications for camouflage. Since dichromats are able to detect less spectral information than trichromats, their ability to locate camouflaged targets through chromatic contrast is comparatively worse (Troscianko et al., 2017). While it has long been argued that there are compensatory benefits in terms of reduced chromatic noise and greater sensitivity to luminance contrast, there is evidence both for (Morgan, Adam & Mollon, 1992) and against (Troscianko et al., 2017) better camouflage-breaking abilities in dichromats. Fennell et al. (2019) provided further evidence for poor camouflage-breaking abilities in dichromats, showing that tigers (*Panthera tigris*) only appear a different colour from green (orange) under trichromatic vision; when adjusting for dichromatic vision, their coat becomes indistinguishable from the hues of the background vegetation. Since their prey are dichromats, the camouflage is successful, and there is no selection pressure for further evolution of their coat colours.

If an animal has multiple photoreceptor types, the potential for non-spectral colour perception arises. Non-spectral colours are not part of the electromagnetic spectrum, instead being perceived when two different types of photoreceptor are simultaneously stimulated (Stoddard et al., 2020). Stoddard et al. showed that hummingbirds (*Selasphorus platycercus*) can accurately discriminate between non-spectral colours composed of UV and visible wavelengths, concluding that birds might perceive many natural colours as being non-spectral. This could be important to the perception of iridescence. Since iridescent structures can reflect both human-visible and UV wavelengths (Doucet & Meadows, 2009), there is potential for

human-non-visible non-spectral colour production, resulting in a surface whose appearance might be fundamentally different for, for example, avian compared to mammalian observers. Interestingly, there is some evidence that colour discrimination might not be entirely restricted to multichromatic animals. Stubbs & Stubbs (2016) describe a way that monochromatic species could potentially perceive spectral differences, exploiting a combination of pupil shape and chromatic aberration.

### **1.3.1.2 | Visual Processing**

There are two aspects of visual processing that are important to visual search: figure-ground segmentation and target-distractor discrimination. Both are fairly self-explanatory: in figure-ground segmentation, objects (figures) are separated from the background (ground; Kimchi & Peterson, 2008); in target-distractor discrimination, objects of interest (targets) are separated from surrounding, already segmented, objects (distractors; these may be irrelevant, or not-of-interest at a particular time, e.g., non-targeted prey individuals within a group; Pashler, 1987). Figure-ground segmentation is a two-stage process, involving low-level detection of simple edge information, then high-level grouping of target edge information (which also involves rejecting edges belonging to the background; Troscianko et al., 2009). Figure-ground segmentation is interesting because it seems to be possible in the absence of complete focal attention (Kimchi & Peterson, 2008). Target-distractor discrimination, on the other hand, might require more 'cognition' because, unless targets and distractors can be separated along one simple stimulus dimension (e.g., luminance), it potentially involves attention to separate targets and distractors. Both processes can be influenced by the visual appearances of targets and distractors (Ralph et al., 2014). As such, camouflage is able to interfere with and impair these processes. For instance, camouflage often involves distractors and targets that resemble one another, which prevents efficient target-distractor discrimination (Troscianko et al., 2009). Although exploited by camouflage, these processes are still helpful in detecting camouflaged prey, especially when camouflage fails. Motion is one of the main constraints on effective camouflage (Ioannou & Krause, 2009; Hall et al., 2013), and movement enhances figure-ground segmentation by making targets more easily discernible from the background (Regan & Beverley, 1984). In addition to the visual appearances of targets and distractors, these processes are affected by the target-distractor ratio. This is particularly true for target-distractor discrimination, which is much less efficient when the number of distractors is high (Pashler, 1987). Prey can exploit this through behavioural choices that increase the difficulty of target-distractor discrimination. The confusion effect is perhaps the best example, whereby predators have difficulty targeting individuals within a group (Landeau & Terborgh, 1986; Scott-Samuel et al., 2015). It is also the case that these two types of visual search can overlap.

Similar distractors can sometimes be treated as part of a texture rather than as individual items, and so a target-distractor task becomes a figure-ground separation task (Cuthill & Troscianko, 2009; Cuthill, 2019).

Because visual search is important in many different contexts, it has fitness implications. Presumably, efficient visual search in most contexts should increase an individual's fitness. For instance, if an animal is able to forage efficiently and effectively, they will gather more resources and should thus fare better than their less-efficient conspecifics. Any mechanism that increases the efficiency of visual search (and thus an individual's fitness), without counterbalancing costs, should be favoured. Learning is a key mechanism that can enhance visual search, especially in a foraging and hunting context. Search image formation is a classic example of learning that can increase the speed with which cryptic prey targets are detected and recognised (Tinbergen, 1960; Pietrewicz & Kamil, 1979; Plaisted & Mackintosh, 1995; Langley, 1996; Bond & Kamil, 1999, 2002, 2006). Such patterns of learning may be influenced by limitations in visual processing capabilities. Perhaps some features are easier to learn over others because of attentional deficit, limiting what can be learned. It seems that many species show biases in learning, whereby single salient traits overshadow other traits and are disproportionately important to the extent that other cues may be ignored entirely. Kazemi et al. (2014) trained blue tits (*Cyanistes caeruleus*) to discriminate between rewarded and unrewarded prey, all with various colour, pattern and shape combinations, and found that prey discrimination was based on colour alone. Despite being the likely result of limitations in visual processing capabilities, overshadowing is clearly an adaptive strategy, allowing faster detection and recognition of prey. This is particularly important when dealing with aposematic prey and Batesian mimicry, where the costs of misclassification may be high. The overshadowing effect of colour in avian visual processing has become relatively well-documented and has repeatedly been shown to increase the efficiency of visual search (e.g., Gamberale-Stille et al., 2018; Lawrence & Noonan, 2018; Corral-Lopez et al., 2020). However, iridescence might present a case where prioritising colour cues might not be so sensible. Assuming colour cues are disproportionately important in avian visual search both before and after learning, the colour-changing nature of iridescent surfaces might prevent or impair detection and recognition processes by confusing avian predators. Perhaps iridescence can function as a form of camouflage by exploiting a loophole in avian visual perception. That is, the seemingly dominating importance of colour signals, which, in the case of iridescence, are unstable and unreliable cues.

### 1.3.2 | HOW CAMOUFLAGE WORKS

#### 1.3.2.1 | Exploiting Receiver Psychology

Camouflage works by exploiting visual processing capabilities of the receiver. There are two main ways it achieves this: firstly, camouflaging patterns act to reduce the signal-to-noise ratio, and secondly, camouflage exploits both shared shortcomings and species-specific aspects of information processing (Kelley & Kelley, 2014; Merilaita, Scott-Samuel & Cuthill, 2017; Cuthill, 2019; Galloway et al., 2020).

##### 1.3.2.1.1 | *Signal-to-Noise Ratio*

Biological signals are produced against background noise. These signals (elements of interest) have to be separated and filtered from the noise (uninteresting and irrelevant elements in the background) to be detected. The function of camouflage is to mask those signals that allow detection or correct identification, and it does this by reducing the signal-to-noise ratio (SNR) (Merilaita, Scott-Samuel & Cuthill, 2017; Galloway et al., 2020). SNR is a framework that compares the amount of relevant information (the signal) to the amount of irrelevant information (the noise) in a visual scene. Camouflage successfully reduces the SNR by either reducing the signal or increasing the noise, or both – each of the three main camouflage strategies reduces the SNR in different ways (Merilaita, Scott-Samuel & Cuthill, 2017). Background matching reduces the signal itself, such that the animal becomes less distinguishable from the background noise. Disruptive colouration reduces true edge signals through edge disruption, but also increases noise through false edges – these become salient and hide the true edges (Stevens & Cuthill, 2006; Stevens et al., 2008). With masquerade, the signal is not reduced because the animal is entirely perceptible; instead, it is mistakenly identified as irrelevant by the receiver. Masquerade reduces the SNR by increasing the level of noise through false information. Some animals may modify their SNR through their behaviour (Cuthill, Matchette & Scott-Samuel, 2019; Stevens & Ruxton, 2019). Background complexity is important here. Since complex backgrounds are characterised by increased visual noise, and prey hiding against complex backgrounds are unsurprisingly harder to locate (e.g., Dimitrova & Merilaita, 2009; Xiao & Cuthill, 2016), active background choice provides a potential way for species to reduce their SNR by maximising the level of background noise. Indeed, some species have been shown to favour high-complexity backgrounds, where their camouflage is most successful (e.g., Merilaita, 2003; Kjærnsmo & Merilaita, 2012). The demonstration that iridescent objects are harder to detect if their backgrounds have high specular reflectance ('gloss') may be an example of this (Kjærnsmo et al., 2020).

#### 1.3.2.1.2 | *Information Filtering*

All visual information is processed and filtered in species-specific ways (Endler, 1978; Endler et al., 2005). Yet humans are deceived by many examples of animal camouflage, suggesting that there are in fact fundamental similarities in the visual processing pathways of different species. Indeed, all species experience a loss of data during visual processing (Troscianko et al., 2009; Merilaita, Scott-Samuel & Cuthill, 2017) at three main bottlenecks: the eye, the optic nerve and attention (Cuthill, 2019). Such losses of information result in spectral, spatial and temporal resolution limits. The spectral resolution of visual information is limited primarily by the number of different photoreceptors within the eye. As already discussed, most species have between two and four photoreceptor types (Kelber, Vorobyev & Osorio, 2003), which reduces the spectral information content considerably. The density of photoreceptors within the retina limits the spatial resolution of visual information (Woog & Legras, 2018; Cuthill, 2019). Finally, the rate at which an animal is able to sample their visual environment limits the temporal resolution of visual information. This is determined by a species' critical flicker fusion frequency (CFF), which describes the point at which a flickering visual stimulus is perceived to be continuous (Boström et al., 2017). Since the colour-changing nature of iridescence could be considered somewhat analogous to a flickering visual stimulus, CFF is likely to be important in determining how perceptible iridescent colour changes are. For instance, birds – the primary predators of insects associated with camouflaging iridescence (Kjernsmo et al., 2020) – tend to have a high CFF (Lisney et al., 2011; Boström et al., 2016, 2017), so it is possible that iridescent colour changes are fully detectable.

After visual information is received by photoreceptors in the eye, signals are sent to the optic nerve. Here, there is massive loss of visual information – in humans, this represents a 10,000-fold reduction in the quantity of data being processed (Zhaoping, 2014). Many species counter this loss of information by behaviourally adjusting their level of attention. Eye-movement is a common method of achieving increased attention. Saccades (rapid eye movements) help to reduce blur (Land, 1999) and keep relevant aspects of the visual scene at the fovea, where visual acuity is at its highest (Carrasco, 2018). Changes in body orientation provide another example of behavioural modification of attention. These movements can be either active or automatic responses, and they allow attention to be focused on specific aspects of the visual scene, maximising the amount of visual information being received (Carrasco, 2018).

Putting aside inter-species similarities in visual processing, the fact that all visual information is still processed and filtered in species-specific ways has important implications in the context of camouflage. All forms of animal camouflage are adaptations to the visual system(s) of the

species from which concealment is required (Cuthill, 2019), and any camouflage strategy will succeed in providing concealment if it deceives the observer(s). Evolutionary change in the ‘hider’ would only be expected if one (or more) of the observers is not fully deceived by the camouflage and the cost of change does not outweigh the benefits. Fennell et al.’s (2019) example of the tiger’s (*Panthera tigris*) orange colouration illustrates this perfectly. Since tiger prey have dichromatic vision, they cannot perceive differences between orange and green hues. While these colours are fundamentally distinct to species with visual systems capable of detecting the differences, to those from whom concealment is sought, the tiger is indistinguishable from the background, the camouflage is thus perfect, and there is no selection pressure for further evolution of the colour pattern. Such examples highlight the importance of approaching the study of animal camouflage from the perspective of the species being deceived.

## 1.4 | Aims and Objectives

Until recently, Thayer’s (1909) ideas of camouflage through iridescence were largely ignored and lacked empirical support. Now, several studies have shown that iridescent colouration can indeed have a camouflaging effect (Kjernsmo et al., 2018; Kjernsmo et al., 2020) or interfere with prey capture (Pike, 2015). As mentioned in Section 1.2.3.1, using moving iridescent targets, Pike (2015) showed that iridescence compromises accurate targeting of moving objects by Japanese quail. Interestingly, in his writings, Thayer noted that iridescence is often found on active species, suggesting – as Pike later confirmed – that changeable iridescence helps to distort the perception of motion. Presumably, iridescent colouration in such active species either makes focusing on signals difficult, makes useful signals weak, or generates sufficient noise to mask any potentially useful cues. Of course, Thayer’s observations are biased: iridescence is taxonomically widespread, existing on more than just active species (Doucet & Meadows, 2009). Kjernsmo et al. (2018) showed that iridescence on static artificial flowers can impair shape recognition in bumblebees (*Bombus terrestris*). This suggests that, in at least some cases, iridescence might enable concealment through disruptive colouration, the form of camouflage that arises from colour patterns that interfere with edge detection and so perception of shape (Stevens & Merilaita, 2009b). The strongest empirical evidence for camouflaging iridescence comes from the experiments of Kjernsmo et al. (2020), in which iridescent beetle-like targets were shown to survive significantly better than most non-iridescent control targets (except black) under predation by both birds and humans. In the case of humans, we can be confident that it was detection that was affected. Although these studies provide strong empirical support for Thayer’s ideas of iridescence as



camouflage, they do not address the mechanisms – that is, the inherent characteristics of iridescent surfaces that enable iridescence’s camouflaging effect. Thayer suggested that colour (particularly the changeable nature of iridescent surfaces) was important. Conversely, or perhaps in addition, Kjernsmo et al. (2020) suggested that specular reflectance is important. In their experiments, although iridescent targets survived best, there was no significant difference in the survival of iridescent and black targets under both avian and human predation. Since these targets did not share any spectral characteristics and were only similar in their levels of gloss, specular reflectance was suspected to have an important impact. Specular reflectance is a form of gloss that is characterised by bright white highlights that appear across a surface (Franklin & Ospina-Rozo, 2021), and it has been hypothesised to have disruptive-like effects. The investigation presented henceforth aimed to explore and understand the mechanisms of iridescence as camouflage. The experiment that follows was heavily inspired by Kjernsmo et al. (2020), using a near-identical, but-expanded, method that was devised to specifically investigate the relative contributions of colour and gloss in maximising the camouflaging effect of iridescent surfaces.

## **2 | Exploring the mechanism(s) of iridescence as camouflage.**

### **2.1 | Introduction**

Iridescence is a taxonomically widespread form of structural colouration that tends to be characterised by bright, vibrant and rainbow-like hues (Doucet & Meadows, 2009; White, 2018), often showing blueshift, whereby wavelengths become increasingly short-wave with deviations in viewing angle (Vigneron et al., 2006). Although there are three structural mechanisms that can produce iridescent colouration (Kinoshita, 2008; Seago et al., 2009), the most common in nature is the multilayer reflector (Seago et al., 2009), which is responsible for – among others – the iridescence seen in many beetles (Seago et al., 2009; Yoshioka et al., 2012) and butterflies (Vukusic et al., 2001). Because iridescence is so taxonomically widespread, it has many hypothesised biological functions (Meadows et al., 2009), including species recognition (e.g., Rutowski, 1977), age identification (e.g., Papke, Kemp & Rutowski, 2007), sex identification (e.g., Lim, Land & Li, 2007), mate choice (e.g., Kemp, 2008) and thermoregulation (e.g., Heilman & Miaoulis, 1994; Biró et al., 2003).

Camouflage is another – albeit somewhat counter-intuitive – function of iridescence that was first suggested by Abbott Thayer in the early Twentieth Century (Thayer, 1909). Widespread among Metazoa, camouflage describes the various strategies that animals use to avoid being detected or recognised by other animals (Endler, 1991; Stevens & Merilaita, 2009a; Ruxton et al., 2018; Cuthill, 2019). Thayer explained that iridescence allows animals to “appear dissolved into many depths and distances”, describing it as “one of the prime factors of disguise” (Thayer, 1909). According to Thayer’s statements, both background matching – in which animals have colours and patterns that match those in their background environments (Merilaita & Stevens, 2011) – and disruptive colouration – in which colours and patterns intersecting salient features of an animal, such as the body outline, disrupt the true edges of features and generate false edges (Stevens & Merilaita, 2009b) – may be particularly important when considering the role of iridescence as camouflage. Until recently, Thayer’s ideas lacked empirical support, but iridescence is now known to provide effective camouflage (Kjernsmo et al., 2020). However, exactly how iridescence provides camouflage remains unclear. Thayer (1909) believed that iridescent surfaces achieved camouflage through their colour, while Kjernsmo et al. (2020) suggested that specular reflectance might be an important factor. Specular reflectance – one of five forms of gloss (Franklin & Ospina-Rozo, 2021) – is characterised by bright white highlights that appear across a surface. It has been suggested that this appearance may have disruptive effects, and that this might enhance the camouflaging effect of iridescent surfaces. Based on these ideas, one could hypothesise that a combination of iridescent colouration and gloss would provide the most effective camouflage.

In this investigation, the survival of artificial beetle-like targets under natural avian predation was monitored. The aim of the research was to start exploring the mechanisms behind iridescence as camouflage, with a particular focus on separating the relative contributions of target colour and target gloss.

## 2.2 | Methods

This study followed a similar experimental procedure to Kjernsmo et al. (2020), albeit with some modifications and expansion to investigate the effects of both target colour and gloss, and any possible interactions with background colour and gloss, on survival. The experiment followed a 2x5 factorial design, which allowed all possible combinations of target colour (iridescent; ‘static rainbow’; green; blue; black) and target gloss (glossy; matt) to be

investigated, with natural variation in background colour and gloss recorded as unmanipulated covariates.

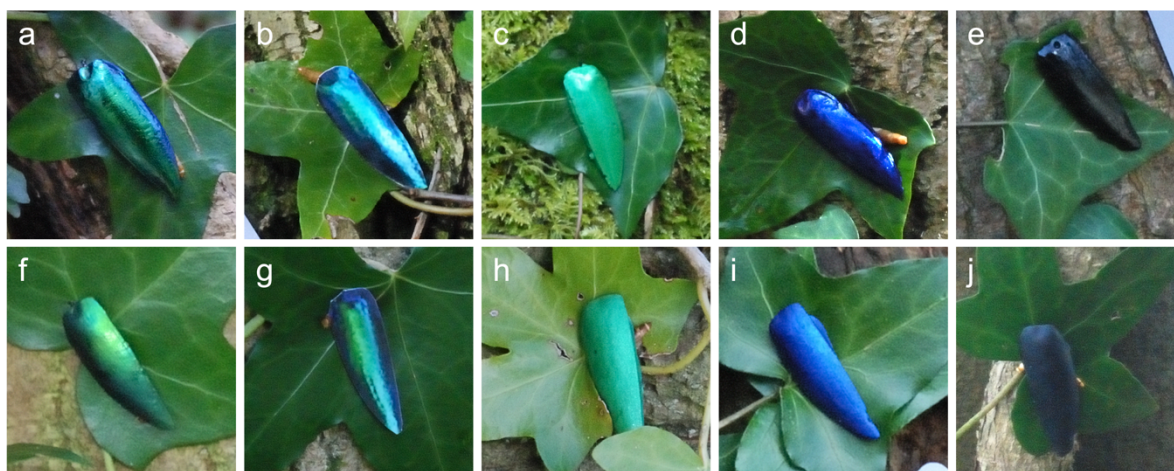
### 2.2.1 | Target Production

Targets were produced using a mixture of real and artificial elytra of an Asiatic jewel beetle (*Sternocera aequisignata*; Fig. 2.1). Real elytra were used for the iridescent targets as natural iridescence would be almost impossible to replicate artificially in a realistic way; the four non-iridescent control targets were artificially created. Green, blue and black targets were created from 2-Ton Epoxy resin (Devcon, ITW Performance Polymers, Shannon, County Clare, Ireland). A 50:50 mixture of resin and hardener (6.5 g each) was mixed with 150 mg of black pigment (L. Cornelissen & Son, London, UK) and poured into elytra-shaped moulds. The elytra-shaped moulds had been created by gently pressing real elytra into Elite HD+ Light Body silicone dental putty (Zhermack, Badia Polesine, Italy) to produce negative impressions. Several elytra were used to create a variety of differently sized targets, accommodating for the morphological variation seen in wild beetle populations. Nail varnishes were used to paint the artificial targets, as selected by Kjernsmo et al. (2020) to match the reflectance peaks of the main colours observed when viewing the iridescent target at different angles. Green targets were painted with two nail varnishes ('163 Metallic Green', Kleancolor, Santa Fe Springs, USA; 'Peacock Green', N°7, The Boots Company PLC, UK), mixed in a 50:50 ratio. Blue and black targets were each painted with a single nail varnish ('661 Ocean Blue' (Maybelline, New York, USA) and 'Blackjack2' (Collection, LF Beauty, UK), respectively). All three targets received two coats of nail varnish. Although Kjernsmo et al. (2020) created a purple target, purple is only seen in the real beetle from extreme viewing angles, and – in addition – the difference in survival between this and the blue target was relatively small, so the purple target was omitted from this study. The 'static rainbow' (SR) targets were created to separate the effect of multiple colours *per se* from the angular change in colour exhibited by iridescence. To create the SR targets, a selection of real beetle elytra was photographed from directly above under natural lighting using a Nikon D90 DSLR camera (Nikon Corporation, Tokyo, Japan). An X-Rite ColorChecker Passport (X-Rite, Grand Rapids, Michigan, USA) was included in each photograph so that they could be calibrated. Photographs were printed onto photographic paper (Epson Premium Glossy Photo Paper S042155), using an Epson SureColor SC-P600 (Seiko Epson Corporation, Suwa, Nagano, Japan), ensuring that the size of the printed beetles matched the size of the real beetles. The printed beetles were carefully cut and then shaped around a plastic pipette tip to give a slightly rounded appearance akin to the real beetles. To be able to pin targets to vegetation in the field experiments, drawing pins were stuck to the backs of all targets. For the green, blue and

black targets, these were embedded into the target itself while the resin was still malleable; for the iridescent and SR targets, these were stuck using a few small drops of 2-Ton Epoxy resin (50:50 mix of resin and hardener, with added pigment, as before). All targets were given a single layer of transparent nail varnish ('SuperStay 3D Gel Effect', Maybelline, New York, USA) to control for any differences in olfactory cues and to limit the possibility of targets exhibiting UV reflectance signals. Finally, targets were sprayed with three layers of one of two types of fixative (Professional Gloss Varnish / Professional Matt Varnish, Windsor & Newton, London) so that half the targets had a glossy and half a matt surface appearance.

## 2.2.2 | Field Experiments

The experiment was a randomised block design, with each of the 10 experimental blocks conducted in a different area of Leigh Woods National Nature Reserve, North Somerset, UK (51°27'20.7"N 2°38'28.9"W) between March and April 2020. Within each block, consisting of a ca. 1 km path, 10 replicates of each of the 10 treatments were randomly assigned to substrates. The beetle-like targets were pinned on English ivy (*Hedera helix*) leaves against tree trunks, roots, or plant shoots (Fig. 2.1), and their survival over a 96-hour period was monitored. Although Kjærnsmo et al. (2020) pinned their targets to various plant species, English ivy shows substantial variation in glossiness (Fig. 2.2), allowing us to eliminate possible plant-species effects on predation rates. The artificial prey targets consisted of two parts: an inedible elytron and an edible frozen-then-thawed mealworm (*Tenebrio molitor*), which was pinned beneath the elytron. After picking a suitable leaf between ground level and a height of ~2 metres, a target was selected at random, by drawing it blindly from a well-mixed bag, and pinned to the leaf. After pinning, the targets were checked at 24-hour intervals (24, 48, 72, and 96 hours) for signs of avian predation. Avian predation was inferred from the partial or full consumption of the mealworm (and provided that the inedible elytron was still pinned to the leaf). If a target had been dislodged, or showed signs of spider or slug predation (hollow exoskeleton or slime trails, respectively), it was considered predated-but-censored (see below). Predated targets were collected when found, along with the leaves they had been pinned to. Any remaining targets after 96 hours were also collected (along with their leaves). When the leaves were collected, they were labelled, using a permanent black marker pen, with a code that corresponded to the target, and placed in a plastic bag for subsequent measurement.



**Figure 2.1** Artificial beetle-like targets pinned to English ivy (*Hedera helix*) leaves. From left to right, colour treatments are: iridescent; static rainbow; green; blue; black. Targets in images *a – e* have a glossy surface appearance; targets in images *f – j* have a matt surface appearance.

### 2.2.2.1 | Gloss Measurements and Colour Analysis

Leaf gloss measurements were made in GlossTools v2.1 using a Zehnter ZGM 1120.268 glossmeter (Zehntner Testing Instruments, Sissach, Switzerland). Although the glossmeter measures specular light reflectance at three angles (20°, 60° and 85°), measurements were only taken from the 60° angle because this is particularly suitable for surfaces with small sizes (Whitney et al., 2012). Five measurements were taken from each leaf (avoiding veins) so that an average reading could be calculated. Leaves were kept completely flat when taking measurements. The glossmeter was calibrated using the included black polished glass standard (refractive index 1,567, defined as 100 gloss units) before any measurements were made and the 'gloss units' recorded are gloss relative to that standard. All measurements were saved in Excel files, which were combined in R (v. 4.0.0; R Core Team, 2020), using the 'readxl' package (Wickham & Bryan, 2019) to load the Excel files.

A Nikon D80 DSLR camera (Nikon Corporation, Japan) was used to photograph the leaves. All leaves were photographed alongside an X-Rite ColorChecker Passport (X-Rite, Grand Rapids, Michigan, USA) so that the photographs could be calibrated. All photographs were taken from directly above, under natural lighting. Photograph calibrations (linearisation and white-point balancing) were performed using a custom program written by I.C.Cuthill in MATLAB, following Stevens et al. (2007). Then, RGB colour values for a well-illuminated point on each leaf and the grey ColorChecker square were determined from pixel coordinates obtained in R (v. 4.0.0; R Core Team, 2020) using the 'tiff' package to read in photographs (Urbanek, 2013a). Data were mapped to both human and avian colour spaces, based on blue

tit (*Cyanistes caeruleus*) cone spectral sensitivities (Hart et al., 2000), these being typical of the woodland passerines seen in Leigh Woods. The latter include, besides blue tits, great tits (*Parus major*), wren (*Troglodytes troglodytes*), chaffinch (*Fringilla coelebs*), dunnoek (*Prunella modularis*), long-tailed tit (*Aegithalos caudatus*), chiffchaff (*Phylloscopus collybita*, towards the end of the study period) and, near the woodland's edge, house sparrow (*Passer domesticus*). The avian colour space did not include the ultraviolet cone's calculated photon catches because neither the ivy backgrounds nor the targets reflected UV (the varnish used blocked any such reflections; Kjærsmo et al., 2020). The Euclidean distance between the 3D coordinate of the leaf and the mean of the target, as specified by the photon catches of the shortwave-, mediumwave- and longwave-sensitive cones in a 'woodland shade' illuminant (Endler, 1993; Maia et al., 2019) was used as a measure of colour contrast.

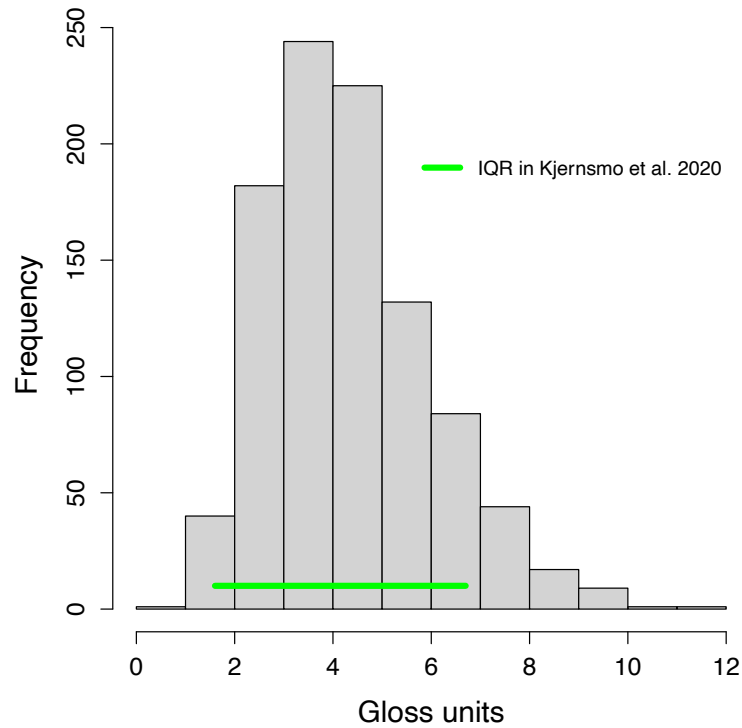
### 2.2.3 | Statistical Analyses

All statistical analyses were performed using R (v. 4.0.0; R Core Team, 2020). The main survival analysis used the 'coxme' package (Therneau, 2020a) to produce mixed-effects Cox regression models. Unlike standard Cox models which treat all factors as fixed effects and limit the generalisability of the results, using mixed-effects models allowed 'Block' to be considered as a random effect so that the results could be generalised to all possible blocks in Leigh Woods. Target gloss, target colour, leaf gloss and colour distance were the four fixed effects in the Cox regression models. Sequential simplification based on non-significance of terms, starting with the highest-order interactions, was used to identify a minimally adequate model that retained only the significant factors and, for significant interactions, their component main effects (Crawley, 2012). Survival plots based on the data from the survival analysis were produced using the 'survival' package (Therneau, 2020b). Post-hoc Tukey contrasts comparing the different target colour treatments were performed using the 'multcomp' package (Hothorn, Bretz & Westfall, 2008). Additional packages installed for use during the analyses included 'png' (for reading in PNG images; Urbanek, 2013b), 'grid' (for attaching images to figures; R Core Team), and 'car' (which has the useful 'recode' function; Fox & Weisberg, 2019).

## 2.3 | Results

Before analysing the data, the repeatability of the leaf gloss data was calculated. The intra-class correlation coefficient of 0.836 shows that leaf gloss can be measured reliably, justifying its inclusion as a factor in the analysis. Kjærsmo et al. (2020) included leaf gloss in their

secondary analysis and showed that it had a significant effect on target survivability. Since there is more variation in background glossiness in the present study than in Kjærnsmo et al. (Fig. 2.2), its inclusion in the analysis is important.



**Figure 2.2** Variation in glossiness (recorded in gloss units) of English ivy (*Hedera helix*) leaves against which beetle-like targets were pinned. The inter-quartile range (IQR) of leaf glossiness recorded in Kjærnsmo et al. (2020) is indicated by the solid green line (note: in that study, English ivy was one of various plant species against which beetle targets were pinned).

In the avian predation experiment, 73.4% of beetle targets showed evidence of avian predation; the remaining 26.6% of targets were classed as censored in the survival analysis, including two that were eaten by slugs, two that were eaten by spiders and 48 that survived until the end of the 96 h experimental period. In order to compare multiple models, the sample sizes had to be equal. As such, a small percentage of the data (2%) had to be excluded from the analysis to account for targets missing data on leaf gloss (0.3%), colour (0.6%) or both (1.1%). Terms were removed sequentially from the models until the minimally adequate model was identified, which retained only the main effects of leaf gloss (Table 2.1;  $\chi^2 = 11.53$ ; df = 1;  $p < 0.001$ ), target gloss ( $\chi^2 = 9.08$ ; df = 1;  $p = 0.003$ ) and target colour ( $\chi^2 = 125.51$ ; df = 4;  $p < 0.001$ ).

**Table 2.1** Sequential simplification (Crawley, 2012) of multiple mixed-effects Cox regression models was used to identify a minimally adequate model that retained all the significant terms in a survival analysis of beetle-like targets under avian predation. Leaf gloss, target gloss and target colour are significant terms, so model 11 is the minimally adequate model; all other models are presented to show the sequence of simplification.

Model no.	$\chi^2$	d.f.	p	Variable(s)
1	3.22	4	0.521	Target colour*Target gloss*Leaf gloss*Colour distance
2	2.27	4	0.686	Target colour*Target gloss*Colour distance
3	1.63	4	0.802	Target colour*Target gloss*Leaf gloss
4	3.96	4	0.411	Target colour*Leaf gloss*Colour distance
5	1.77	1	0.184	Target gloss*Leaf gloss*Colour distance
6	0.38	1	0.537	Target gloss*Colour distance
7	1.39	1	0.238	Leaf gloss*Colour distance
8	1.27	4	0.866	Target colour*Colour distance
9	1.76	4	0.780	Target colour*Target gloss
10	2.58	4	0.630	Target colour*Leaf gloss
11	3.71	1	0.054	Target gloss*Leaf gloss
12	11.53	1	<0.001	Leaf gloss
13	9.08	1	0.003	Target gloss
14	125.51	4	<0.001	Target colour

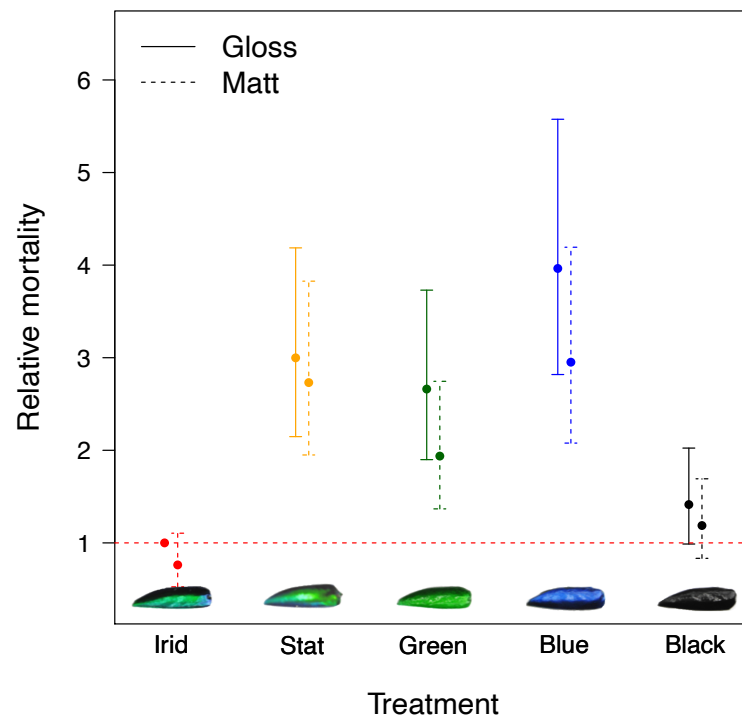
**Table 2.2** Pairwise comparisons of iridescent treatment to four other colour treatments (static rainbow; green; blue; black) using Tukey contrasts showed that iridescent targets survived significantly better than the other colours. P values are presented in the upper right-hand corner; z values are presented in the lower left-hand corner. The z scores have been calculated by subtracting the survival of the row colour from that of the column colour, such that a positive z-score indicates that the column survived better than the row treatment in the pairwise comparison.

	Iridescent	Static	Green	Blue	Black
Iridescent	–	<0.001	<0.001	<0.001	0.023
Static	9.34	–	0.248	0.528	<0.001
Green	7.43	-2.03	–	0.011	<0.001
Blue	9.40	1.56	3.23	–	<0.001
Black	3.00	-6.60	-4.60	-7.11	–

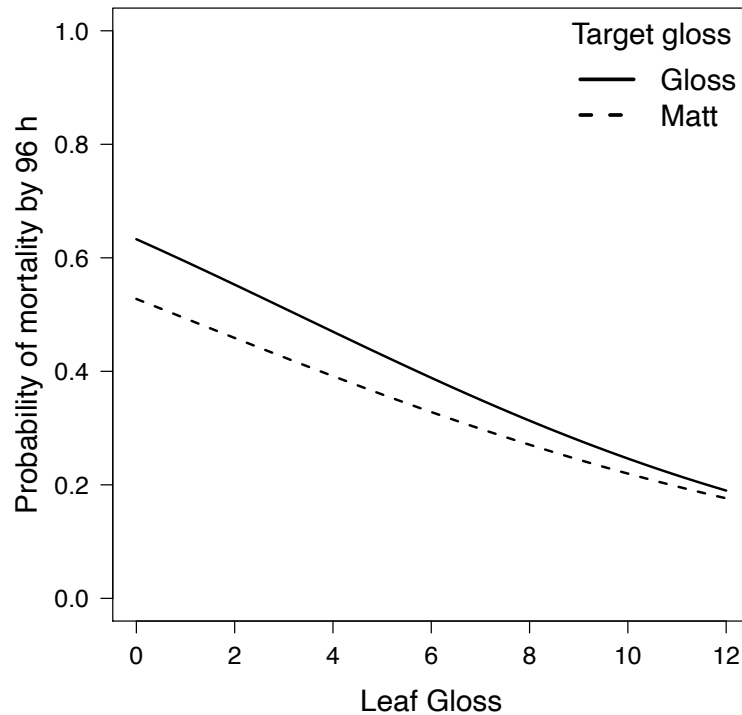
Targets survived significantly better on glossier leaves than on less-glossy leaves, and matt targets survived significantly better than glossy targets (Table 2.1; Fig. 2.3). Although the target gloss\*leaf gloss interaction was not quite significant (Table 2.1;  $p = 0.054$ ), the trend was for a greater difference in survival between matt and glossy targets on matt than on glossy leaves (Fig. 2.4). Target colour was also significant, pairwise comparisons of the iridescent treatment to all other colour treatments showing that the iridescent targets survived significantly better than each of the four other target colours (Table 2.2). The lack of interaction



between colour and any other factor suggests that colour had a similar effect on target survival regardless of target glossiness (Fig. 2.3). Of the other treatments, black survived significantly better than blue, green or static rainbow, and green survived better than blue. The survival can be summarised as iridescent > black > green = static rainbow > = blue, where green survived significantly better than blue, and where there was no significant difference in survival between static rainbow and blue.



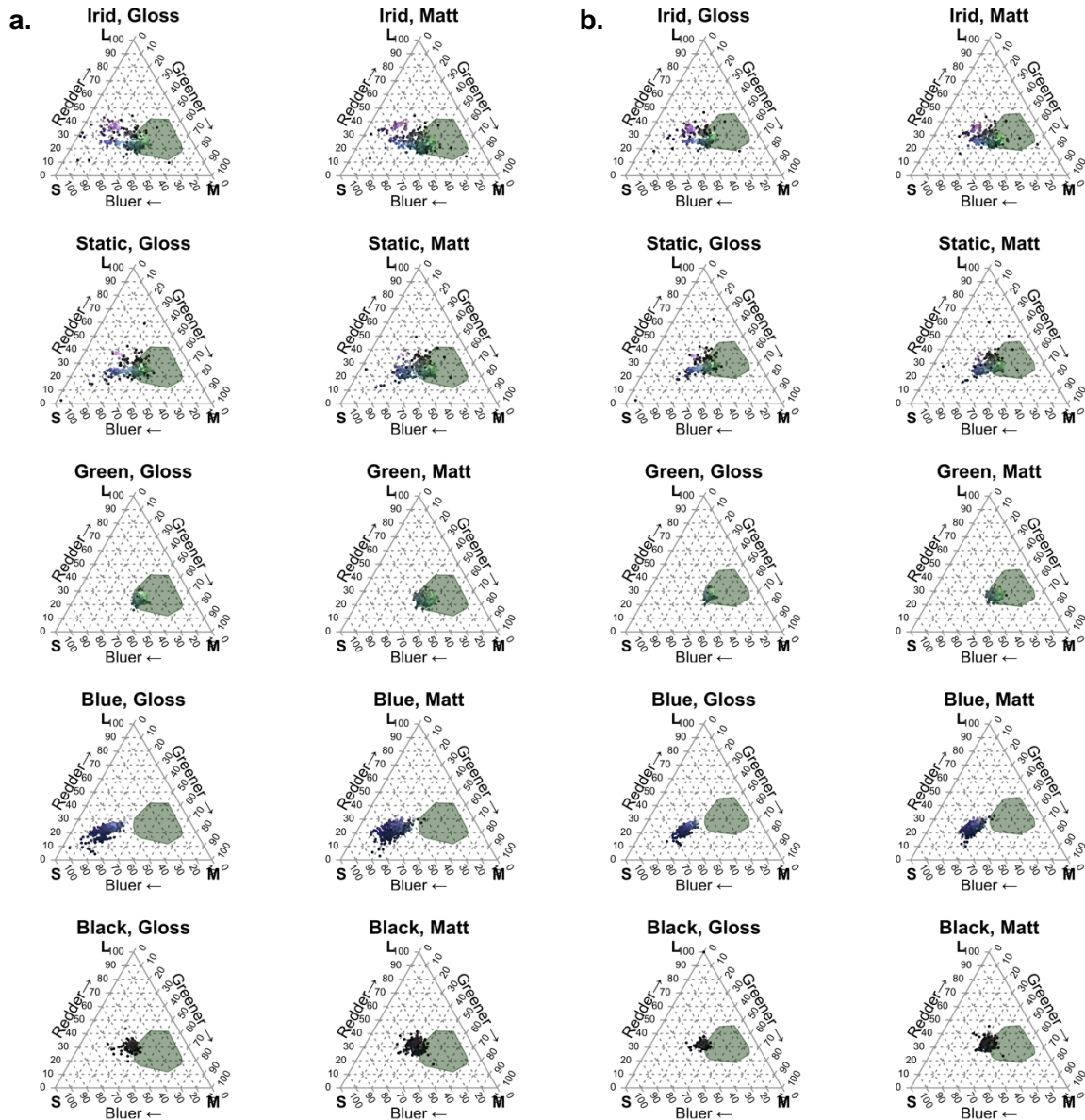
**Figure 2.3** Odds ratios ( $\pm 95\%$  confidence intervals) showing relative mortality of five colour treatments (iridescent; static rainbow; green; blue; black) under avian predation. Odds ratios were obtained from a mixed-effects Cox regression model. All colour treatments are compared to the glossy iridescent treatment. Glossy targets are indicated by solid 95%-confidence-interval lines; matt targets are indicated by dashed interval lines.



**Figure 2.4** Odds ratios showing the probability of mortality by 96 h for glossy (solid line) and matt (dashed line) targets on leaves of increasing glossiness (measured in gloss units), under avian predation. Odds ratios were obtained from a mixed-effects Cox regression model.

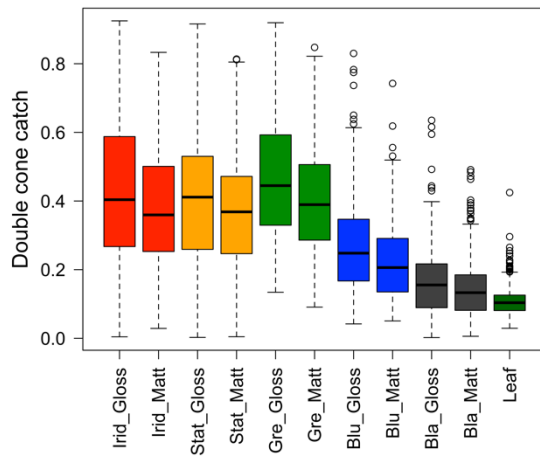
Additional analyses explored the visual differences between targets and their backgrounds in qualitative and descriptive ways. Maxwell triangles were produced to map the colours into avian (Fig. 2.5.a) and human (Fig. 2.5.b) colour space, using the R package ‘ternary’ (Smith, 2017). Although there is some overlap, the general pattern is that most background colours are different from target colours, which fall elsewhere in the colour space; the colours of targets and backgrounds are easily discriminable. The same pattern of differentiation is seen when comparing the luminance of targets and backgrounds, where targets are lighter than leaves in both avian (Fig. 2.6.a) and human (Fig. 2.6.b) vision. To confirm these qualitative conclusions, Support Vector Machines were used to classify colours as from target or leaf, for each treatment separately. ‘SVMs’ are a machine-learning tool for classification that allows non-linear boundaries between two classes of points in a feature space (see, e.g., Lantz, 2013; Barnett et al., 2018). Here, the feature space is colour as defined by three variables: the cone photon catches. To do this, half the targets/leaves for each treatment were randomly selected, using R’s ‘sample’ function, as training data for models fitted using the R package e1071 (Meyer et al., 2019), and then tested on the other half of the data. Receiver Operating Characteristic (ROC) curves were produced from these models (Fig. 2.7), to show the trade-off between correctly classifying targets (at the expense of falsely classifying leaves as targets) and correctly classifying leaves (at the expense of falsely classifying targets as

leaves). Using the area under the ROC curve as a summary measure of classification accuracy (where 0.5 is random and 1 is perfect), they confirm conclusions from qualitative inspection of the Maxwell triangles: targets and leaves are easily discriminable based on colour alone, with all areas-under-curve at least 0.96, for bird or human vision. The conclusions are similar using hue only, ignoring luminance (Fig. 2.7.a), or using both hue and luminance (Fig. 2.7.b).

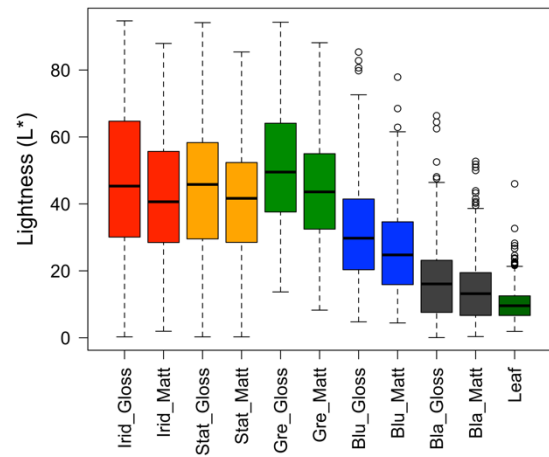


**Figure 2.5** Maxwell triangles for all colour/gloss treatment combinations. These show how the colours of beetle-like targets (coloured dots) and English ivy (*Hedera helix*) leaves (green shaded area) map into avian (a) and human (b) colour space. The three axes show the percentage of photon capture by short-wave (S), medium-wave (M) and long-wave (L) cone cells.

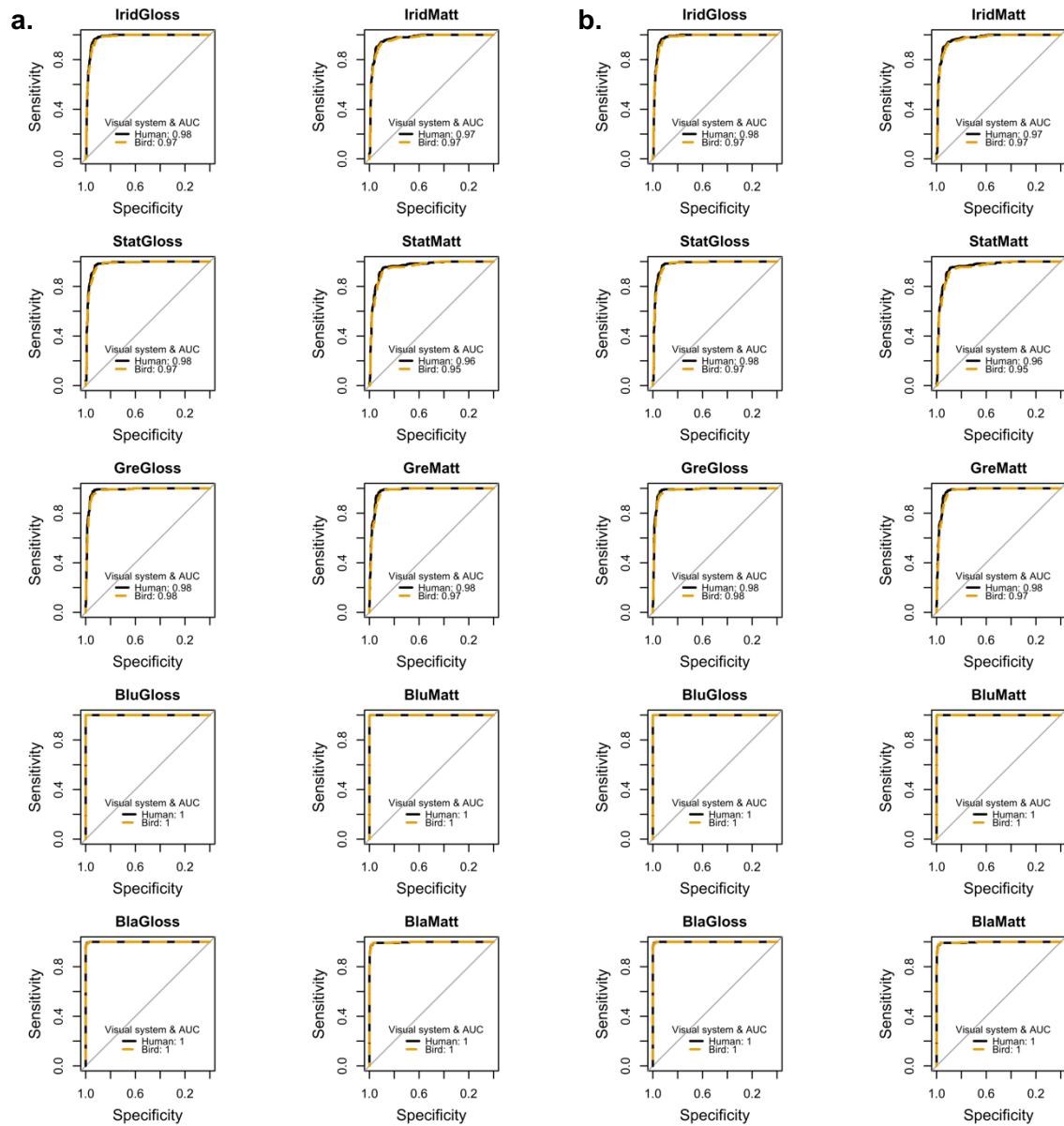
a.



b.



**Figure 2.6** Luminance of beetle-like targets and English ivy (*Hedera helix*) leaves in both avian (a.) and human (b.) colour vision. Luminance in avian vision is plotted as double cone catch; luminance in human vision is plotted as lightness in the  $L^*a^*b^*$  colour space (CIE, 1976). Thick lines represent the median value; boxes represent upper and lower quartiles (inter-quartile range); whiskers represent maximum and minimum values. Outliers are presented as hollow circles.



**Figure 2.7** Receiver operating characteristic (ROC) curves showing sensitivity of avian (yellow lines) and human (blue lines) visual systems to the differences between all colour/gloss treatment combinations of beetle-like targets and English ivy (*Hedera helix*) leaves. Targets and backgrounds are easily discriminable, regardless of whether colour alone (a) or colour and luminance (b) are considered.

## 2.4 | Discussion

The main aim of this research was to start exploring the mechanisms behind iridescence as camouflage. The results suggest that colour is the most important aspect of camouflaging iridescence, with iridescent targets surviving significantly better than all other colour treatments. The survival can be summarised as iridescent > black > green = static rainbow > = blue. Interestingly, although iridescent targets survived significantly better than black targets,

black still seemed to survive surprisingly well. Perhaps black targets were misclassified by predators as being shadows, holes, faeces, or – though perhaps unlikely – diseased leaves, and so tended to be ignored. Although not the most important aspect of camouflaging iridescence, target gloss still had a significant impact on survival, with matt targets surviving significantly better than glossy targets. Finally, all targets survived significantly better on glossier leaves than on less-glossy leaves. In a broader sense, the results of this investigation contribute to a widening literature on camouflaging iridescence, supporting conclusions from previous research that have shown that biological iridescence can function as a particularly effective form of camouflage (Pike, 2015; Kjernsmo et al., 2018; Kjernsmo et al., 2020).

#### 2.4.1 | THE IMPORTANCE OF COLOUR

Writing over 100 years ago, Abbott Thayer suggested that iridescence provides concealment because iridescent colours make species “appear dissolved into many depths and distances” (Thayer, 1909). Now, a century later, the results of this study prove that Thayer was right: it is indeed the colour aspect of iridescence that provides its camouflaging effect. However, the exact mechanism(s) by which iridescent colours provide camouflage remains somewhat speculative. There may be some background matching. Many iridescent insects, including the *Sternocera aequisignata* jewel beetle elytra used in this study, appear green from a range of angles (Sun, Bhushan & Tong, 2013), a hue that is commonly associated with typical background vegetation (Endler, 1993). Since background matching requires similarities in the colours and patterns of targets and their backgrounds (Endler, 1984; Merilaita & Stevens, 2011; Cuthill, 2019), it is easy to see how the green hues of iridescent surfaces could provide camouflage through background matching, and correlational evidence suggests that this might indeed be true for some species. DeSilva et al. (2005) describe how adult manuka beetles (*Pyronota festiva*) are found on the green leaves of manuka plants (*Leptospermum scoparium*). The adults’ iridescent colouration is composed predominantly of green hues, so the possibility of background matching may be implicit from their habitat. However, a lack of spectral measurements makes it impossible to quantify the visual similarities (if indeed there are any) of manuka beetles and manuka leaves; the assumption of colour matching is based solely upon qualitative assessment under human vision. In the present investigation, colour and luminance information for both targets and their backgrounds were calculated. However, analyses of my data (Fig. 2.5.; Fig. 2.6.; Fig. 2.7.) suggested that the beetles and their backgrounds should be easily discriminable in both avian and human colour space. For background matching to be successful, there need to be similarities in the visual properties of targets and backgrounds, such that the two are (mostly) indistinguishable, so the fact that the beetles and their backgrounds are spectrally and visually different suggests that background

matching may not be a suitable explanation for iridescence as camouflage (at the very least, in relation to the targets used in this study). That said, colour and luminance measurements were extracted from single photographs per target, which may not fully or accurately characterise the iridescent targets – the angle of photography, for example, might have influenced the colour values obtained, such that the conclusion that targets and backgrounds should be easily discriminable (at least in the case of iridescent targets) may be flawed. In addition, limitations in visual systems mean that the visual similarities between targets and backgrounds need not be exact for some degree of background matching to be achieved, so iridescence as background matching cannot be conclusively excluded. Regardless, most iridescent surfaces – including those of the beetles in this study – exhibit blueshift, whereby reflected wavelengths become increasingly short-wave with deviations in viewing angle (Vigneron et al., 2006; Stuart-Fox et al., 2021), so any background matching is only going to be effective at specific viewing angles. However, this could actually be advantageous. When viewed from above, the *S. aequisignata* targets appear green against the English ivy (*Hedera helix*) background leaves, possibly gaining their survival advantages through background matching. As the viewing angle deviates sideways, the target colours become increasingly short-wave, which no longer provide background matching against the ivy leaves. But, from such extreme viewing angles, the leaves that form the immediate background may not be visible, so the blue-shifted surfaces might actually be providing matching against backgrounds beyond the leaves to which the targets are attached. In other words, iridescent surfaces might provide some degree of background matching camouflage against different backgrounds at different viewing angles. Ultimately, a background matching explanation is undermined by the fact that the iridescent targets survived significantly better than the green control targets, which should theoretically have achieved background matching themselves.

Since – for the reasons discussed – angle-variable background matching does not seem to provide a satisfactory explanation, perhaps disruptive colouration is a better and simpler explanation of iridescence as camouflage. Disruptive colouration is the type of camouflage that arises through the interruption of edge and body features by contrasting colours and patterns cut across those features (Cott, 1940; Cuthill et al., 2005; Stevens & Merilaita, 2009b). Iridescent colour ‘patches’ occur across surfaces in such ways that they could very feasibly act to disrupt the outline or create false edges. This, combined with the colour-shifting nature of iridescent surfaces, could create some sort of ‘dynamic’ disruptive colouration that is effective independent of viewing angle, with the shifting colours introducing disruption and false edges. Kjærnsmo et al. (2018) demonstrated that multilayer iridescence interferes with object recognition in bumblebees (*Bombus terrestris*), suggesting that iridescence could indeed enable camouflage through disruptive colouration. However, this might not necessarily

explain the results found in this study, because the visual systems of bees and birds differ such that their perception is different (Whitney et al., 2020). Disruptive colouration is often thought of as an enhanced version of background matching as it typically combines background colours with features that interfere with edge detection ('differential blending', Cott, 1940; Stevens et al., 2006; Fraser et al., 2007). Perhaps iridescence as camouflage is enabled through both background matching and disruptive mechanisms, depending on the angle at which the surface is being observed. Perhaps, for example, when viewed from above, the *S. aequisignata* jewel beetle targets used in this study are concealed through background matching, but then as the observer moves and the viewing angle deviates sideways, the shift in colour disrupts the outline and generates false edges across the surface, providing concealment through disruptive colouration. Although perhaps rather removed from biological realism, Bora (2017), using modelling, suggested that colour (in comparison to grey-scale images) can indeed interfere with and hinder accurate edge detection.

Because iridescence and its properties are so different from the pigmentary colours normally associated with camouflage, attempting to categorise it according to traditional classifications of camouflage mechanisms may be misguided. Instead, it is best to explain iridescence as camouflage using a signal-to-noise ratio (SNR) framework. SNR compares the amount of relevant information (the signal) to the amount of irrelevant information (the noise) in a visual scene. For camouflage to be successful, it must act to reduce the SNR (Merilaita, Scott-Samuel & Cuthill, 2017; Galloway et al., 2020). Perhaps iridescent colouration provides a mechanism for reducing the SNR through the generation of chromatic and achromatic noise. Because iridescence is taxonomically widespread (Doucet & Meadows, 2009), it has many signalling functions, including species recognition (e.g., Rutowski, 1977), age identification (e.g., Papke, Kemp & Rutowski, 2007) and mate choice (e.g., Kemp, 2008). But for iridescence to function effectively as a signal, it must be combined with structures and/or behaviours that enhance its detectability and reliability (Stuart-Fox et al., 2021). Without such detectability-enhancing mechanisms, iridescent signals are unstable, and the iridescent colouration likely generates noise. The *S. aequisignata* jewel beetle targets used in this study have, on account of them being manipulated and non-living, neither structures nor behaviours that enhance the detectability of their iridescent colouration, so their high survivability suggests that camouflage may indeed be the result of iridescence generating noise, potentially masking any useful signals, such as those of the body outline. This is important in the context of edge detection through achromatic cues at the body boundary because iridescence perhaps generates sufficient noise to interfere with edge cues such that effective edge recognition is either impaired or impossible (most likely the former, as other factors, such as lighting, may affect iridescence's noise-inducing effectiveness). Since many biological signals involve colour



(Cuthill et al., 2017), it may seem somewhat unusual that iridescent colours could generate noise. However, previous research comparing visual search in dichromatic and trichromatic humans has suggested that colour might actually be a key source of noise (Morgan, Adam & Mollon, 1992; Saito et al., 2006). In the case of iridescence, it might not even be the colours themselves that produce noise, but rather the changeability of the colours: the fact that the perceived hue changes with viewing angle. In this study, as in Kjærsmo et al. (2020), the 'static rainbow' targets were created to control for the changeability of colours seen in the iridescent targets. Since the iridescent targets survived significantly better than the 'static rainbow' targets, it is not simply the colours themselves that are important, it is the fact that there is changeability. This changeability makes iridescent surfaces unstable, preventing reliable signals being transmitted, and potentially generating noise (or at the very least, reducing the signal among background noise). Iridescent colours tend to be bright and assumedly salient (Doucet & Meadows, 2009), yet signal instability might make it difficult for animals to attend to colour cues, or easier for useful colour cues to be missed. Pike (2015) found that iridescence interferes with targeting of moving targets in Japanese quail, concluding that this is the result of colour changeability making it harder to track iridescent surfaces. In the case of a foraging animal hunting static prey, when an iridescent surface is noticed, the animal may be initially attracted to the hue that is detectable at their current viewing angle. But as they move closer to investigate, the viewing angle and thus the perceived hue changes, meaning the surface no longer appears as expected, potentially becoming undetectable (though perhaps only temporarily). This might be a particularly plausible scenario, given that many predators are themselves trying to avoid predation and are thus constantly alert to potential threats (Lima & Dill, 1990). It may be that it takes just a simple predator-checking saccade away from prey for an iridescent target to 'disappear' following an initial detection. In a COVID-free world, human search experiments using relatively new, field-portable, eye-tracking technology will enable this very possibility to be explored. At the very least, a colour-changing iridescent surface might elicit hesitancy responses in predators, allowing prey to escape or 'disappear'. Another effect of colour changeability on predators could be that the changeable iridescent surfaces prevent search image formation. Search images are short-term perceptual filters that predators develop through frequent prey encounters and subsequent learning that enable fast identification of specific prey features (Tinbergen, 1960; Pietrewicz & Kamil, 1979; Langley, 1996; Troscianko, Skelhorn & Stevens, 2018), and in avian predators, learning seems to be heavily based on colour (Kazemi et al., 2014; Gamberale-Stille et al., 2018; Lawrence & Noonan, 2018; Corral-Lopez et al., 2020). Because iridescent surfaces are unstable, showing colour changeability, and noisy, they might interfere with learning, such that search image formation is not possible. That said, an argument could be made that colour changeability is sufficiently distinctive and memorable that it could be

learned, potentially allowing some predators to overcome the effectiveness of iridescent camouflage.

Finally, the role of aposematism, however unlikely, must be briefly addressed. Aposematism involves conspicuous signals that warn predators of prey defences (Poulton, 1890; Rojas, Nokelainen & Valkonen, 2017; Caro & Ruxton, 2019), and it has previously been suggested that iridescence might have a role in aposematism (e.g., Bowers & Larin, 1989; Schultz, 2001). While the results of this investigation do not directly reject aposematism as a reason for higher survival in iridescent prey, there are several important reasons why it is unlikely. *Sternocera aequisignata* is found across much of Southern Asia (Ek-Amnuay, 2008), so it and its iridescent colours are unfamiliar to avian predators in the UK. This means that there will never have been any opportunities for specific learnt avoidance to develop, and so any aposematic effect would have to be through generalisation from a similar, co-occurring, chemically defended iridescent insect. Candidate species common in North Somerset include the musk beetle (*Aromia moschata*) and rose chafer (*Cetonia aurata*), but the former is found in wetlands not woodlands, and the latter is not known to be chemically defended (it appears in the diet of at least some birds; Hebda, Kata & Zmihorski, 2019). An argument could be made that unfamiliarity means an increased likelihood of avoidance through neophobia or dietary conservatism (Marples & Kelly, 1999); however, all my prey treatments were novel as such, and previous research has shown that human ‘predators’ struggle to locate iridescent prey in the same environment as my experiment was carried out (Kjernsmo et al., 2020). So, an effect on detectability rather than acceptability is the parsimonious explanation for my results. Ultimately, although iridescence could function as an aposematic signal or induce neophobia in some systems, there is little evidence for iridescence as aposematism or neophobia in the context of my study.

#### 2.4.2 | THE ROLE OF TARGET GLOSS

Target gloss had a significant impact on survival, with matt targets surviving significantly better than glossy targets. Kjernsmo et al. (2020) suggested the opposite – that gloss could have a prominent role in camouflaging iridescence – so this result may be somewhat surprising. It has been suggested – and often assumed – that specular gloss might have disruptive effects (Franklin & Ospina-Rozo, 2021). Specular gloss is characterised by highlights of high reflectance that appear white. The way that these highlights appear across the body surface, both within the body and at the edge, could theoretically create false edges and edge disruption. In addition, specular surfaces often have subtle mirror-like reflective qualities and have been suggested to, in some cases, potentially provide perfect background matching

through mirroring of surrounding hues and patterns (Thomas, Seago & Robacker, 2007). However, no empirical evidence exists for either hypothesis, and the results of this study strongly suggest that gloss is actually somewhat costly in the context of concealment. Previous research may help to explain the apparent costs of gloss. It has been suggested that gloss can increase the salience of three-dimensional (3D) body cues (Adams & Elder, 2014; Chadwick & Kentridge, 2015). When the target and/or the observer changes position relative to the other, the position of specular highlights across a glossy surface shifts, following the contours of the body, revealing – and potentially drawing attention to – the 3D shape (Chadwick & Kentridge, 2015). Since 3D cues are important in visual search (Penacchio et al., 2015; Penacchio, Lovell & Harris, 2018; Cuthill et al., 2016), this might enhance the process of recognition. Another possibility is that gloss can influence the perceived brightness of a surface. Across a glossy surface, there is contrast between specular and diffuse components, such that glossy surfaces often appear visually darker than matt surfaces (Chadwick & Kentridge, 2015). Toscani, Valsecchi & Gegenfurtner (2017) assessed humans searching for glossy and matt targets, finding that humans essentially ignore specular reflections and perceive glossy surfaces as being darker. Depending on the visual conditions, perceiving glossy surfaces as being darker might make them appear sufficiently different from the background that they become more detectable.

Despite the apparent costs of gloss, many iridescent insects (and indeed many non-iridescent species too) have a glossy surface appearance. Clearly, at least in the sort of environment investigated in this study (mixed deciduous woodland), for iridescence to be maximally effective as camouflage, it should be combined with a matt surface appearance. That many species are glossy is interesting as it suggests that there may be other benefits to a glossy surface appearance. While it is indeed true (within the context of the background and environmental conditions studied here) that matt iridescence enhances camouflage, concealment is not the only component of fitness; there are many other life-history considerations, and all animals face trade-offs. Perhaps the best explanation for the abundance of gloss is that it arises from an important non-visual function. For instance, gloss is very often the result of surface structures that maximise hydrophobicity (Franklin & Ospina-Rozo, 2021). In addition to offering protection through water-repellence (Wang et al., 2020), hydrophobicity may provide a mechanism for efficient water collection, which would be particularly useful in arid terrestrial habitats or environments where water is scarcely available. In the Namib Desert, the head-stander beetle (*Onymacris unguicularis*) ascends dunes to collect water from wind-blown fog (Hamilton & Seely, 1976; Seely, Henschel & Hamilton, 2005). Their surface microstructure allows water droplets carried within the fog to condense along the body and be directed towards the mouthparts (Guadarrama-Cetina et al., 2014).

The beetles have a glossy surface appearance, and this appears to be due to the properties of their surface microstructure. This example illustrates how gloss might not have a visual purpose, instead being the result of a vital-but-nonvisual function, and why it is not necessarily sensible to maximise concealment, when there are many other important processes that require energetic attention. That colour is the most important factor in determining the success of camouflaging iridescence is interesting in that it suggests that glossiness might ultimately be irrelevant to camouflage, and insects can still achieve effective concealment irrespective of whether they have a glossy or matt surface appearance.

#### 2.4.3 | THE EFFECT OF BACKGROUND GLOSS

Background gloss influenced survival, with targets surviving significantly better on glossier than less-glossy leaves. This can be explained very simply using a SNR approach. There have been suggestions that glossy backgrounds are associated with background complexity and high levels of background noise (Franklin & Ospina-Rozo, 2021). Since camouflage works by reducing the SNR (Merilaita, Scott-Samuel & Cuthill, 2017; Galloway et al., 2020), increased background noise through gloss may provide a sufficient change in SNR to provide targets with some degree of concealment irrespective of their own spectral or visual characteristics. Interestingly, while matt targets survived significantly better than glossy targets, the differences in survival between the two tended to be greater on matt than on glossy leaves. Although the interaction was not significant, this could be further evidence that background gloss generates noise enough to help better conceal prey. If matt surfaces generated noise, glossy targets would probably survive satisfactorily on matt leaves. But they did not, though glossy targets did survive relatively well on glossy leaves, and this is presumably the result of benefits provided by the background rather than (for reasons discussed above) target gloss. The fact that background gloss influences the success of concealment has important implications for camouflage. Many species show habitat choice, whereby a preference for backgrounds that maximise camouflage is observed (e.g., Kang et al., 2012, 2013a, 2013b; Stevens et al., 2017). Perhaps some species may select backgrounds that maximise the amount of gloss-induced noise and thus camouflage. Consideration should also be given to the fact that background glossiness may vary temporally, with factors such as weather (in particular, rainfall) potentially influencing the level of specularity across a surface.

#### 2.4.4 | CONCLUDING REMARKS

While this study has produced reliable data and results, it is not without its limitations. During target production, the fixatives did not adhere particularly well to all the targets, with the real

jewel beetle elytra being particularly problematic. This meant that some of the targets lost sections of their glossy or matt covering either during pinning or over the course of an experimental block. The resultant damaged surfaces appeared 'blotchy', with patches differing (at least to the human eye) in both their colour and gloss. The effect was more noticeable on matt than glossy targets, and some ended up with glossy patches where the fixative had been scratched away. However, this is unlikely to have had much of an impact on the investigation because damaged targets were – as much as possible – replaced during pinning so that they would not be included in the study. In addition, targets were continually produced throughout the experimental period so that any that became damaged (or lost) could be replaced at the start of the next block. A larger problem with the fixatives is the possibility that the two types (glossy and matt) differed in terms of their odours, which – if true – could have influenced the predation rates observed. However, in addition to being virtually impossible to control, the likelihood that this occurred is very slim, especially as – based on my olfactory senses – neither seemed discernibly different from the other. The biggest limitation to the conclusions that can be drawn from the investigation (in terms of the mechanism by which survival was enhanced) was the lack of human search experiments. Ideally, human search experiments would have been performed to corroborate the results of the avian predation experiment, and to allow definitive conclusions about the mechanism by which iridescence affected survival. However, the absence of these experiments is not critical because the results of this study align completely with those of Kjærsmo et al. (2020). Indeed, despite these potential limitations, the main findings (at least those that have previously been studied) are consistent with existing research (e.g., Pike, 2015; Kjærsmo et al., 2020).

The results of this study provide an insight into the mechanisms behind iridescence as camouflage. Colour – specifically, the changeability of hue and/or brightness observed across iridescent surfaces – is the most important factor in iridescence as camouflage. Although there are many possible explanations for this, using a SNR framework to explain camouflaging iridescence is perhaps best in that it does not exclude traditional descriptions of camouflage, but rather includes them through the acknowledgement that successful camouflage could theoretically be achieved through any mechanism that reduces the SNR. Exactly how iridescence reduces the SNR (i.e., which mechanism(s) is/are at play) may depend entirely on the context in which it is perceived. In addition to target colour, lowered target gloss has a significant beneficial impact on target survivability, but this is not as important in maximising concealment as the colour itself. The success of camouflaging iridescence is strongly influenced by the level of background glossiness, with all targets surviving significantly better on glossier than less-glossy leaves, again consistent with a SNR interpretation.

Although this investigation provides some advancement in our understanding of iridescence as camouflage, there is still much to be researched. Iridescent signals are strongly dependent on illumination conditions, with directional, as opposed to diffuse, lighting maximising the iridescent effect (Stuart-Fox et al., 2021). In addition, different habitats tend to be associated with different light environments (Endler, 1993), and this might limit the range of hues that are even perceptible across an iridescent surface. Since the changeability of colour seems to be the most important factor in iridescence in camouflage, these could have important implications for the effectiveness of concealment under different conditions. Understanding how different illumination conditions influence iridescence as camouflage would provide a valuable insight into the generality of iridescence as a form of camouflage, and whether it can reliably conceal species in a multitude of scenarios; many species possess iridescent colouration, but – given its perceptual variability – can it be a consistently successful form of camouflage under all lighting conditions? Iridescence as camouflage seems to work because the colour changeability introduces visual noise, which reduces the SNR. Any change in illumination conditions or the context of perception may influence the level of noise generated by iridescence, and thus its success as camouflage. It would be very interesting, therefore, to investigate how different conditions affect iridescence as camouflage through the exploration of visual noise and its implications on successful concealment. Of course, this would first require a method for confirming and subsequently quantifying iridescent noise to be devised, but metrics of ‘visual clutter’ based on salience would be a promising place to start (Rosenholtz et al., 2005; Rosenholtz, Li & Nakano, 2007; Xiao & Cuthill, 2016). Finally, the influence of the background on iridescence as camouflage should be explored in detail. Since targets survive significantly better against glossy than less-glossy backgrounds, there may be potential for species to choose the backgrounds against which they live. It would be interesting to explore whether iridescent species tend to occur against glossy backgrounds more often than expected by chance, either through active choice or because selection only favours iridescence-as-camouflage in such environments. The influence of background gloss on camouflage extends beyond iridescence too – perhaps species with all sorts of colour patterns prefer (and achieve better concealment against) glossy backgrounds due to the noise-inducing effects of gloss. It is likely that background gloss is influenced by environmental factors, such as rainfall, which may temporarily alter the level of specularly within a background. Some species may have evolved to exploit this, be it behaviourally (through background choice) or developmentally. For instance, many insects emerge from pupation to coincide with specific seasonal events (Tauber, Tauber & Masaki, 1986) – perhaps the emergence of adults of some species is correlated with seasonal periods of wet weather, in which background gloss may be highest, and during which camouflage (and thus survival) can be maximised.

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