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Rowe, Zeke W

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**How background complexity impairs
target detection and can mitigate
poor camouflage.**

MSc(R) thesis by Zeke W Rowe.

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of MSc(R) in the Faculty of Biological Sciences, School of Biological Sciences, submitted October 2021.

Word Count: 17999

Abstract

Avoiding detection through camouflage is often key to survival. However, an animal's appearance is not the only factor affecting conspicuousness: background complexity also alters detectability. This has been experimentally demonstrated for both artificially patterned backgrounds in the lab and natural backgrounds in the wild, but only for targets that already match the background well. Therefore, we do not know whether habitats of high visual complexity provide concealment to even relatively poorly-camouflaged animals. By measuring predation rates of artificial prey which differed in their degrees of background matching to tree bark, whilst also measuring the natural background complexity, I was able to explore this issue. Higher background orientation clutter (edges with varying orientation) reduced the detectability of all but the poorest background matching camouflaged treatments; higher background luminance clutter (varying achromatic lightness) reduced average mortality for all treatments. Another gap in our knowledge is the precise mechanism in which visual complexity affects target detectability. By using artificial grey-scale targets and backgrounds, I was able to isolate and manipulate the normally covarying factors which comprise 'complexity' in natural habitats. By doing this, I showed that reduced detection by humans is not explained by greater information content (entropy) or higher variance in the background's features (feature congestion) per se, but instead by reduced signal-to-noise ratio in the perceptual dimension that potentially distinguishes target from background. This combination of field and laboratory experiments suggests that, although highly salient targets will always be easily detected, even relatively poor camouflage (in terms of background matching) can be mitigated by a more complex background. This has implications for both camouflage evolution and habitat preferences, and opens questions into when the term complexity should be used, and how viewers learn the characteristics of the background.

Keywords: background complexity, camouflage, detectability, visual search, protective coloration, visual clutter.

Acknowledgements

I would like to give an enormous thanks to my primary supervisor, Professor Innes Cuthill, for his incredible expertise and support throughout all aspects of this MSc, and to my secondary supervisor, Professor Nick Scott-Samuel, for his help and advice, especially regarding experimental design. Thank you also to Daniel Austin, Nicol Chippington, William Flynn, Finn Starkey and Edward Wightman for their assistance in the field, to all the participants of the laboratory experiments, and to my parents, girlfriend and close friends for their continued moral support.

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: Zeke W Rowe DATE: 20/10/2021

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1. Literature Review

1.1 The importance of concealment

Predation is one of the largest selection pressures that many animals face and this has resulted in a vast arsenal of defensive strategies. Using a common framework found within the military, the survivability onion, we are able to peel away the potential layers of such defences and home in on specifics (Figure 1.1). Normally used within the context of warfare, the survivability onion is utilised for the vital task of reducing the likelihood of a lethal strike against a target. It does this by using the following requirements, don't be: there, detected, identified, acquired, engaged, hit, penetrated, or affected. The comparisons within biology to the defences of prey are directly related to when a prey item has an 'encounter situation' with a potential predator (Lima and Dill, 1990, Edmunds, 1974, Cuthill, 2019). The best way is to simply stay away from danger, either from selecting habitats with low predation or remaining vigilant and moving away from danger when it arrives. If this cannot be done, however, the second tier is employed, which is to remain concealed to the threat either by remaining out of the predator's vision (or other sensory modalities) by straightforwardly hiding or by remaining undetected and/or unrecognised via crypsis. Due to its effectiveness, this second tier is commonly used within the animal kingdom.

The survivability onion

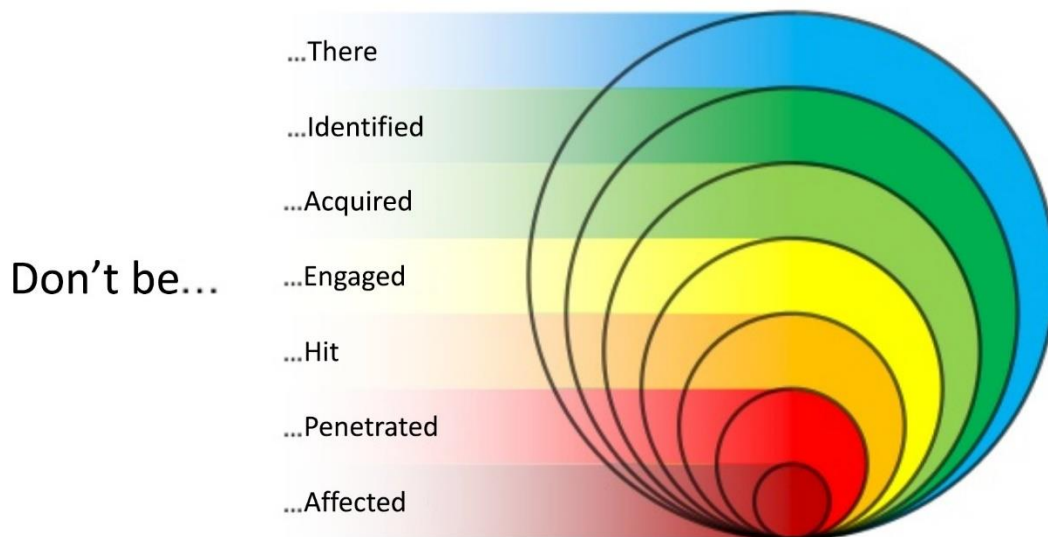


Figure 1.1 - The Survivability Onion. Slide 17, 13 January 2015 Enduring Challenge Briefings for the Centre for Defence Enterprise, UK Ministry of Defence © Crown Copyright 2015. Reproduced under the terms of the Open Government Licence <http://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/>.

When prey are visually selected by predators, they often evolve colouration and patterning which is able to deceive their attackers, fulfilling the first tier of the onion (Stevens, 2015). One of the most common of these strategies is camouflage, whereby the probability of detection and recognition is decreased due to the colours and patterns of the animal (Cuthill, 2019, Stevens and Merilaita, 2009a). The study of camouflage has a long history, with it being first recognised as an important example within the animal kingdom for illustrating the workings of natural selection and adaptation (Darwin, 1859, Wallace, 1877, Wallace, 1889, Poulton, 1890). Surprisingly the precise mechanisms by which camouflage is able to conceal from viewers were not examined until 1896 and 1940, when the artist Abbot Thayer and zoologist Hugh Cott published their significant works, using art to connect the functions within biology (Thayer, 1896, Cott, 1940). After a significant gap in studying crypsis, there was an attempt to look at defensive colouration through the eyes of predator perception (Endler, 1980, Endler, 1981, Endler, 1978). This revived enthusiasm for the study of camouflage once more, with the past couple of decades finally yielding empirical evidence for these theoretical mechanisms, with most gaining quantitative support (Ruxton et al., 2018).

Remaining concealed may be incredibly useful for prey species to increase their survival from predator's hunting attempts, and thus have a higher fitness, but it is also utilised in many other aspects of an animal's life. Predation is not the only case where being concealed is evolutionarily beneficial. The reverse can be true, where a predator is able to remain visually undetected to its prey item and therefore increases its chances of a successful hunt (Pembury Smith and Ruxton, 2020), either by remaining concealed whilst static and allowing the prey to haplessly wander into its striking distance or by pursuing the prey without initiating a vigilance response (just picture a lion stalking its prey). This is achieved by crypsis, masquerade (the idiom 'a wolf in sheep's clothing' comes to mind) or mimicry. Being undetected can also be useful when attempting to gain mating opportunities, particularly when there is plenty of competition for the access to females and such access is well guarded. We see this in Australian giant cuttlefish (*Sepia apama*), where subordinate males mimic the female colouration and patterning so as to fly under the radar of the dominant male and gain access to the female; such a tactic is often referred to as 'sneak mating' (Stevens, 2016). Similarly, it has been well documented that individuals living in groups are often attacked and persecuted by more dominant members of the group and, therefore, for these submissive individuals it is better to be inconspicuous so as to not be targeted.

1.1.1 The different mechanisms of camouflage

Although we can class all of the above examples as camouflage, this is really an umbrella term for colour patterns that exploit a series of perceptual mechanisms. Perhaps the most obvious of these is where an animal's pattern and colouration matches that of the background which it is seen against, somewhat obviously called 'background matching' camouflage (Merilaita and Stevens, 2011).

Consistent with the importance of matching the background, research has showcased that there are correlations between the colouration of species to their naturally evolved habitats (Merilaita and Stevens, 2011), suggesting that there may be some potential anti-predator benefit to this. Kang *et al.* (2012) even saw behavioural evidence that when moths land on bark they arrange their patterning to align with that of the backgrounds in such a way that reduces detection and increases matching (Webster *et al.*, 2009). Marshall *et al.* also demonstrated a similar behavioural effect that a lizard's choice of microhabitat aids its camouflage, showing that the animals naturally select backgrounds which better conceal themselves (Marshall *et al.*, 2016). Interestingly, species which have colour altering abilities are seen to adhere to the rules of background matching and change their own colour to become more concealed against new backgrounds (Duarte *et al.*, 2016, Duarte *et al.*, 2018, Josef *et al.*, 2015). Perhaps more convincingly however, in terms of a direct link to fitness, work done on the clutches of ground-nesting birds showed how local background-matching camouflage is a good predictor for survival, with the egg colour contrasts which better matched their backgrounds surviving a greater length of time (Troscianko *et al.*, 2016), showing there is indeed an anti-predator benefit to this phenomenon.

Background matching is not a failsafe strategy, however, with unaligned patterning between target and background, shadowing of the animal's shape, and the outline of the target all being important key cues for detection. This has allowed another mechanism to evolve - disruptive colouration (Thayer, 1909). One useful formal definition is as follows: 'a set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object's, or part of an object's true outline and shape' (Stevens and Merilaita, 2009b). Cuthill *et al.* provided empirical support for this mechanism by manipulating 'moth-like' targets to have varying edge disruption, and by monitoring the wild avian predation it was found that indeed there is a benefit to survival to breaking up the outline (Cuthill *et al.*, 2005). Further work showed how the camouflage strategies used are habitat-dependent, with those shore crabs (*Carcinus maenas*) utilising disruptive colouration being more common in highly variable habitats whilst those in homogenous habitats had a higher level of background matching (Price *et al.*, 2019), demonstrating that which mechanism is selected for is contingent upon the features of the habitat which it is seen against.

Some distinct mechanisms work by simply enhancing the level of background matching in visually challenging scenes. By comparing landscape paintings to animal colouration, Thayer saw a trend where animals are 'darkest on those parts which tend to be most lighted by the sky's light, and vice versa' (Thayer, 1896). The phenomenon he was describing is now called countershading, possibly the most common colouration patterning. Two anti-predator functions to why such colouration occurs have been proposed (Kiltie, 1988, Rowland, 2009, Ruxton et al., 2004). First, that it improves background matching when viewed from below against a light background or from above against a dark background; such a situation can be found in the open oceans for example. The second, as originally described by Poulton (Poulton, 1890), is that this colouration limits the visual salience that self-cast shadows may cause (Allen et al., 2012, Cuthill et al., 2016, Penacchio et al., 2015)

You might be thinking the best form of camouflage is to be completely invisible; however, outside of science-fiction, this is impossible. Within nature, some animals have evolved the next best thing - to be transparent. This is ideal as allowing light to pass through you from the background means you are always able to match your background and therefore your background matching camouflage is no longer context-dependent on your background or behaviour. This is not foolproof however, as if the two media the light is passing through are not equal in refractive index there will be some refraction and reflection of light, a key cue to detection (Johnsen, 2001). Additionally, as many tissues have a structural orientation, this can cause light polarisation, resulting in a detectable contrast with the natural light (Shashar et al., 2000, Shashar et al., 1998, How et al., 2015). That said, even semi-transparency can be effective (Barnett et al., 2020).

If remaining undetected is impossible, it is best to disrupt the next stage of the cognitive process - recognition. Called 'special resemblance' by Poulton (1890), masquerade is the mimicry of inedible or unimportant items in the environment (Endler, 1981, Skelhorn et al., 2010b). This differs from Batesian mimics due to the behaviour and cognition of the receiver, as predators actively avoid mimics of aposematic prey items but are indifferent to those masquerading as unprofitable items (Skelhorn et al., 2010a). Studies on naïve domestic birds (*Gallus gallus domesticus*) have shown how for such a strategy to work, the predator needed to experience the object (a twig in this case) as unprofitable before they would show any latency or concern attacking the twig-mimicking caterpillars (Skelhorn et al., 2010b).

1.1.2 Signal-to-noise ratio

A key determinant of detectability is the signal-to-noise ratio (SNR) as it compares the content of useful information to detect a cue to the misleading or useless information (Merilaita et al., 2017, Galloway et al., 2020). The analogy here is that the target is the signal (i.e., something the perceiver

is trying to detect) and all factors impeding the detection of the signal is noise. Looking at some of the above examples, both background matching and disruptive colouration aim to minimise the signal to reduce the ratio, but disruptive colouration also increases noise through false edge signals (Merilaita et al., 2017). You may believe in the case of masquerade and mimicry that the signal is reduced, however this actually increases the noise due to the false but very salient features from the target. This is a very useful framework to demonstrate how the varying mechanisms of camouflage aids concealment and are exploited by animals. Although the SNR is not needed to be calculated in this thesis, it will be utilised throughout as a tool to further the clarity in which complexity can decrease detection.

1.2 Introduction to visual complexity

Complexity or ‘clutter’ is an important aspect of our day-to-day lives; for example, anecdotally when you are trying to search for your lost keys it is harder in a messy room than a tidy one. Clutter is defined as ‘the state in which excess items, or their representation or organization, lead to a degradation of performance at some task’ (Rosenholtz et al., 2007). Within human psychology many perceptual effects are increased by a higher level of ‘complexity’, with items which are in excess and disorganised able to cause crowding or so called ‘separation difficulty’, where objects which are presented away from the fovea have a reduced recognition by the presence of ‘flanking’ objects (Levi, 2008). Masking is also seen in such contexts with the target appearing to have reduced contrast, meaning its detectability is reduced (Legge and Foley, 1980). Even the limits of short-term memory can be reached due to visual clutter, not only increasing number of objects but also the object’s features (luminance, colour, and orientation), with the threshold higher for simple features over more complex ones (Miller, 1956, Alvarez and Cavanagh, 2004). It is therefore clearly important to take complexity into account when developing critical human displays, for example a pilot noticing a warning light on the display of an aeroplane. Such detrimental perceptual effects are not always the case with increasing clutter, however. Having ‘more items’ can sometimes increase visual clarity by being in a regular pattern, meaning you can easily predict the appearance of a neighbouring item from the target item. In such instances it can be easier, for example, to detect a trend where all items point to that trend or easy grouping with items of the same characteristics. More items therefore can assist the detection of any outlier characteristics of groups of trends. Humans have been shown to be able to determine the level of visual clutter in maps effectively, suggesting that they are able to perceive when a scene is complex (Rosenholtz et al., 2005).

When is a scene deemed as cluttered? How can you quantitatively measure complexity? Consider you are attempting to leave a note to yourself to remember to buy milk; instead of leaving it on the untidy and cluttered kitchen surfaces, you instead put it on the uncluttered cupboard door so it will draw your attention later. This example suggests that the level of visual complexity is connected to how easy it is to add an attention-drawing item to the scene. Rosenholtz has developed a model based on this idea, the Statistical Saliency Model (Rosenholtz, 1999, Rosenholtz, 2001a, Rosenholtz, 2001b), which indicates that the more difficult it is to add a new item to a scene which will be salient, the more complex the scene is visually. This is predicted by the scene's variance in three features: luminance, colour and edge orientation. This has led to a new metric being developed by Rosenholtz: feature congestion, a surprisingly simple measure of complexity which uses the local variation of luminance, colour and edge orientation to successfully measure complexity of any given scene (Rosenholtz et al., 2005).

A less perceptual and more mathematical metric of complexity is subband entropy. The more items which are grouped together, have similar characteristics or are aligned, the more 'organised' a scene becomes and therefore the less cluttered it appears. Entropy is how efficiently a scene can be coded either in the brain or a computer and still allow the image to retain all its features (Rosenholtz et al., 2007), so a more organised scene takes less computational power to process. Lower entropy would show a lower complexity, with feature repetitions and groupings shown as redundant and removed.

Previously there have been other attempts to quantify visual complexity. Information density, first coined the data-ink ratio by Tufte and Goodwill (1983), was a metric used within the field of information visualisation in an effort to show the optimal amount of information to present without making it perceptually difficult for the viewer to extract the information. With this in mind, Woodruff et al. looked into both the number of visible objects and the number of vertices as possible metrics for this (Woodruff et al., 1998). The digital electronics company Dynamic Logic did similar research looking into the number of 'elements' on a Web page, where a word, graphic or so-called 'interest area' were defined as an 'element' (Dynamic Logic, 2001; cited in Rosenholtz *et al.*, 2007). Even basic metrics such as the amount of ink on black and white maps have been suggested (Frank and Timpf, 1994). Such basic metrics have a multitude of problems and very few have been properly applied to real world scenarios. Of course the visual complexity of a background is affected on some level by the number of objects, graphic tokens or entries in source code of the display. Conversely the amount of plain space has been shown to have an effect on task performance whilst using maps (Phillips and Noyes, 1982) and a directory assistance search task (Springer, 1987). Nevertheless, within the directory assistance task it was shown that when aligned in columns, the task was easier and when reading maps, tasks became harder when the clutter was similar to the target of the task

(Phillips and Noyes, 1982). Edge density is also sparsely used within the literature in an attempt to measure clutter, which is defined as the ratio of number of edges in a particular image (Mack and Olivia, 2004), but has failed to produce reliable results (Rosenholtz et al., 2007). Even simply counting Web page 'elements' did not show a good alignment with clutter and advertisement effectiveness (Dynamic Logic, 2001; cited in Rosenholtz et al., 2007). We see on the other hand how both feature congestion and entropy can be good metrics for determining visual complexity (Rosenholtz et al., 2005, Rosenholtz *et al.*, 2007).

1.3 Background complexity and the evolution of camouflage

As previously mentioned, visual complexity has been seen to be detrimental to the perception of targets. However, how is this important to our understanding of the evolution of camouflage and an animal's behavioural ecology? To answer this question, a feedforward neural network which contained three-layers was used to examine how the visual complexity of the background affected the evolution of cryptic colouration in prey (Merilaita, 2003). By modelling the predator's visual processing based on vectors with eight cells, the virtual predator was able to detect samples of its environment as either prey or background. As the prey evolved, they became coloured to confuse this classification by the predator's selection; in short, they became more camouflaged.

Two features of the model were varied, one feature of the background and one of the prey. The first was that visual complexity varied in the background, controlled simply by the number of differing visual elements which were presented in the habitat. Such 'elements' were classed as items of the background's colour and pattern which consist of different colours or characteristics, such as stripes or spots for example. The complex habitat contained four of such features, whereas the simple habitat only three. This is a very loose version of 'complexity', with no exact metric and little control for the variation in these elements. The visual complexity here was designed to be at a smaller scale than the size of the predator's visual samples and therefore should not be confused with larger scaled heterogeneity (Bond and Kamil, 2006). When it came to create the eight-cell samples, one of the visual features was selected as the 'basal element', where each condition had two cells of this basal element but either had two cells of the three remaining elements in the complex condition, or three cells of the two remaining elements in the simple condition. The final varying feature in the model was the ability of the prey to evolve, either being able to evolve all the background characteristics unconstrained, or constrained to reproduce all but one of the elements. Once the model was run, ultimately the prey's fitness was measured by the output the network gave for that particular colour and pattern phenotype, with outputs which varied the most from the 'unity' having

the greatest fitness. As expected, this caused the prey to evolve towards greater crypsis in all four scenarios, becoming better background matching and having less predation (or in this case network outputs for prey decreasing). The prey continued to evolve until 200 generations had been produced or when predation was below the threshold value.

In every single condition in which the habitat was 'complex', the detectability of the evolved prey dipped below the threshold value in both constrained and unconstrained evolutionary conditions. In direct contrast, in the simple condition this only happened when the evolution of the prey was unconstrained. The threshold was only reached in the constrained evolution situation in 34% of the simulations. We can therefore see that evolutionary constraint in colouration and pattern had a much more damning effect in detectability by predations in the simple habitats versus the more complex ones, ultimately suggesting that it is harder to evolve camouflage in more simple habitats and perhaps that other protective colouration strategies will be utilised instead (Merilaita, 2003). A good analogy for this is the way you would analyse data with a two-way ANOVA, with two factors being the animal's colouration and the background colour. We think of camouflage as a two-way interaction in that the animal and the background need to match for concealment to be effective. However, this study has pointed out that there may be a 'main effect' of the background too, with background complexity providing concealment independent of animal colour.

Within this study, Merilaita suggests that the mechanism which causes this effect is the limited capacity of the predator's brain to process visual information (Dukas, 1998). This is a limitation which has been shown as a trade-off between search rate and detection rate in predators (Gendron and Staddon, 1983, Gendron, 1986). In this case if the brain's processing capacity is consistent then an increase in background visual complexity (a larger diversity of the visual information) makes visual search and detection harder. Therefore, even prey which have constrained and consequently imperfect crypsis will be less likely to be detected. There are two main benefits from using an artificial neural network: first it produces an effective and convenient way to study animal colouration evolution, as in other modelling methods colouration and crypsis are often entangled together and are confused; second, predators' brains and artificial neural networks (allegedly) work in very similar ways to process information, meaning that findings are applicable to nature.

1.4 Effects of visual complexity on detection in human search tasks

As previously discussed, there has been a multitude of attempts to test the effect of visual 'clutter' or complexity on human search and detection. In this section I will discuss the human perception studies which are most influential to further the understanding of camouflage evolution and behavioural ecology. By using humans as proxy 'predators', these studies assume that the general principles underlying cognition are similar to non-human predators to draw parallels into the natural world.

In 1989 Duncan and Humphreys proposed a new theory of visual search (Duncan and Humphreys, 1989), in contradiction to the commonly discussed Feature Integration Theory (Treisman and Gelade, 1980), which instead of seeing detection become more difficult between serial and parallel search (search attending to one stimulus at a time compared to multiple stimuli) or between feature and conjunction search tasks (where search tasks are achieved pre-attentively for a one-feature target compared to search which occurs with two or more features together and are identified serially), instead saw difficulty increase with an heightened similarity between targets and non-targets. Interestingly for this thesis, however, this work also parallels the effect of visual complexity on human search. When the participants were tasked with trying to find a target amongst the non-target 'distractors', the background diversity had an effect on the reaction time. The study showed the participants scenes with a target amongst non-targets or just non-targets, and asked participants to react when they detected whether the target was present or absent. The target was an upright L placed amongst other Ls rotated at 90°, with a varying degree of non-target homogeneity (greater homogeneity was displayed by all the distractors facing one way) (Figure 1.2). The results of the study showed that an increased heterogeneity of the non-target distractor Ls was a good predictor for a longer reaction time for the participant to detect the target. Such heterogeneity was a basic metric for visual complexity as although features such as luminance and colour contrasts remained the constant, there was an increased complexity in terms of the orientation of the letters and therefore gave a greater diversity in the background (Figure 1.2). This may suggest that human visual search is impeded by complexity; however it is rare that such basic and minimal scenes are used day-to-day in human life or that such simplicity would be found in nature.

(a) Homogeneous

(b) Heterogeneous

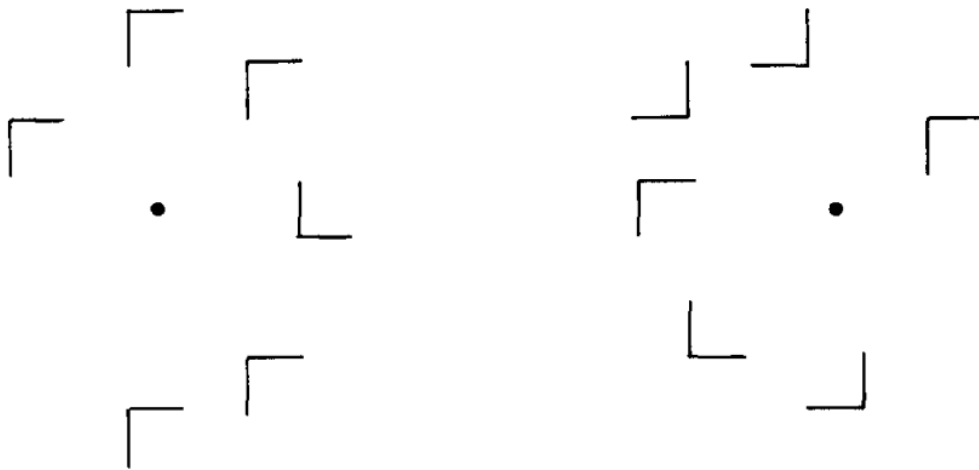


Figure 1.2 - The homogenous (a) and heterogenous (b) conditions of the search tasks in Duncan and Humphreys, 1989.

As Rosenholtz et al. began to develop Feature Congestion as a metric it was vital they tested the usefulness of this for human-perceived clutter. To begin with, they showed how humans are able to rank maps of the USA on which their perceived complexity correlated successfully to the ranks the maps were given when measured using Feature Congestion (which at the time only used colour and luminance contrast as measurements) (Rosenholtz et al., 2005). However, more extensive work needed to be done by collecting performance data on other more varied displays to solidify the use of Feature Congestion as a metric for visual 'clutter'. Two years later work which rectified this area of weakness was published (Rosenholtz et al., 2007), in which human participants were tasked with finding a single grey-scale Gabor patch (a sinewave convolved with a Gaussian) on coloured geographic maps of varying complexity as measured by Feature Congestion (this time including edge orientation into how complexity was measured). This was conducted on a computer screen and participants were tasked at either marking the target as present or absent. With the target being a Gabor instead of a something you might 'naturally' find on a map, this is advantageous as symbols or features found on a map will not have the same distinctiveness and therefore be less salient. This adds another layer of variance to the data whilst also being able to vary the target (scale, orientation, and phase) and maintain control over its appearance. The complexity was measured for each background before the target was added using the metrics of Feature Congestion, Entropy and Edge Density. Each metric was a good indicator for poorer reaction time in the human search, showing that a higher complexity was detrimental to detection.

A big difference between the metrics is their handling of colour variability, so to further separate the effects of the metrics on human search tasks, this same paper modified maps from the first experiment to reduce their colour variability (by either turning the map into grey-scale or by converting them to CIE Lab colour space and locking the a to b ratio to a consistent red-hue). Again, participants were told to search for a Gabor patch on these maps and to either say whether the target was present or not with the reaction time being recorded. The Feature Congestion metric of complexity, as predicted, showed that human search reaction time is greater when the map has a larger amount of colour variance, whereas both entropy and edge density showed no difference between the low and high colour variance maps.

Murali et al. began to research such effects in human search to explore ideas within camouflage evolution with biologically relevant backgrounds (Murali et al., 2021a). They wanted to see how visual complexity can alter the optimal camouflage of a species in the face of background heterogeneity. Participants were tasked with finding a target and 'attacking' it as quickly as possible by touching it on a touch-sensitive computer screen. The target was square-shaped and contained the same or similar features as the background it was viewed against. The backgrounds could be simple or complex, with the simple ones having solely basic shapes (quadrilaterals, circles and triangles) whilst the complex backgrounds had more complex shapes (stars, swirls and symbols). These backgrounds also varied in their heterogeneity by differing in their variance in both the size and colour of these features. These backgrounds were designed to mimic naturally occurring pebbles in shape and size but were still artificially produced. Again, as the previous studies have found, a higher visual complexity of the background was seen to be detrimental in 'attack' latency. However, the finding was novel in that this effect was only found when the target had some level of background matching. This was concluded as the targets which were generalists (matched all of the backgrounds but to a low level) had a higher attack latency than the specialist targets (matched one of the backgrounds perfectly) when seen against the background which had a higher complexity but was less heterogeneous. Contrastingly, specialists fared better than generalists in highly heterogeneous backgrounds, irrespective of complexity. When the target was completely non-matching to the background it is assumed to be too salient and is easy to detect and therefore is attacked even when against complex scenes. However, these results should be treated with caution, as element shape is only one of many ways to measure complexity, and it may be that it was simply the match to the average localised background luminance which drove the data, as this cofactor was not controlled for.

The effect of the complexity of natural backgrounds on detection of a unicoloured triangular target has been examined in humans (Xiao and Cuthill, 2016a) by taking photos of the target and their

localised background once placed on oak tree bark; the complexity was then able to be precisely measured using Feature Congestion and Entropy, two of the metrics discussed previously. The researchers took human participants along a roughly 1 km transect, giving them the task of detecting and pointing out the same unicoloured targets as the previous bird experiment in the same paper. Each participant was given a laser range finder to point to the target when they had found them, giving two detection variables: detection of the target, and its localisation (how close they were to the target to the nearest centimetre). They found that a higher background complexity did indeed impede detection of the targets. This effect of complexity on target detection was poorly predicted by the more abstract metric of entropy, but was more strongly related to the metric based on low-level vision feature congestion. In particular, the study showed that with a lower orientation clutter (less variation in the angle of edges) of the backgrounds, the target was detected at a greater distance. This gives us an insight into how complexity may be a factor in wild predation and search tasks involving natural complexity, in this case oak bark.

1.5 The effects of visual complexity in non-human search tasks

In natural environments, visual complexity can vary massively across both time and space. Therefore, it is sensible to assume that such complexity variations could produce important selection pressures on the way that animals conceal themselves and the way their visual systems are exploited. Such relationships were first examined in the laboratory by monitoring predation by blue tits (*Cyanistes caeruleus*) on artificially produced targets and backgrounds (Dimitrova et al., 2009). By examining the effects of having higher and lower contrast backgrounds (and therefore higher and lower luminance complexity) on effective search time, the study showed that targets either with a high or low contrast on a background with a higher contrast had a longer search time. This therefore potentially demonstrated how a higher background complexity can be detrimental to predation and visual search; however, with reference to the studies discussed above, it seems likely that just using the range of luminance variation alone as a metric for complexity is not sufficient. Studies then attempted to demonstrate this effect using the same method, but with a more quantitative form of background complexity. These series of experiments had two backgrounds against which the targets were viewed, being defined as simple or diverse (Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012). In both experiments, the backgrounds differed in the number of different shapes within the background, five for simple and eight for diverse (see Figure 1.3). Both backgrounds were identically coloured so colour background matching would be equal on each. With increasing shape number, the background complexity does not increase linearly due to the nature of the shapes used,

as they vary in the number of sides and angles. Again, these two studies saw that no matter what target was used on the backgrounds, a higher complexity was detrimental to the bird's success in searching for them. A similar study used density of elements as a metric of complexity instead of number of different element shapes (Dimitrova and Merilaita, 2014). Two backgrounds were used, a high density and a low density variant, with the colour background matching being equal on each treatment. They showed that no matter the target, a higher density background made the visual search task more difficult for the birds. All these studies fail to precisely measure complexity, either in terms of information content or perceptual clutter, and each has its own set of confounding factors, with each measure of complexity not controlling for the level of variance which may instead provide better concealment due to a higher chance of partial local background matching.

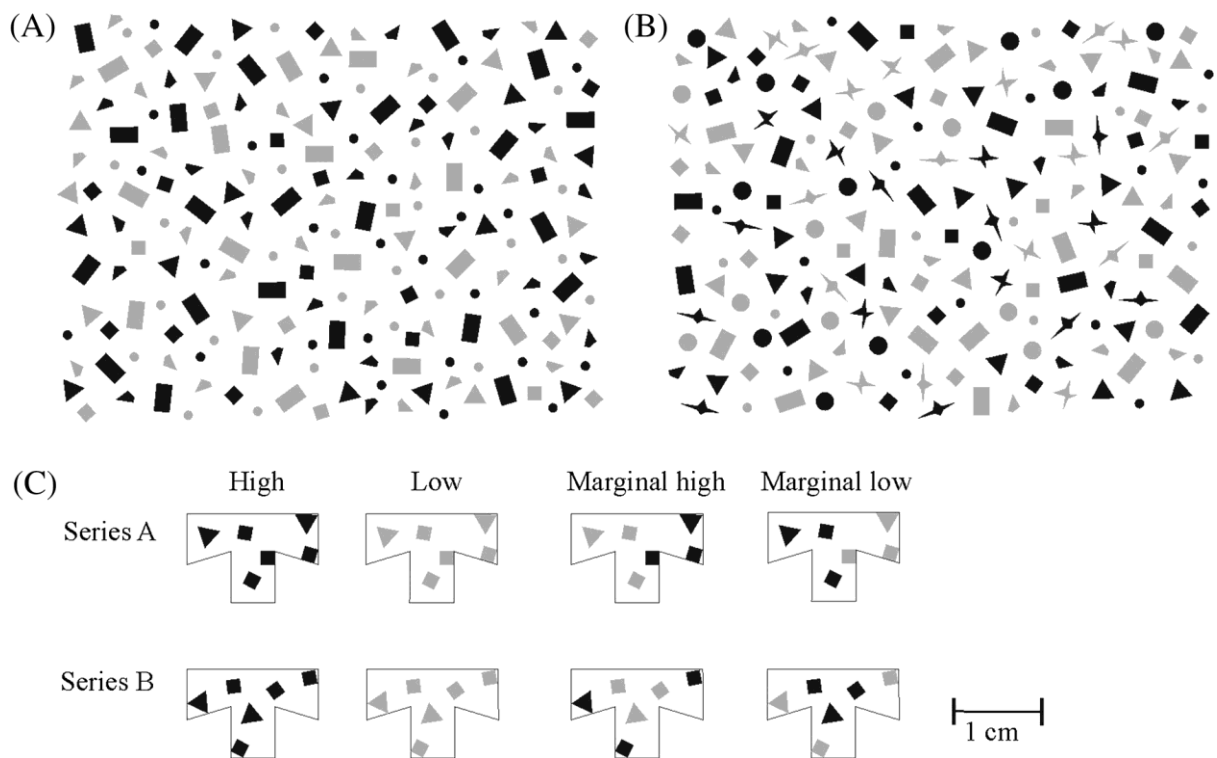


Figure 1.3 - The backgrounds and targets of Dimitrova and Merilaita (2010). As discussed, (A) – the simple background and (B) – the diverse background only differed in the number of the different shapes, 5 and 8 respectively. (C) The targets for both A and B with the differing contrasts.

Although these studies are convincing indications that there might be a detrimental effect of higher background complexity on detection, no natural backgrounds have been used and complexity has not been quantified directly, only using proxy measures such as element density and number. Work

by Xiao and Cuthill (2016) fills this gap by using a single type of background matching target placed on natural backgrounds and monitoring the wild avian predation on these targets. As previously mentioned, in relation to their assessment of target detection by humans, by taking photos of the target and their localised background once placed on oak tree bark, complexity was able to be precisely measured using Feature Congestion and Entropy, two of the metrics discussed previously. Now complexity has been precisely measured on natural backgrounds we can begin to confidently conclude that any effect seen has implications on the behaviour and the evolution of animals within the natural world. This study showed that predation was reduced by a higher complexity, but for only part of the perceived complexity which was measured. This may be due to the backgrounds used, as such bark is often lacking in high contrasts in luminance and colour, perhaps a different effect would be found against other backgrounds. Entropy was a much poorer predictor than Feature Congestion, and only one of the three components of Feature Congestion seemed important: edge orientation, with both colour and luminance having no additional predictive value (Figure 1.4).

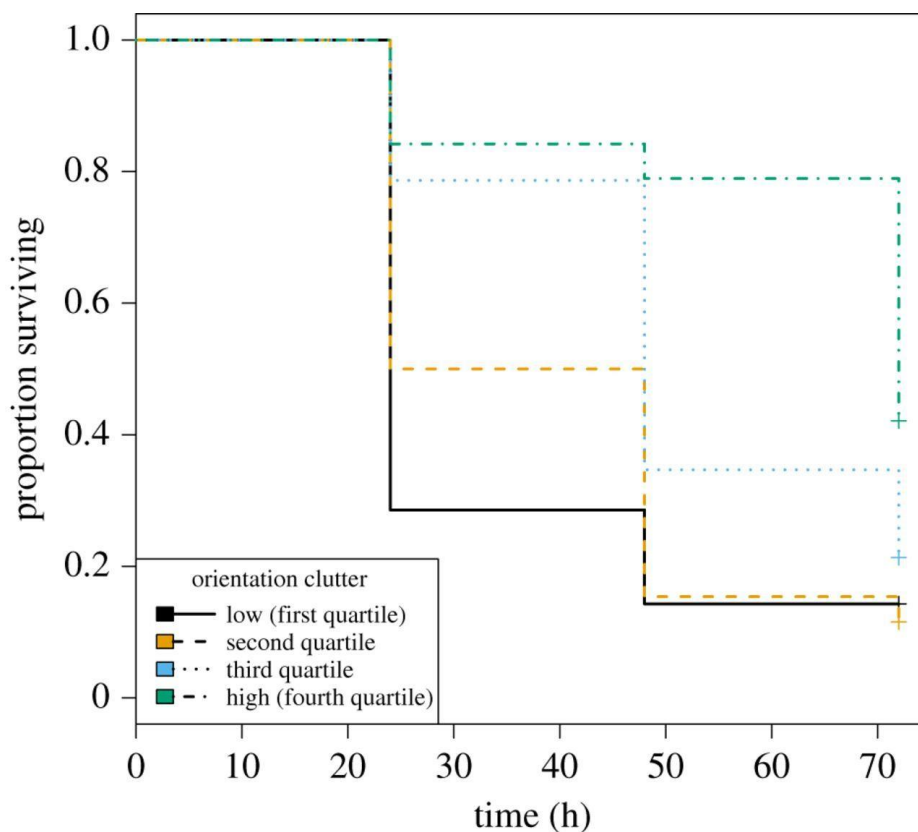


Figure 1.4 - The beneficial effect of orientation complexity on a target's survival from avian predation (figure reproduced from Xiao and Cuthill, 2016). For illustration purposes, orientation was

categorised into four approximately equal samples sizes from low to high; in the analyses it was treated as a continuous variable.

Complexity is not always as simple as being complex spatially but can also be complex temporally; i.e., complexity via motion (Cuthill et al., 2019). This is interesting as the actual content of the scene stays the same but complexity increases due to the motion of the features. This works to conceal in the same way, by increasing the visual noise of the background and therefore blanketing any signal the target is producing, reducing the SNR. By utilising domestic fowl chicks as proxy wild foragers, the effect of dappled light on search was examined by Matchette et al. (2019). Newly hatched naïve birds were taught to peck at simulated prey on a computer screen. Dappled light (spotted light which typically passes through gaps in leaves), produced either by a mirror ball or by computer simulation, was projected over these computer screens. When there was this visual complexity over the scene in the form of dynamic visual noise, then the efficiency of foraging was decreased, shown by an increase in the latency for the birds to both fixate and peck the simulated prey.

Similarly, caustic light has been shown by Matchette et al. (2020) to have the same effect with wild-caught Picasso triggerfish (normally produced by water, but in this case by sophisticated gaming software). This paper suggests that the presence of these dynamic caustics would affect detection by both prey and predators, potentially by increasing the visual complexity of the scene, and its presence would alter survival. However, this study simply used caustics in a monochromatic fashion, whereas naturally there are colour differences in the borders. Therefore, the whole picture of complexity might not be told here, especially since many marine animals are tri- or tetrachromatic which leads us to believe colouration might play a vital role in detection and therefore how detection can be impeded. These water-produced caustics vary spatially when portrayed on differing substrates, therefore the importance of wave pattern and coastal characteristics should be explored to understand how marine complexity might alter predation levels. Similarly to this, Kjernsmo et al. (2020) suggested that when moving against backgrounds with a higher level of specular reflection, also known as gloss, then detection and recognition may be hindered. This was done by showing that the rate of survival was greater when static targets were against such backgrounds by predation by wild avian attackers. As direction and intensity of 'gloss' changes by the angle in which it is perceived, when an animal is moving the background is no longer visually static and has increased in its dynamic complexity. It makes sense that these habitats impede detection due to complexity; however this has yet to be confirmed and more work needs to be done to see if this is feasible within an animal's sensory ecology.

1.6 Evidence of habitat selection for higher complexity

If visual complexity does indeed impede detection, you would expect that animals would choose their habitats depending on the level of complexity which their current needs dictate, either choosing habitats with a higher complexity to remain concealed or choosing habitats with a lower complexity to increase saliency for visual signalling (e.g. an individual performing a mating display wanting as many potential mates as possible to see it). In the first case there is a small amount of experimental evidence: Kjærnsmo and Merilaita (2012) used least killifish (*Heterandria formosa*) to demonstrate this. They tested whether the fish would select either a more visually matching background or a visually complex background to increase concealment. By placing a predator in a separate container within the centre of the experimental tank of the killifish, the fish was able to choose between two of four artificial backgrounds to be seen against in an attempt to remain concealed (Figure 1.5). The backgrounds were manipulated to match the horizontal stripes of the fish, with the first two backgrounds varying in whether the fish would match or mismatch the orientation of the background stripes. The other two backgrounds had a complex orientation of these same stripes or a complex pattern shape with no matching occurring. When the fish were given the choice to be seen against a background they matched the orientation of, or a complex stripe orientation background, females selected the complex one (it is not clear why males did not show the same tendency). This makes sense in terms of real-world living: although the horizontal stripes of the fish match the horizontal striped background, this only occurs when the fish itself is horizontal. Once the fish behaviourally changes its orientation, it becomes mismatched and stands out, risking higher predation levels. In the complex setting, when the fish moves there is a higher chance that the fish will match some level of the background and still remain concealed. There is uncertainty whether this is the level of complexity per se or perhaps the level of variance with background matching needing to be able to occur, shown by the lower selection of the complex habitat in which background matching is not possible (Figure 5). Work conducted on corn snakes (*Pantherophis guttatus*) also shows a similar pattern (Kravchuck and Watson, 2020). The snakes were given a choice of two backgrounds on which they could hide from the human experimenter. Similar to the previous experiment, the snakes chose complex backgrounds over plain ones – even when there is, according to the authors, no background matching occurring.

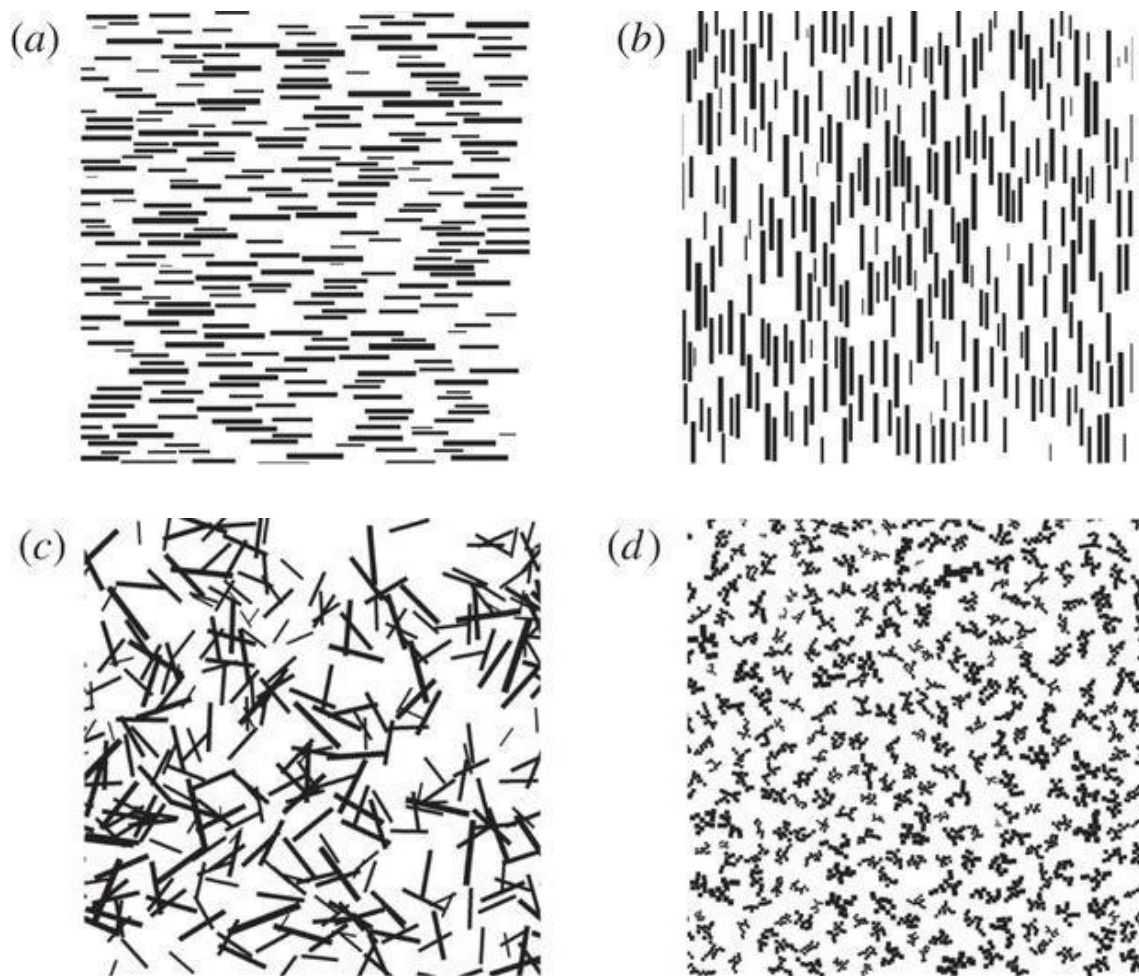


Figure 1.5- The backgrounds used in Kjernsmo and Merilaita, 2012, in which horizontal striped killifish (*Heterandria formosa*) were given a choice of being seen against when predator pressure was applied. Matching orientation background (a), mismatching orientation background (b), complex orientation background (c) and a complex pattern shape (d).

We would also expect that when the background has a high dynamic complexity, caused by features such as illumination or foliage movement, that animals would choose this habitat to perform unintentionally salient behaviours in as to be better concealed to potential predators. We see this with sit-and-wait lizard predators of the genus *Sceloporus* that have been seen to change their foraging site, but only do this when the wind is blowing at a higher than average speed (Jackson, 1974). This higher wind rate will be correlated with higher motion of dappled light and leaf resulting in a great level of visual complexity. As motion breaks concealment (Ioannou and Krause, 2009, Hall et al., 2017, Hall et al., 2013) moving when there is a higher background temporal complexity will help conceal this movement and therefore predator risk of these lizards is reduced. It has been

suggested that this behaviour could be an alarm response, however this seems trivial as *Sceloporus* is exposed to such movement daily so is likely to become habituated to this environmental trait.

The same has been seen in the behaviour of predators, which select for lower dynamic noise aquatic habitats to hunt in (Attwell et al., 2021). By placing threespined sticklebacks (*Gasterosteus aculeatus*) into habitats where they differed in their spatial levels of simulated water caustics, this study demonstrated the fish chose to spend less time in the high complexity areas. These same fish were less likely to respond to virtual 'prey' in these high complex conditions. We can expect that like how animals choose their foraging patches because of profitability (Krebs, 1979, Milinski, 1979), the reason in which the fish chose the lower complexity environments is for better information gathering in these conditions and therefore a higher hunting success.

If this is true, we could also expect the reverse to be true: that animals wanting to become salient for signalling would select simpler backdrops as to stand out and further convey their visual cues. However, this is a particularly understudied area of research, with the little work done here suggesting that it does not matter (Milner et al., 2008). In this paper, female crabs were shown the exact same mating cues given by a robot male-mimic in both a simple and a complex environment. However, females showed no preference in which habitat the signal was given against. It could be, however, that the male's signal is incredibly conspicuous and complexity simply cannot hinder such a motion-salient visual cue. This does not say anything about whether the males have a preference for habitat whilst signalling. Perhaps one reason on why such habitat preference is not widely seen in nature is that drawing attention to themselves by doing a salient cue combined with doing this against a visually quiet background is far too exposing to a predator's perceptual ability and so predation sky-rockets. Maybe instead it could be better to signal whilst being in complex habitats, as to reach the detection threshold for the intended receiver but remain undetected to a less sensitive predator.

1.7 The goals of the thesis

Xiao and Cuthill, as previously stated, demonstrated how natural complexity (by using feature congestion and entropy as measures) is detrimental to the predation of moth-like targets from wild avian predators (Xiao and Cuthill, 2016a). A limitation of this study, however, was the use of a single target colour which is the average colour of the background of the trees on which they were seen. Therefore, the limits of visual complexity to conceal have not been fully explored in a natural setting. Previous work suggested that complexity will impede the detection of the target no matter the level

of background matching camouflage (Merilaita, 2003). When this was examined in human search this was found not to be the case, and targets needed to match some of the background for complexity to have any effect on the latency of attack (and consequently detection time) (Murali et al., 2021a). However this study failed to control for average luminance correctly, and therefore the actual effect of complexity here was not fully explored. The extent to which these findings are analogous to non-human predation in natural habitats is not clear, however, and further research is needed involving wild predation using variations in natural complexity -- this is what the first data chapter in this thesis aims to explore.

Surprisingly, whether it is actual complexity per se which impedes the detection of targets has not yet been fully examined. A good analogy to explain this can be drawn from Kjernsmo and Merilaita (2012). As previously discussed, when given the choice under predation pressure female killifish chose a background with lines varying in direction over a background with only horizontal lines which it was better matched against. We can see this makes sense as if the fish changes its orientation, suddenly it mismatches the horizontal line background and becomes salient to the predator, whereas when it does this against the other background it can remain concealed. This leads to the question of why the fish chose this habitat for better concealment: is it complexity per se or perhaps a greater variability in the background in which you can match to? We can see how such confusion can be paramount in experimental studies by examining studies where shape diversity has been used as a proxy for 'complexity' whilst not measuring or controlling for the variability of these shapes (Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012, Murali et al., 2021a). The second data chapter aims to explore this question by separating out the covarying factors of complexity which may hinder detection.

The use of artificial targets to monitor wild predation rates have been widely utilised for studying protective colouration, and has provided many valuable insights (Cuthill et al., 2005, Mappes et al., 2014). However, often the full picture is not discovered until similar experiments are done within the more controlled laboratory conditions (for example Wainwright et al., 2020). Therefore, we can examine how complexity truly affects detection by examining the deleterious effects in both avian and human visual systems. Previous studies examining other features and mechanisms of camouflage by using biologically relevant targets have shown results align well between humans and birds (Xiao and Cuthill, 2016a, Stevens et al., 2013, Michalis et al., 2016, Cuthill and Szekely, 2009). By combining data and findings from a multitude of different methods, the deleterious effects of visual complexity on a target's detection is beginning to be understood. However, only after the effect of naturally occurring colouration on the inhibition of the complexity is examined, and we fully know the mechanisms by which this occurs, will we have an idea of the relevance in the natural

world of complexity. Examining the questions proposed here in greater depth will improve how animals have evolved their specific anti-predator colourations and aid our understanding of behavioural choices in habitats. By examining effects on both bird and human search behaviour, we can attempt to answer these questions with relative ease and add to this great and advancing field, over 80 years after Cott's landmark book on "Adaptive Colouration in Animals" was first made public.

2. Background complexity can mitigate poor camouflage

2.1 Introduction

Remaining undetected is frequently important for a number of reasons, including predator-prey interactions, avoiding social harassment and seeking sneak mating opportunities. Camouflage is the most widespread means of achieving concealment 'in plain sight', arguably the most important factor being the similarity of the object's colour and pattern to that of its immediate background (Endler, 1978, Endler, 1981, Endler, 1984, Merilaita and Stevens, 2011). However, a factor extrinsic to the camouflaged object also affects its concealment: background complexity (Merilaita, 2003, Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012, Kjernsmo and Merilaita, 2012, Xiao and Cuthill, 2016a). Merilaita (2003) argued, based on results from neural network models, that the visual complexity of the background is a key determinant of detectability, and that higher background complexity relaxes the requirement for precise background matching. He proposed that this is because more complex backgrounds impose higher information-processing costs, and that predators are limited in their processing capacity; I return to this issue in the Discussion. Analogously, the effect of many, highly salient, visual features in the background, known as 'visual clutter', has been investigated in humans in applied contexts such as visual display design (Rosenholtz et al., 2005, Rosenholtz et al., 2007), and also in a few other species. First, by monitoring predation on artificially patterned backgrounds by birds or fish (Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012, Kjernsmo and Merilaita, 2012) and second, by measuring wild avian predation, and human visual search, for artificial targets against natural backgrounds (Xiao and Cuthill, 2016a). Although these studies demonstrate a detrimental effect of background complexity on detection, they do not tell us how important it is relative to matching the background. Somewhat surprisingly, Xiao & Cuthill's (Xiao and Cuthill, 2016a) experiment suggested that, for birds, background complexity was far more important than matching the immediate background. A key limitation of Xiao & Cuthill (Xiao and Cuthill, 2016a) is that the effect of background complexity was demonstrated for only a single target colour: that of the average background. This leaves open the question of whether the benefits of background complexity for concealment are independent of background matching, as Merilaita (2003) suggested, or whether some level of background matching is required. Murali et al. (Murali et al., 2021b) have addressed this question using humans searching on artificial backgrounds, concluding that background heterogeneity aids concealment, but not when the targets fail to match the background. However, whether such effects apply to non-human predators in the field, and the sort of complexity variation seen in natural backgrounds, needs to be addressed. My present study fills that gap, by systematically varying the degree of background

matching and establishing the limits of background complexity's ability to impede detection by wild predators searching on natural backgrounds in the field.

Here, I determine the extent to which background complexity can mitigate poor camouflage. Understanding the interaction between conspicuousness and background complexity is important for two main reasons: the first is to understand what pattern of camouflage evolution will be favoured in different habitats (Merilaita, 2003); the second is to understand which habitats animals prefer if complexity does indeed decrease detection (Kjernsmo and Merilaita, 2012). Most habitats are heterogenous in colour and pattern, and many animals move between visually different habitats. So an open question is whether it is better to have coloration that is a compromise between different backgrounds, or specialised to one (Hughes et al., 2019, Merilaita, 2003, Merilaita et al., 1999, Duarte et al., 2016). Modelling suggests that a critical factor is the trade-off between improved survival on one background and reduced survival on another (Houston et al., 2007, Merilaita et al., 1999). Background complexity will affect that trade-off if it mitigates any mismatch of specialist camouflage to alternative backgrounds, and of compromise strategies to all backgrounds. Furthermore, animals benefiting from concealment could potentially select backgrounds with higher complexity (Kjernsmo and Merilaita, 2012) and those benefiting from salience (for signalling) could select habitats with lower complexity (White et al., 2020).

By monitoring the survival of artificial prey 'moths' in natural woodland, I examined the effect of natural levels of background complexity ((as in Xiao and Cuthill, 2016a)) on the survival of different degrees of background matching ((as in Michalis et al., 2017)). By recording the frequency of colours across a large sample of European oak tree (*Quercus robur*) bark within the woodland, I produced treatments which spanned the background luminance frequency distribution. This allowed me to test whether higher background complexity interferes with detection of all targets regardless of how well they match the background, or whether complexity cannot mitigate poor camouflage. I predicted that high background complexity would only reduce detectability for targets that already match the background well. By manipulating one simple feature, the average luminance or achromatic lightness, that is known to influence the salience of camouflaged objects in our experimental paradigm (Stevens et al., 2006), I sought to determine just how mismatched the target needs to be to the background for complexity to cease to affect detectability. Whether the effect is sudden or continuous is an empirical question that our experiment should help address. To measure background complexity I used feature congestion (Rosenholtz et al., 2005, Rosenholtz et al., 2007), which is based on features from the early stages of visual processing, namely variation in luminance, colour and edge orientation. It has been shown to predict interference in both human and bird

search (Rosenholtz et al., 2005, Xiao and Cuthill, 2016a). For avian colour vision, I used Xiao & Cuthill's (2016a) adaptation of the model of Rosenholtz *et al.* (2005, 2007).

2.2 Material and methods

2.2.1 Stimuli

The targets were designed to resemble a non-specific Lepidopteran: right-angle triangles at 45 mm wide × 32 mm high. Nine treatments were produced, all having the average hue of oak bark but varying in achromatic lightness. The colour information was derived from 1000 calibrated photographs of oak tree bark, taken in the same woods as the experiment was carried out in (Leigh Woods National Nature Reserve, North Somerset, UK, 2°38.6' W, 51°27.8' N) the previous year. Photographs were taken at head height, approximately one metre away from the oak trees, of areas of bark that were free from lichen and not in direct sunlight. The camera was a Nikon D3200 DSLR camera with 35 mm Nikon AF-S DX NIKKOR f/1.8G lens (Nikon Corp., Tokyo, Japan), set at ISO 1600, f8 and automatic integration time. A colour standard, Colorchecker Passport (XRite, Grand Rapids, Michigan, USA), was pinned to the trees in the bottom left-hand corner of the frame for later calibration (as in (Stevens et al., 2007, Westland and Ripamonti, 2004)). These photographs were linearised and normalised to control for variation in light intensity and colour balance, and then mapped to the cone photon-capture colour space of a typical passerine predator, using cone spectral sensitivity data for the blue tit (*Cyanistes caeruleus*) (Hart et al., 2000). The procedures were carried out using custom MATLAB scripts (MATLAB 2019b, The MathWorks, Natick, MA, USA), using the same procedures as described in (Westland and Ripamonti, 2004, Xiao and Cuthill, 2016b). One hundred random target-sized samples were taken from each photograph (the xy coordinates being pairs of random numbers drawn from a uniform distribution), and the average colour for each was calculated. The measure of lightness was the photon catch of the avian double cones (Kelber et al., 2003), scaled from 0 (black) to 1 (white), and two opponent channels to represent the relevant variation in hue: red-green (the contrast between mediumwave- and longwave-sensitive cones) and blue-yellow (the contrast between shortwave- and the average of mediumwave- and longwave-sensitive cones), both also scaled to lie between 0 and 1 (for further details see Xiao and Cuthill, 2016a). Neither oak bark nor the printed targets reflected ultraviolet, so this component of avian colour could be ignored (for bark reflectance spectra see Cuthill et al., 2006). The 'avian luminance' of the 100,000 samples ranged between 0.07 and 0.85, and had two modes (Figure 2.1). The treatments of 0.05, 0.15, 0.25, 0.35, 0.45, 0.55, 0.65, 0.75, 0.85 luminance units were chosen to span the range from exceedingly rare and dark to exceedingly rare and light, with treatments also

approximating the two peaks and the trough between them (Figure 2.1). All treatments had the same red-green and blue-yellow contrasts (0.013 and -0.155 respectively), matching the average of the 100,000 bark samples, so they varied in tone/lightness but not hue. These targets were printed on waterproof paper (Rite-in-the-Rain, J.L. Darling LLC, Tacoma, WA, USA) using a calibrated printer (Canon imageRUNNER ADVANCE C5535i; Canon Inc., Tokyo, Japan), see Figure 2.2 for example targets.

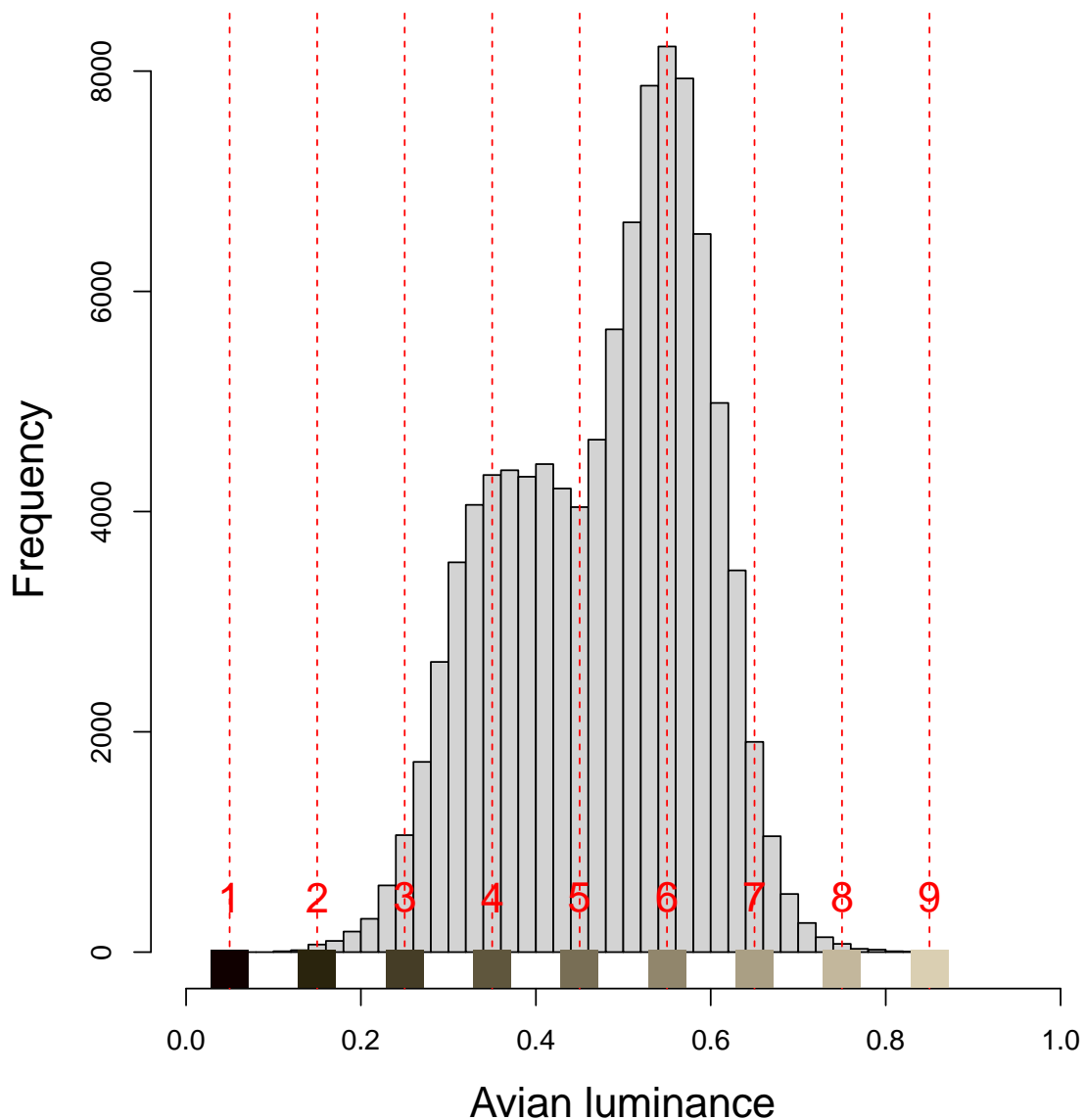


Figure 2.1 - A histogram showing the frequency of the avian luminance of 100,000 oak tree (*Quercus robus*) bark samples. The red dotted lines show where on the distribution the treatment luminance values fall, with the darkest designated as treatment 1 and the lightest as 9.

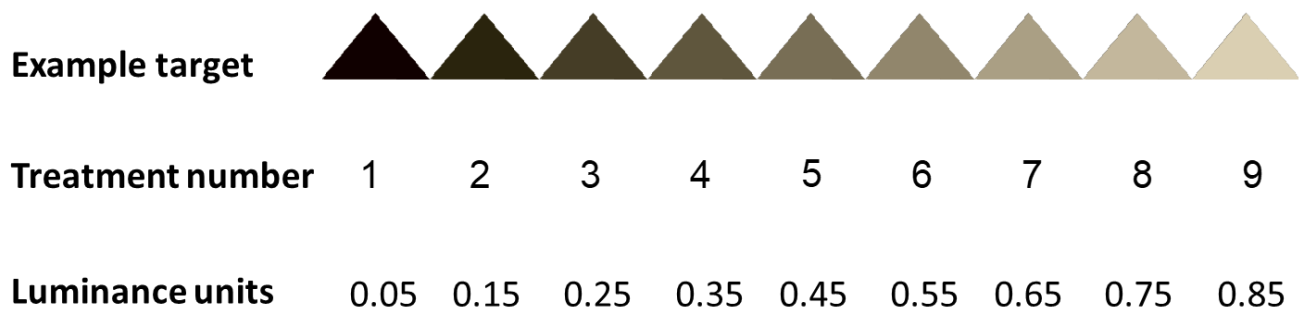


Figure 2.2 – Example targets for each of the treatments used and their respective luminance units.

2.2.2 Procedure

The experiments were run from October to December 2020. The general experimental protocol followed that of Cuthill *et al.* (2005), with the artificial ‘moths’ pinned to mature oak trees along non-linear transects with a dead mealworm (*Tenebrio molitor*) larva frozen at -80°C then thawed underneath the ‘wings’, with a small portion showing. Each transect comprised a block within an overall randomised block design. The transects varied in length from ca 500 to 1000 m, according to variation in oak tree density within different areas of the woodland. The meandering nature of the transects would make them hard to define in terms of area, but they did not overlap each other. Younger oak trees (trunk circumference at head height < 0.9 m) were avoided, with no more than one target per tree, pinned at roughly head-height, facing away from paths to minimise interference from the public. Once pinned, a photograph was taken of the target and its respective background; four mobile phones were used, two of which were iPhones (iPhone 8 and 11, Apple Inc., Cupertino, CA, USA) and two of which were Samsungs (Samsung SM-A405FN and SM-G970F, Samsung Group, Seoul, South Korea). The known size and reflectance of the target, coupled with calibrations based on photographs of a colour chart (Colorchecker Passport; X-Rite, Grand Rapids, MI, USA), were used to normalise and linearise the photographs, then map them to avian colour space. These photos were then used to extract the same measures of background complexity as in Xiao & Cuthill (2016a), using Rosenholtz’s principles of feature congestion (Rosenholtz *et al.*, 2005, Rosenholtz *et al.*, 2007). The calculations were carried out using the custom MATLAB scripts described and explained in (Xiao and Cuthill, 2016b), based on the original Matlab functions of Rosenholtz and colleagues (<https://dspace.mit.edu/handle/1721.1/37593>). Rosenholtz *et al.*’s “feature congestion” can be thought of as a perceptual measure of the variation in three components of a visual scene: luminance, colour and edge orientation. A scene with high levels of local contrast in brightness will score highly on the luminance clutter measure; analogously, spatial variation in colour contributes to

the colour clutter metric, and variation in the orientation of edges (lines) contributes to the orientation clutter metric. “Local contrast” is in fact calculated at three spatial resolutions (i.e. capturing variation in each of coarse, medium and fine detail) and summed to provide a single measure of each of what Rosenholtz *et al.* (Rosenholtz *et al.*, 2005, Rosenholtz *et al.*, 2007) call contrast (luminance), colour and edge orientation ‘clutter’. The feature congestion metric is a weighted sum of the three, based on empirically derived estimates of the contribution of each to perceived differences. Xiao & Cuthill (Xiao and Cuthill, 2016a) showed that the orientation clutter measure of perceived image complexity, and an equivalent for avian vision, predicted the detectability of triangular (notionally moth-shaped) targets on natural bark backgrounds, for humans and birds respectively. The supplementary material of Xiao & Cuthill (2016a, 2016b) has a figure that, in a simple intuitive way, demonstrates how the Rosenholtz *et al.* clutter metrics relate to image features.

Targets were checked at 24, 48, 72 and 96 h, with disappearance of all or most of the mealworm being marked as avian predation, and predation by invertebrates (spiders, slugs, wasps) and ‘survival’ up to 96 h being marked as ‘censored’. Invertebrate predation was determined by either direct observation (one instance of a wasp), a hollowed-out exoskeleton (spiders) or the presence of mucus near the target (slugs). The large sample size that our method allows precludes direct observation of most predation events, so we cannot be certain that birds were responsible for all events scored as bird predation. However, one would expect birds to be the predominant visual predator for such prey in winter in UK woodland, and non-visual predators would only add noise to our data. In each block, 90 targets were placed (10 replicates of each of the nine treatments). Overall, 27 blocks were completed, totalling 2,430 targets.

2.2.3 Analysis

Mixed-effects Cox regression was applied using the ‘coxme’ function from the ‘coxme’ R package (Therneau, 2020; R Core Team, 2020). Block was fitted as a random effect, treatment and the three metrics of feature congestion of the background were treated as fixed effects. The significance of effects were tested using an analysis of deviance comparing the unexplained variation of models with and without the factor in question, tested against a χ^2 distribution. Starting with a maximal model including interactions between treatment and each of the feature congestion metrics, models were step-wise simplified based on non-significance of terms. Effect sizes are presented as odds ratios with 95% confidence intervals. Treatment 5 was chosen as the baseline for comparison with other treatment levels, as this lay close to the mean of the whole distribution (0.48) and was also close to the luminance of the single treatment used in Xiao & Cuthill (2016a).

The following is the process in which the mortality rates were analysed using mixed effects Cox regression, as seen in Table 2.1. The final model (step 5 on the table), retaining only significant terms and the main effects associated with the interaction between orientation clutter and Treatment. Values are the estimates of the coefficients of each term (Coef) and the associated standard error (SE(Coef)), the exponential function or odds ratio of the coefficient ($\exp(\text{Coef})$), the z-test for the difference between the estimated coefficient and zero, and associated p-value. The odds ratio of 0.866 for the main effect of (standardised) luminance clutter on mortality means that for every increase in luminance clutter of one standard deviation, mortality is reduced by 13.4% ($1 - 0.866$). The intercept of the whole model is the mortality rate for treatment 5 (a luminance close to the mean of all backgrounds) and the contrasts for the main effects of Treatment therefore are the differences between the mean mortality rate of each level of Treatment compared to the mean mortality rate of treatment 5. So, for example, the odds ratio ($\exp(\text{Coef})$) for the main effect contrast of treatment1 indicates that mortality of treatment 1 (the darkest targets) is, on average, 2.278 times that of treatment 5 (average bark luminance targets). Analogously, the contrasts for the Treatment by orientation clutter interaction are the slopes of the effect of orientation clutter within each treatment level, compared to the slope of the effect of orientation clutter for treatment 5. For example, the statistically significant odds ratio of 1.789 for the comparison of the slope of orientation clutter in treatment 1 with that in treatment 5 means that the slope is 78.9% steeper in treatment 1 than 5. However, this is not because there is a stronger effect in treatment 1 than 5; the opposite in fact, as the slope is close to 1 (not significant) and significantly negative in treatment 5 (i.e. orientation clutter reduces mortality in treatment 5, but not treatment 1). I use the R notation for model terms, such that “:” indicates the interaction term.

2.3 Results

Overall, 27% of targets were censored (8.6% eaten by spiders, 6.6% by slugs, 3.3% lost, and 8.7% remained uneaten after 96 h). The main effect of treatment, ignoring background complexity, affects target mortality in a pattern that loosely mirrors the frequency of each luminance in the background ($\chi^2 = 376.41$, d.f. = 8, $p < 0.001$; compare Figure 2.3 with Figure 2.1). Targets which have a more common background shade (treatment 2 to 7) have a lower relative mortality than rarer shades.

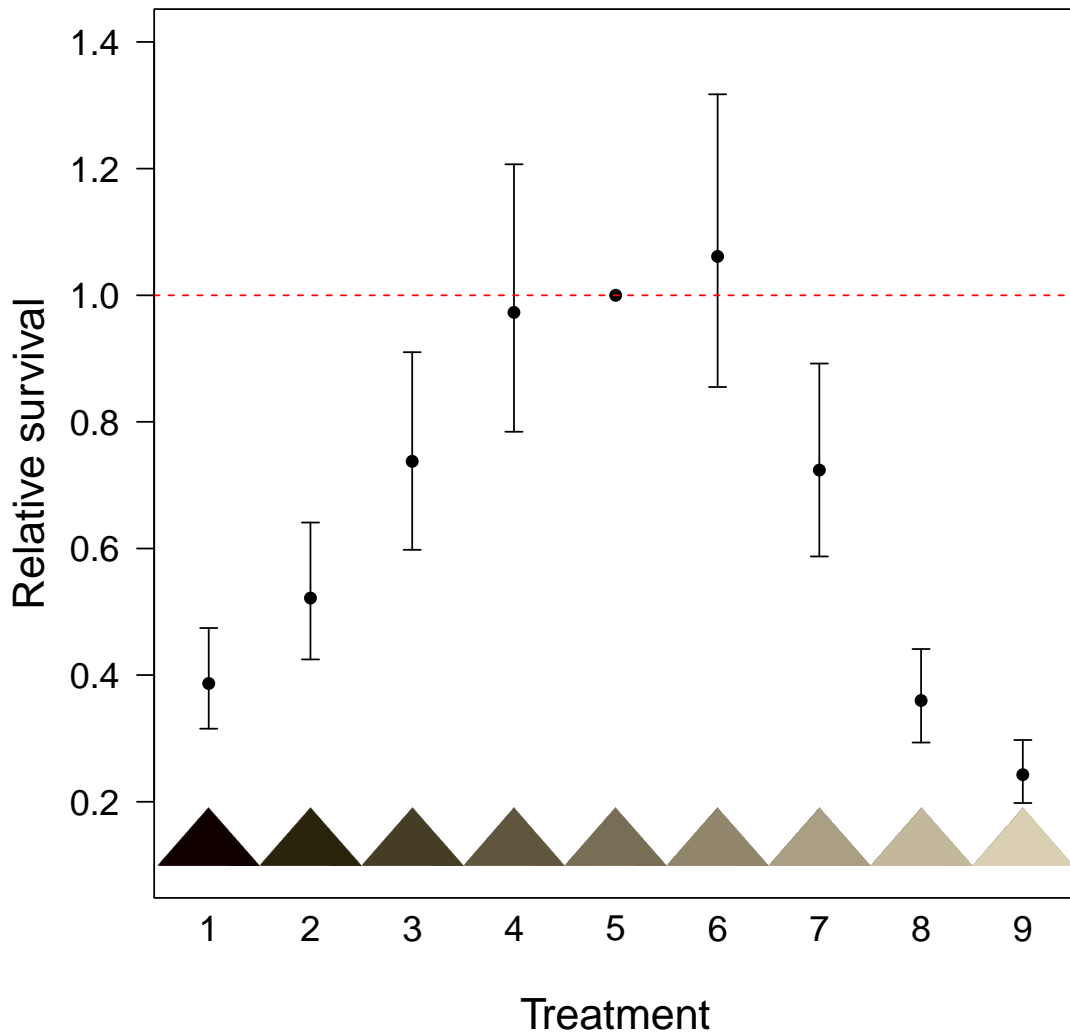


Figure 2.3 - More common background shades have enhanced survival. Odds ratio plot for the relative survival of each treatment compared to treatment 5, which lies near to the mean of the whole distribution. Treatments with 95% confidence intervals not overlapping the red dashed line have a lower relative survival (< 1) than treatment 5. Odds ratios and 95% confidence intervals (bars) were estimated using a mixed-effects Cox regression.

We then examined how the metrics of background complexity altered the survival of the targets; all steps in the statistical modelling can be found in the Table 2.1. There was no significant interaction between treatment and colour clutter ($\chi^2 = 5.09$, d.f. = 8, $p = 0.748$), treatment and luminance clutter ($\chi^2 = 10.05$, d.f. = 8, $p = 0.262$), or a main effect of colour clutter ($\chi^2 = 0.00$, d.f. = 8, $p = 0.979$). However, the interaction between treatment and orientation clutter and the main effect of luminance clutter remained in the minimal adequate model ($\chi^2 = 57.04$, d.f. = 8, $p < 0.001$ and $\chi^2 =$

22.89, d.f. = 1, $p < 0.001$, respectively). Survival was higher with greater luminance clutter (odds ratio 0.866, 95% c.i. 0.818 to 0.918). The effect of orientation clutter was also found to boost survival, but only for those treatments with commoner background shades (treatments 2 to 7), with no significant effect for the treatments representing very rare shades, both dark (1) and light (8, 9); see Figures (3a,b).

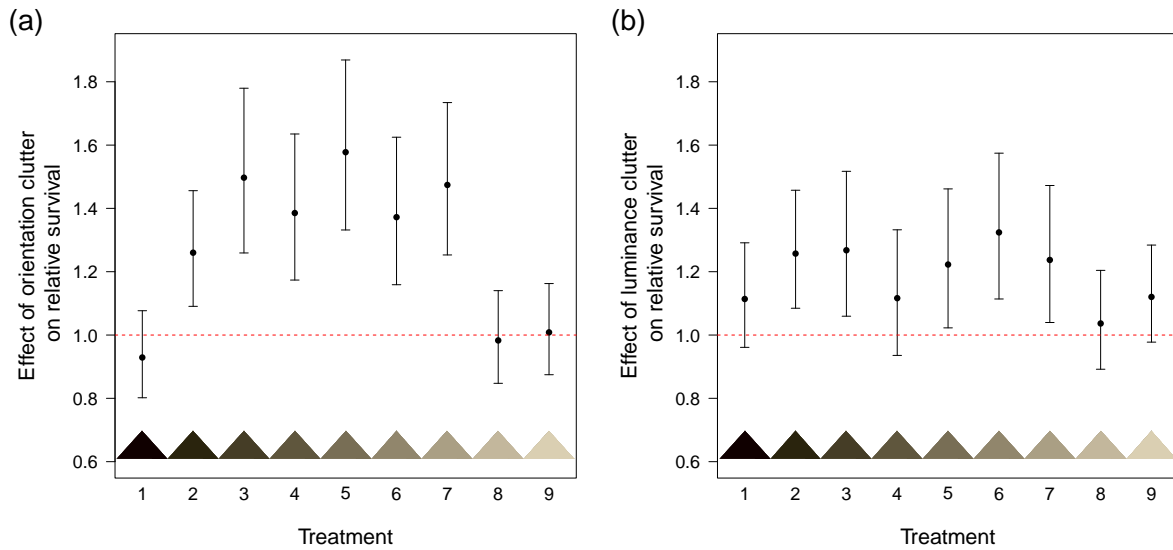


Figure 2.4 - Odds ratios of the effect of (a) orientation clutter and (b) luminance clutter on the relative survival of the treatments. Background complexity only enhances survival for targets that match the background to some degree (treatment 5 is close to the average background luminance, with treatment 1 much darker, and treatments 8 and 9 much lighter, than any background colours). The red dotted line signifies no effect (= 1); data above the line have a higher relative survival on more complex bark (> 1). Odds ratios and 95% confidence intervals were estimated using a mixed-effects Cox regression.

Table 2.1 - A table demonstrating the five steps of the analysis of mortality rates using mixed effects Cox regression and the respective outputs. The following are the abbreviations used, ori = 'orientation', lum = 'luminance', col = 'colour'.

Step	Model	Term removed	Chi	df	p
1	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(lum.clutt) +	Treatment:scale(col.clutt)	5.092	8	0.748

	Treatment:scale(col.clutt) + Treatment:scale(ori.clutt)				
2	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(lum.clutt) + Treatment:scale(ori.clutt)	Treatment:scale(lum.clutt)	10.045	8	0.262
3	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(ori.clutt)	Treatment:scale(ori.clutt)	57.042	8	<0.001
4	Treatment + scale(lum.clutt) + scale(col.clutt) + scale(ori.clutt) + Treatment:scale(ori.clutt)	scale(col.clutt)	0.000	1	0.979
5	Treatment + scale(lum.clutt) + scale(ori.clutt) + Treatment:scale(ori.clutt)	scale(lum.clutt)	22.886	1	<0.001

2.4 Discussion

My results support Merilaita's (2003) conclusion, based on neural network modelling, that background complexity has an important influence on detectability, and that higher background complexity enhances the benefits of background-matching camouflage. When examining the three visual characteristics of feature congestion (luminance, colour, and orientation of edges), I found that two of them had a significant effect on predation rates. A higher background orientation clutter reduced the detectability of all but the rarest background-matching camouflaged treatments (treatment 1, 8 and 9) (Figure 2.4a). With regards to a higher background luminance clutter, there was also a pattern of lower mortality (Figure 2.4b). This effect was similar to, but weaker than, that seen with orientation clutter, but with no detectable treatment-by-background interaction. Therefore, unlike orientation clutter, I cannot confidently conclude that the concealment benefits of high background luminance contrast disappear for rarer background matching samples. The effect of orientation clutter has been previously found in experiments involving humans and wild birds (Xiao and Cuthill, 2016a). Although luminance clutter was not significant in that study, I note that my sample size was an order of magnitude greater, so capable of detecting smaller effects. I make no claims that orientation clutter will be the most important factor in all situations; oak bark is characterised by deep linear ridges, and my targets have linear edges, so an effect on the signal-to-noise ratio in the domain of edge detection is expected. Oak bark also has low chromatic variation (mainly different shades of brown), so it will be interesting to carry out analogous experiments with backgrounds, and targets, with different chromatic and structural characteristics.

A corollary of background complexity aiding concealment is that background complexity mitigates less-than-perfect camouflage (Merilaita, 2003). Targets which are matched to at least some of the

background are less detectable on visually complex backgrounds than those on backgrounds of lower complexity. These findings have implications for habitat selection and thus animal distributions. If an animal benefits from concealment, all things being equal, it should choose a complex background (Kjernsmo and Merilaita, 2012). Conversely, those benefiting from conspicuousness (e.g. to convey a visual signal) should choose to be seen against a less complex background to maximise their saliency (Itti et al., 1998). Habitat choice with respect to habitat complexity could be an effective means of changing the balance between salience and crypsis (Barnett et al., 2016), with different costs and benefits from changing appearance per se. We also found that the rarest background shades were little affected by the complexity of the background. Background complexity does not mitigate a very poor match to the background.

Moving beyond the effect of background complexity, on average the treatments with more common background shades survived better than rarer shades (Figure 2.3). This is expected as, all things being equal, the best camouflage strategy is expected to be the most probable background sample (Michalis et al., 2017). Settling at random (as in our experiment), a common sample has a higher chance of being against a background that is a similar colour to itself, reducing detectability. In my data, survival generally matched the peaks in background luminance (Figures 1 and 2), although there was no detectable dip in survival in treatment 5 compared to 4 and 6, as might be expected from the bimodal luminance distribution (Figure 2.1). This could be a lack of statistical power (although our sample size was large, the benefits of a precise match to the background may be small), or an example of where there is an advantage to a 'compromise' strategy intermediate between the two modal background shades (Houston et al., 2007, Merilaita et al., 2001, Merilaita et al., 1999, Hughes et al., 2019).

In summary, the experiments of Murali *et al.* (Murali et al., 2021b), for humans searching on artificial backgrounds, and our findings – using natural backgrounds – suggest that background complexity alters the detectability of background-matched targets. This is true even for those targets which have relatively poor, but not the poorest, background matching. This suggests that visual complexity can play a role in the evolution of camouflage in heterogenous environments (Merilaita, 2003) and can mitigate the costs of a poorer match. One caveat is that none of my targets were maximally cryptic (all lacked patterning) meaning they may have been more salient than natural moths, we did this to avoid adding another dimension into the treatments which we would have had to control for. Additionally, tree bark is relatively homogeneous in comparison with other natural substrates (e.g. leaf litter); it would be of interest to see if similar trends obtain for such environments. Animals could also make habitat choices based on visual clutter, selecting habitats of higher complexity for concealment and lower complexity for signalling. This prediction deserves to be tested. Beyond

biology, the results are also relevant to understanding human visual search in natural environments, and extending approaches familiar to those in applied psychology and ergonomics (e.g. with regard to visual displays) to more naturalistic tasks.

3. How background complexity impairs target detection

3.1 Introduction

One of the most common forms of protective coloration found within the animal kingdom is camouflage (Stevens and Merilaita, 2011), and the study of how surface texture impedes detection or recognition has a long history (Wallace, 1889, Thayer, 1896, Thayer, 1918, Cott, 1940). Many characteristics of the camouflaged individual have been proposed to aid concealment, from matching the background (Bond and Kamil, 2006, Merilaita, 2003, Merilaita and Stevens, 2011) to distracting from vulnerable areas with salient features (Cott, 1940, Dimitrova et al., 2009). Using an artificial neural network model, Merilaita (2003) has demonstrated that an extrinsic factor may also be involved in concealment: the visual complexity of the background. As natural scenes have large variability in their complexity, it is important to understand the effects this will have on the animals which live within them.

The first empirical evidence to show that visual complexity has a deleterious effect on visual search was collected from humans attempting to discriminate targets from already detected 'distractors' (Duncan and Humphreys, 1989), and to detect targets through 'visual clutter' on displays (Rosenholtz et al., 2005, Rosenholtz et al., 2007). The same effect was found in both birds (Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012, Dimitrova and Merilaita, 2014) and fish (Kjernsmo and Merilaita, 2012) when searching for artificial targets on artificial backgrounds, each with abstract patterns of varying diversity in their component features. Similar adverse effects of complexity on search performance have also been shown in a natural setting by monitoring wild avian predation on artificial moth-like prey on tree bark (Xiao and Cuthill, 2016a) (Rowe, submitted ms). However, it appears that the protection that complexity brings may not be unlimited (Murali et al., 2021b, Rowe, submitted ms), and there is no single standard definition of 'complexity': it is frequently unquantified or, when it is, defined in terms of objective mathematical constructs related to entropy, or perceptual metrics of 'visual clutter'. Entropy relates to the degree of randomness in the pattern, and will be inversely related to how 'structured' it is. With a less complex and/or more repetitive background, the amount of information needed to encode it decreases and thus so does its entropy. Quite conceptually distinct from this physics-based approach, perceptual measures of complexity attempt to quantify the amount of 'visual clutter': salient objects in the scene that might interfere with the detectability or identifiability of a target. For example, the 'feature congestion' metric of Rosenholtz and colleagues (Rosenholtz et al., 2005, Rosenholtz et al., 2007) combines the contrast in luminance, the contrast in hue, and the variation in 'edge' orientation, at different spatial scales, as a single measure of complexity (Rosenholtz et al., 2005). Surprisingly, although this

measure has been successful at predicting detection success in experiments on humans and birds (Rosenholtz et al., 2005, Rosenholtz et al., 2007, Xiao and Cuthill, 2016a), the exact process by which complexity impedes detection is, as yet, unclear. Potentially, a more complex scene has more information to encode so the processing itself induces a delay (Merilaita, 2003), or the defining characteristics of the background take longer to learn. However, it may be that a higher variance in features that might be confused with target features reduces detection, as the more variable the background the greater the probability of a match between target and at least some aspects of that background.

It is hard to isolate the mechanisms by which complexity affects detectability, and the related issue of how best to define complexity, using natural backgrounds. A background which has, say, more colour patches than a monotone scene, is not only more complex (*sensu* Physics: higher entropy), but is more variable, and necessarily has certain colours the simple background lacks; any or all of these may affect detectability. Therefore, to separate these different factors which covary in nature, I used artificial monochrome backgrounds, with human participants acting as proxy ‘predators’ in two computer-driven search experiments. In both experiments, targets and backgrounds were random mosaics of greyscale tiles. In all treatments, no component greys of the targets matched any background greys, so the effect of background complexity *per se* could be assessed, rather than higher complexity potentially affecting the probability of a colour match to the target. By independently manipulating the entropy and feature congestion of the backgrounds against which the target was viewed, I was able to separate the influence of these two measures of complexity.

I predicted that in both the experiments, if feature variance (measured by feature congestion) explains the relationship between visual complexity and detection then it should become more difficult to find the target when the background has more shades of grey and these shades are of higher mutual contrast. However, if it is greater information content (measured by entropy) which better predicts detectability, then it should become more difficult to find the target when the background has more shades of grey regardless of within-background contrast.

3.2 Materials and methods

3.2.1 Stimuli

The target and backgrounds were produced in R 4.0.2 (<https://www.R-project.org/>, 2018 #2437), with the target being a 4x4 square of grey blocks randomly placed on a 48x48 background of blocks (see figure 3.1). The ‘palette’ used for the backgrounds comprised nine, equally spaced greys,

ranging from black (RGB pixel values 0, 0, 0) to white (255, 255, 255) in a standard red, green, blue sRGB colour space. This stimulus configuration simplified the specification of target and background attributes to one dimension: lightness. The 4x4 of the target always aligned with the blocks of the background (blocks could not be partially occluded, c.f. (Murali et al., 2021b)) so any difference between the greys in the background and either or both of the target greys was a unique and perfect predictor of target location.

The target was always made up of two shades (sRGB = 191 and 64) whilst the background contained either one, two, three or, in the case of Experiment 1, four shades (figure 3.1). The patterning of background shades was fully and independently randomised (the grey shade of each block was assigned using R's 'sample' function, with replacement, the probabilities of each grey depending upon treatment: e.g. 1/2 for a treatment with two greys, 1/3 for a treatment with three greys, and so on). With so many ($48^2 = 2304$) blocks in every background, although there was random local variation in the density of different grey blocks, the frequency of each grey was close to that expected from the probability. Conversely, every target had exactly eight light grey and eight dark grey blocks, but their positions were independently randomised (again using R's sample function, but without replacement). Randomisation prevented any search images for the target, based on learning of pattern configuration (Troscianko et al., 2018), from occurring. Sampling without replacement (from eight light and eight dark greys) prevented variation in the average colour of targets (as targets comprised only 16 blocks, full randomisation could have resulted in a predominantly light or predominantly dark square, which could affect detectability).

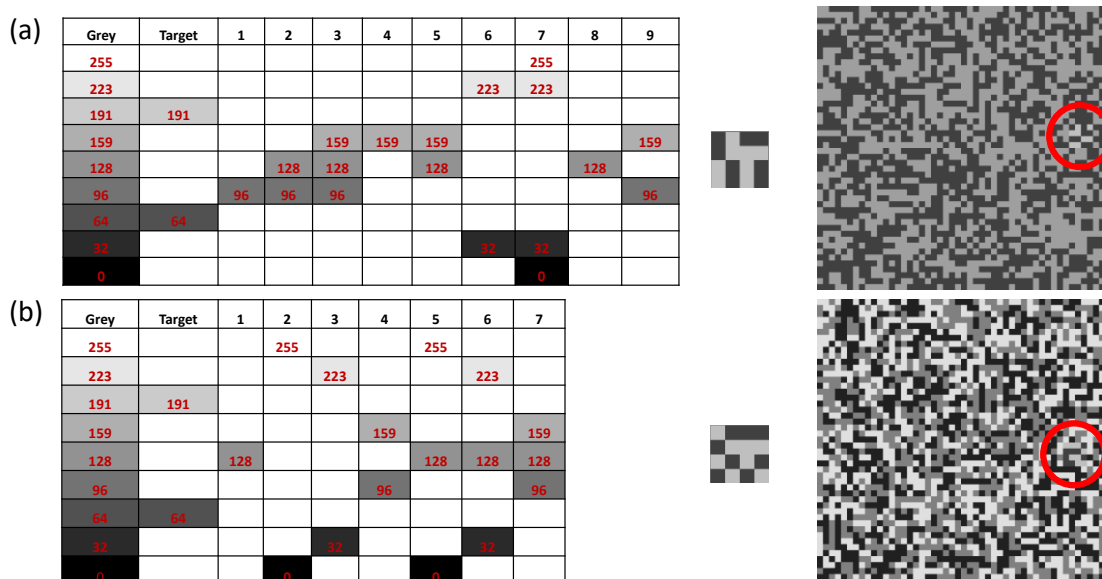


Figure 3.1 - The stimuli in Experiments 1 (a) and 2 (b). Left to right: in the tables, there are nine possible grey levels (column 'Grey') from black (pixel value 0) to white (255), with the target always being a square of eight dark grey (pixel value 64) and eight light grey (191) square blocks, randomly arranged (column 'Target'). An example of a target is shown in the middle panels of (a) and (b) above. The grey levels in each of the nine treatments of Experiments 1 (a) and 2 (b) are shown in the tables to the left, with the RGB values in red (numbered columns). Examples of backgrounds for treatment 9 of Experiment 1, and treatment 6 of Experiment 2, are shown in the right-hand panels of (a) and (b) respectively. The target location is indicated by a circle (not present in the experiment).

Two experiments were performed, varying the number of shades of grey in the background (and hence entropy) and the difference in grey level between them (and hence feature congestion, as this metric rises with the local contrast between blocks). In Experiment 1, the similarity in shade between background greys and target greys could be asymmetrical with respect to the two component target greys (e.g. a background grey could be closer in shade to the lighter of the two target greys than the darker of the two). In Experiment 2, lightness differences were symmetrical (e.g. if there was a background grey similar to the lighter of the target greys, there was another background grey equally close to the darker of the two target greys). The treatments for both experiments are shown in figure 3.1; note that the target greys never matched any of those in the background. This removes the possibility that better concealment may be due to a higher probability of the target matching any part of the background.

3.2.2 Procedure

All the visual search tasks were run using PsychoPy2 (Peirce et al., 2019), using the previously constructed stimuli, saved as PNG files, described above. All participants were briefed in line with the Declaration of Helsinki, were naïve to the purpose of the experiments, and had normal or corrected-to-normal vision. Ethical approval was granted by the joint research ethics committee of the University of Bristol Faculties of Science and Life Sciences.

Each experiment was run twice, on two different sets of participants: once online, with each participant using their own computer/monitor; then again, once COVID restrictions had eased and in-lab participant testing was allowed, in a controlled test environment. The replication was necessary because commercial displays vary in their relationship between pixel (RGB) value and screen brightness, meaning that different participants saw slightly different images (in terms of contrast range and target-background difference), and those differences were unknown. In addition,

the test conditions would have been variable (viewing distance, mouse or touchpad, attention to the task, etc.). Thus the online data were ratified by repeating the experiment with a gamma-corrected (calibrated and linearised) 21.5" iiyama ProLite B2280HS monitor (iiyama; Hoofddorp Netherlands) with a refresh rate of 60 Hz, a resolution of 1200 × 1080 pixels, a screen size of 268.1 mm by 476.6 mm, and a mean luminance of 64 cd m⁻²) at a viewing distance of ca. 50 cm. The monitor was driven by a Macbook Pro (Apple Inc., Cupertino, CA, USA). The main room lights were turned off, and the participant was left alone, after briefing, to complete the experiment.

The participants were given written instructions that they would have to find and click on a two-shade target on a background which varied in the number of shades of grey. They were told that every screen had one, and only one, target in a random location, and they should search until they found it. However, they were also told that, if they really could not locate the target, they could click to the side of the screen to advance to the next image. The experiment was preceded by a random ordering of the same 10 practice images, varying in the number of background greys, where the target was always in the middle of the screen. Following this, treatments were shown to the participants in five blocks of nine screens for Experiment 1, and five blocks of seven screens in Experiment 2. For experimental trials, the target was in a random location. Each block contained one replicate of each treatment, with each participant's five blocks comprising a random subset, without replacement, of 24 possible blocks. Participants saw random subsets of a pool of replicate images, rather than unique target-background combinations, because images were constructed in advance rather than generated in real time during the experiment. Each block was followed with an instruction that a break could be taken before the next block; in practice, most participants only paused for a few seconds. The response time was measured as the latency between the stimulus appearing and the participant clicking on the screen.

The two online experiments involved 130 participants from the Life Sciences undergraduate student cohort from the University of Bristol. Participants were randomly assigned (using the Python random number generator within PsychoPy) to one of the two experiments. The first experiment had 69 participants (46 female, 21 male, 2 undisclosed; aged 19-27, median 20) and the second had 41 (24 female, 14 male, aged 19-26, median 20). The female biased sex-ratio reflects the female bias in the student population for these degrees. For the lab replication, 24 participants (50 % females, aged 20-36, median 22.5) completed both of the experiments in turn, with the order balanced across participants.

3.2.3 Analyses

All data were analysed in R 4.0.2 (<https://www.R-project.org/>, 2018 #2437). Using Linear Mixed Models (function `lmer` in the package `lme4`) (Bates et al.) I tested the effect of treatment (background type) on log-transformed response time (RT). Only trials in which the target was correctly located were used in the analysis of response time. Planned contrasts (a polynomial contrast and set of pair-wise comparisons, fitted simultaneously as one contrast matrix), were obtained using the function `glht` in the `multcomp` package (Hothorn et al., 2008) to maintain the experiment-wise type I error rate at 0.05. To save the reader from having to refer back to this Methods, the details of, and rationale for, the planned contrasts are described in the Results.

The effect of sex on detection was also analysed to assess, post hoc, whether there were any unexpected sex differences. In these secondary analyses, only data for participants who reported their binary sex were analysed, with the instances of undisclosed sex too rare to be included as an additional level. First, a model with the interaction between sex and treatment, and their main effects, was fitted; then, where the interaction was not significant, a model without the interaction was fitted to test the main effect of sex.

It was intended also to analyse the proportion of 'hits' (correctly clicking on the target), as an additional measure of detection success, with Generalized Linear Mixed Models using function `glmer` in the package `lme4`, with binomial error. However, none of the models converged, because misses were rare. Nevertheless, I report the percentage of misses, in order to address the possibility of any speed-accuracy trade-offs.

3.3 Results

3.3.1 Experiment 1

Treatment had an effect on response time in both the online ($\chi^2 = 1587.0$, d.f. = 8, $p < 0.001$) and lab-based ($\chi^2 = 1030.3$, d.f. = 8, $p < 0.001$) versions of the experiment. If the effect of complexity is solely related to information processing, the prediction based on the entropy of the background is that the difficulty for 4 greys > 3 greys > 2 greys > 1 grey, regardless of which shades of grey are present. Thus there should be a monotonic relationship for the response times for treatment 9 > 8 > (7=6=5=4) > (3=2=1). As there are four levels, a cubic polynomial describes this relationship. Response time increases with entropy, but the relationship is not monotonic, with the cubic term significant as well as the linear (figure 3.2; online experiment: linear coefficient = 2.9, $z = 40.0$, $p < 0.001$; quadratic coefficient = 0.6, $z = 20.8$, $p < 0.001$; cubic coefficient = 1.2, $z = 16.4$, $p < 0.001$; lab experiment: linear

coefficient = 2.4, $z = 25.8$, $p < 0.001$; quadratic coefficient = 0.6, $z = 14.6$, $p < 0.001$; cubic coefficient = 1.2, $z = 13.8$, $p < 0.001$).

While the treatment with four greys (9) has the longest response time and the treatments with one grey (1, 2, 3) have among the shortest response times, there are clear differences within the two-grey treatments that indicate strong effects independent of entropy. For example, treatment 7, with two greys, has the second-longest response time, much longer than treatment 8, which has three greys. Particular pair-wise comparisons are illuminating, chosen because the predictions for entropy and feature congestion differ (Table 3.1). As feature congestion is based on the salience of features in the background, which is in turn affected by local contrast, treatments with more widely spaced grey levels generate higher levels of feature congestion. This means that, for example, treatment 8, which is identical to treatment 6 apart from the addition of a third grey level intermediate between the dark and light greys of treatment 6, has lower feature congestion despite having a higher entropy. Wherever these planned pair-wise comparisons are significant, they are consistent with the predictions of feature congestion and not entropy. Although some comparisons that were significant in the online version of the experiment were not significant in the lab version, the overall pattern of the data was consistent across both experiments. The one anomaly in terms of predicted effects is the aforementioned comparison of treatments 8 and 6, which favoured neither hypothesis, the addition of the intermediate grey level having no discernible effect ($p = 0.987$ and 0.117 respectively, for the online and lab versions of the experiment). Misses were too rare to be analysed but, consistent with the response time data, were most common in treatment 9 (7.6% of trials in the online experiment; 0.8% in the lab version) followed by treatment 7 in the online experiment (2.6% of trials); there were no errors in any treatments apart from treatment 9 in the lab version of the experiment. There was therefore no evidence of any speed-accuracy trade-off.

The effect of sex on response time was not significant, either in interaction with treatment (online: $\chi^2 = 8.4$, d.f. = 8, $p = 0.392$; lab: $\chi^2 = 4.5$, d.f. = 8, $p = 0.808$) or as a main effect (online: $\chi^2 = 0.5$, d.f. = 1, $p = 0.484$; lab: $\chi^2 = 0.4$, d.f. = 1, $p = 0.548$).

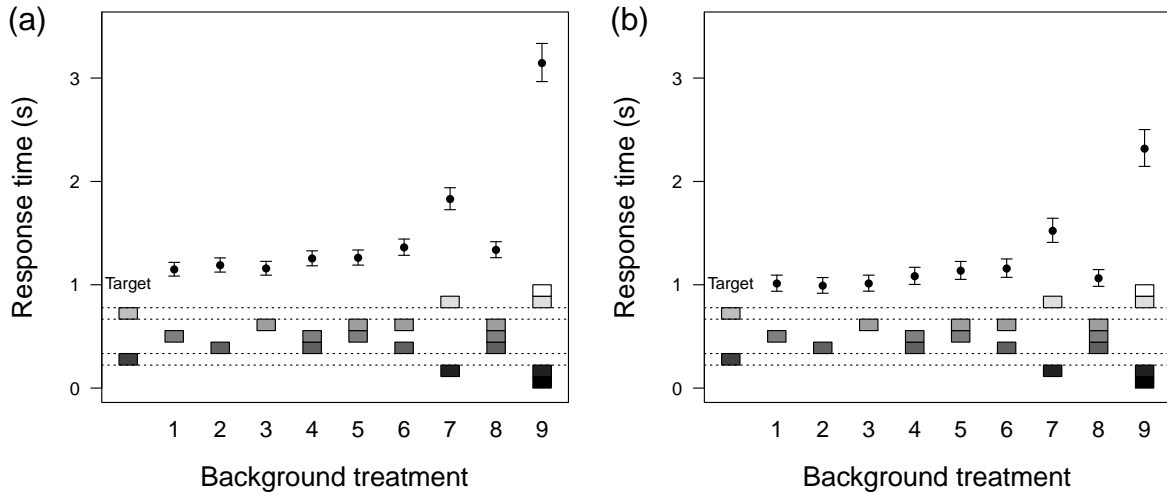


Figure 3.2 - Mean response time ($\pm 95\%$ c.i.s) in seconds for the nine background treatments of the non-calibrated online (a) and calibrated lab versions (b) of Experiment 1. Values are based on the model estimates, back-transformed from the log scale. The bottom key shows which shades were present within the background for each treatment; the two shades of the target are provided for comparison (dotted lines).

Table 3.1 - Experiment 1: results from planned pair-wise comparisons of response times between treatments that differ in predictions for entropy and feature congestion (FC) measures of background complexity. Where the estimate has a positive sign, the first treatment has a longer response time than the second; vice versa for a negative sign (e.g. -0.3 indicates that the response time for treatment 8 was less than that for treatment 7, consistent with FC not Entropy). The experiment was run twice: online with uncalibrated monitors and unknown test conditions, and in a lab under controlled conditions with a calibrated monitor.

		Online experiment				Lab experiment			
Entropy prediction	FC prediction	Estimate	z	P	Support	Estimate	z	p	Support
8 > 6	8 < 6	-0.0	0.6	0.987	Neither	-0.1	2.4	0.117	Neither
8 > 7	8 < 7	-0.3	11.2	<0.001	FC	-0.4	10.1	<0.001	FC

4 = 7	4 < 7	-0.4	13. 5	<0.00 1	FC	-0.3	9.6	<0.00 1	FC
4 = 6	4 < 6	-0.1	3.0	0.024	FC	-0.1	1.9	0.345	Neither
5 = 6	5 < 6	-0.1	2.7	0.044	FC	-0.0	0.5	0.995	Neither
6 = 7	6 < 7	-0.3	10. 6	<0.00 1	FC	-0.3	7.7	<0.00 1	FC

3.3.2 Experiment 2

Treatment had an effect on response time in both the online ($\chi^2 = 1277.0$, d.f. = 6, $p < 0.001$) and lab-based ($\chi^2 = 848.8$, d.f. = 6, $p < 0.001$) versions of the experiment. As with experiment 1, if the effect of complexity is solely related to information processing, the prediction based on the entropy of the background is that the difficulty for 3 greys > 2 greys > 1 grey. The predicted monotonic relationship for the response times is therefore for treatment (7 = 6 = 5) > (4 = 3 = 2) > 1. With three levels, a quadratic polynomial describes this relationship. As with Experiment 1, response time increases with entropy, but the relationship is not linear, with the quadratic term significant as well as the linear (figure 3; online experiment: linear coefficient = 1.2, $z = 28.6$, $p < 0.001$; quadratic coefficient = 0.7, $z = 11.7$, $p < 0.001$; lab experiment: linear coefficient = 1.1, $z = 22.2$, $p < 0.001$; quadratic coefficient = 0.6, $z = 8.2$, $p < 0.001$). Again, as with Experiment 1, there is as great variation between treatments with the same entropy as between treatments with different entropies. For example, treatment 5, with three greys, produced significantly shorter response times than some of the treatments with two greys (Table 3.2). Indeed, the difficulty of target detection was similar to that of treatment 1, with only one grey level, on which the target was immediately detectable (Table 3.2).

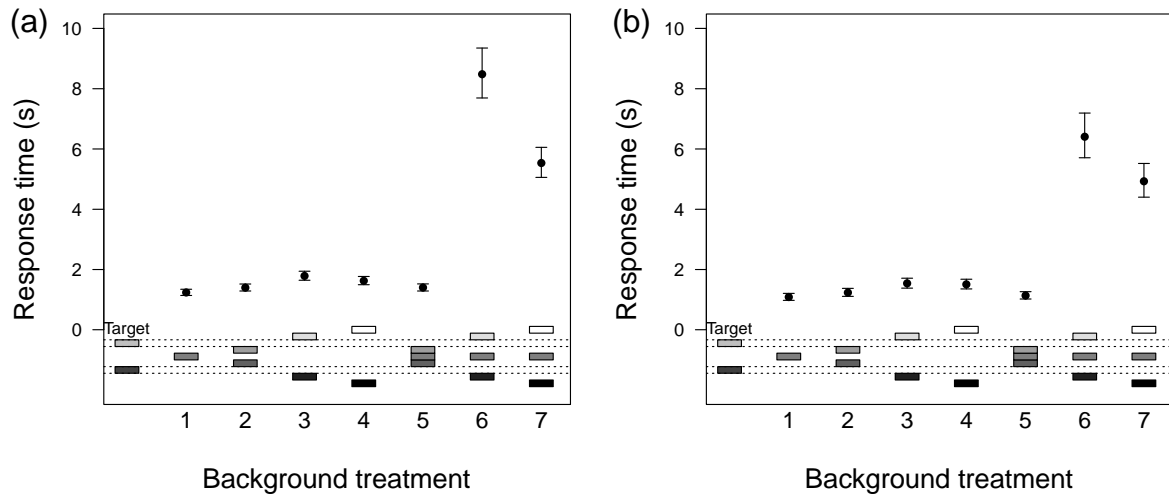


Figure 3.3 - Mean response time ($\pm 95\%$ c.i.s) in seconds for the seven background treatments of the online non-calibrated (a) and calibrated lab versions (b) of experiment 2. Values are based on the model estimates, back-transformed from the log scale. The bottom key shows which shades were present within the background for each treatment; the two shades of the target are provided for comparison (dotted lines).

As with Experiment 1, it is informative to consider cases where the predictions for entropy and feature congestion differ (Table 3.2). Like Experiment 1, the results of online and lab versions of the experiment were very consistent but, unlike Experiment 1, the results do not favour one hypothesis over the other for what constitutes the aspect of 'complexity' that impedes target detection. Misses were too rare in some (but not all) treatments to be analysed but, consistent with the response time data, were most common in treatment 6 (37.1% of trials in the online experiment; 20.8% in the lab version) followed by treatment 5 (22.9% of trials in the online experiment, 15.8% in the lab version); there were no errors in any other treatments in the lab version of the experiment, and they were 6% of trials or fewer in the online experiment.

Table 3.2 - Experiment 2: results from planned pair-wise comparisons of response times between treatments that differ in predictions for entropy and feature congestion (FC) measures of background complexity. Where the estimate has a positive sign, the first treatment is greater than the second (1.2 indicates treatment 7 had a longer response time than treatment 4) and so is consistent with the Entropy prediction; vice versa for a negative sign. The experiment was run twice: online with uncalibrated monitors and unknown test conditions, and in a lab under controlled conditions with a calibrated monitor. The comparison between treatments 5 and 1 does not differentiate between the two measures of complexity, but whether there is a difference it is nevertheless of interest.

		Online experiment				Lab experiment			
Entropy prediction	FC prediction	Estimate	z	p	Supports	Estimate	z	p	Supports
7 > 4	7 < 4	1.2	23.6	<0.001	Entropy	1.2	18.8	<0.001	Entropy
6 > 4	6 < 4	1.7	29.9	<0.001	Entropy	1.4	22.6	<0.001	Entropy
5 > 4	5 < 4	-0.1	3.0	0.019	FC	-0.3	4.7	<0.001	FC
6 > 3	6 < 3	1.6	28.1	<0.001	Entropy	1.4	22.2	<0.001	Entropy
5 > 3	5 < 3	-0.2	4.9	<0.001	FC	-0.3	5.0	<0.001	FC
5 > 2	5 < 2	0.0	0.0	1.000	Neither	-0.1	1.4	0.672	Neither
5 > 1	5 > 1	0.1	2.5	0.083	Neither	0.0	0.8	0.965	Neither

The effect of sex on response time was not significant, either in interaction with treatment (online: $\chi^2 = 9.7$, d.f. = 6, $p = 0.138$; lab: $\chi^2 = 2.7$, d.f. = 6, $p = 0.848$) or as a main effect (online: $\chi^2 = 0.5$, d.f. = 1, $p = 0.485$; lab: $\chi^2 = 1.3$, d.f. = 1, $p = 0.247$).

3.4 Discussion

While, broadly speaking, response times increased with entropy, entropy could not explain the, sometimes very large, differences in response times within entropy classes (i.e. treatments with the same number of grey levels in the background). Importantly, when we compared treatments where the predictions for entropy and feature congestion differed, entropy frequently failed (always losing out to feature congestion in Experiment 1; sometimes, but not always, in Experiment 2). If visual 'complexity' was captured by entropy, we would expect to see that detection would become slower with an increasing number of grey levels, regardless of the contrast between those levels. It does

not. Therefore increased 'complexity' of a background, in terms of mathematical information, is not the driver of increased difficulty in visual search for our stimuli. That entropy is a poorer predictor of visual search than feature congestion has been advanced before in studies of natural and manufactured backgrounds (Xiao and Cuthill, 2016a, Rosenholtz et al., 2007); by designing backgrounds where the predictions of the two metrics are opposed, my study pinpoints that failing. I suggest that when biologists discuss the camouflaging effect of backgrounds that are variable and/or have lots of 'visual clutter', they should not use the term complexity. Complexity has a precise mathematical definition, and it is not the number of bits of information in a scene that impair detection. The goal was not to establish whether entropy or feature congestion is a better measure of the visual complexity seen in nature, but which better predicts the effect of the background on the detectability of a target placed on that background.

The results of Experiment 1 seem to provide clear support for the explanatory power of feature congestion. For example in Experiment 1, comparing two-shade backgrounds only, the longest response times are seen in treatment 7, with the highest feature congestion (highest variance in grey level), followed by treatment 6, with the next highest, then treatments 5 and 4 having the lowest response time and variance (figure 3.2). However, looking more closely, the differences between treatment 6 and treatments 5 or 4 are not that marked (significant only in the online version of the experiment, where screen calibration was absent). What might underpin this deviation from the predicted pattern? First, in treatments 4 and 5, one of the two grey levels is more different in luminance to either of the target greys than in treatments 6 and 7. That is, the targets are a closer match to the background greys in treatments 6 and 7 than in treatments 5 and 4. Second, in treatment 7 which, of the two-grey treatments, produces the greatest increase in response times, both target greys fall within the range of the background greys (i.e. lie between the dark and light shades in the background), whereas in treatments 4, 5 and 6, both target greys fall outside the limits bounded by the background greys. The results of Experiment 2 confirm this interpretation of the true causes of detection difficulty in Experiment 1. All else being equal, having greys closer in luminance to those of the target increases detection times (figure 3; e.g. 3 > 4 and 6 > 7). In addition, the treatments with longest detection times (3, 4, 6 and 7) are those where the target greys fall within the limits bounded by the background greys. This is what makes detection against background 6 so difficult: the target greys are both close to the greys in the background and they fall within a range spanned by greys in the background. Significantly, the addition of a third grey to the background, intermediate between the lightest and darkest shades, even though it decreases feature congestion by reducing variance in luminance, greatly increases search difficulty (compare

treatments 6 and 3). While the entropy of treatment 6 is greater than treatment 3 (3 shades vs 2), it is not greater entropy that causes the increased search times; it is greater confusability between target and background greys. This conclusion is consistent with previous work on prey detection and natural complexity in the field, which showed that greater feature congestion can impede wild avian predation, but only when the target is partially background matching (Rowe, submitted ms).

We can conclude that neither entropy nor visual clutter per se are the mechanism by which background "complexity" aids concealment for our experimental stimuli. It is greater visual clutter that can be confused with target features that improves concealment. When comparing treatment 8 with 6 in Experiment 1, entropy and feature congestion each point to one of the treatments concealing the target better, but the data suggest that adding the intermediate grey makes no difference (figure 3.2, table 3.1). This is because in both treatments the target can be located the simple rule "find the lightest grey" or "find the darkest grey". The explanation also holds in Experiment 2 where there is no detectable difference between treatments 2 and 5. Such a "unidirectional" rule cannot be used where the target greys lie within the limits of the background distribution; instead, a two-component ("greater than x but less than y") rule must be used, or even a search for a unique grey level. Consistent with this, as discussed earlier, concealment is greatly improved by the addition of an intermediate grey, but only when the lightest and darkest background greys lie outside the two target greys (figure 3.3; treatment 6 is a much more difficult task than 3, and 7 than 4, but 5 and 2 are almost identical). When a simple unidirectional "lighter than all" or "darker than all" rule cannot be used, addition of grey levels makes locating a unique target grey even harder. One concern about these findings is the potential use of local rather than 'global' features to detect the target, specifically the pixel to pixel contrast at the boundary of background to target. As this was not controlled for in the experiment, this might have created bias by salient cues. Additionally, the sRGB colour scale I chose in this chapter is linearly related to light intensity as seen on a gamma-corrected monitor (as in this experiment). However, human vision has a non-linear relationship with light intensity, so perhaps this was a poor choice. Nevertheless, the experiment stands regardless as this is a minor visual issue.

Our results imply that the proposition that greater background complexity offers protection independent of the level of background matching (Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012) is wrong. There is always some level of interaction between background and target features, rather than there being a separable independent effect of the background. Camouflage works through reducing the signal-to-noise ratio (Merilaita et al., 2017); as the latter can be via

enhanced noise as well as reduced signal, this is how 'complexity' (increased variance in background features potentially confusable with those of a target) aids concealment. It is interesting that a background with just three grey levels (e.g. treatment 6 of experiment 2; figure 3.3) makes for a difficult search task, even though any of the grey levels used in our experiments are very easily discriminated from those in the target (differences in RGB values of 1 are discriminable, and our greys are spaced 32 units apart). How confusing a background might be is linked to the viewer's estimate of the distribution of features in the background. How viewers learn the nature of the background is an important area of study for future work.

4. Concluding remarks

There are many gaps in our understanding of the mechanisms which cause complexity to have deleterious effects on detection, and the consequences this effect has on the behavioural and evolutionary ecology of camouflaged animals. This thesis has attempted to fill a few of these gaps and has resulted in a multitude of further work being suggested. Are animals which are relatively poorly camouflaged still able to benefit from a higher complexity? To assess this, in chapter 2, 'moth-like' targets which varied in their average background-matching camouflage levels were placed on natural backgrounds which were shown to vary in complexity (as defined by feature congestion). The level of avian predation was then monitored for these targets to see where the effect of this complexity on a target's survival was found. I found that the targets which were extremely poor background-matching saw no benefit. We can deduce that, unlike previously hypothesised (Dimitrova and Merilaita, 2010, Dimitrova and Merilaita, 2012), complexity does not have a universal deleterious effect on detection but, in fact, requires some degree of background-matching to work. These findings have implications for both the evolution and behaviour of camouflaged animals. You could expect to see in more complex environments that camouflaged animals would have evolve less perfect background-matching camouflage, as a trade-off would develop between the cost of colouration and being detectable. A large-scale comparative study which would assess optimal camouflage and complexity of habitats against the camouflage strategies of its occupants could begin to pick this apart, such as has been done for other camouflage strategies such as countershading (Allen et al., 2012).

My results would also suggest it would be beneficial for animals to be able to perceive the level of complexity and adjust their choice of backgrounds when performing different behaviours. If benefiting from remaining concealed, it would be better to be seen against a background of higher visual complexity, and animals would presumably select for this. Contrasting to this, camouflaged animals wanting to be salient for signalling would avoid such habitats, and opt for a lower complexity scene. Further studies examining this would be beneficial: for example, giving animals a choice of backgrounds which vary in complexity to either hide against when predators are present, or signal against when in the presence of potential mates. To strengthen this, studies examining the natural settings in which animals choose to do these behaviours should also be conducted. In the same experiment, I also saw that a higher background orientation clutter (edges with varying orientation) explained the highest amount of the variation in survival. Whilst a higher background luminance clutter (varying achromatic lightness) reduced detectability of all treatments rather than only in less salient targets. That said, the pattern was similar to that for orientation clutter and so the lack of an interaction with target salience could have been due to lack of statistical

power (because most of the variation in survival was used up by the treatment by orientation clutter interaction). It would be interesting to see if, with different background habitats, the same metrics can be used to determine detectability, or if these are simply reliant on the types of background scenes used in my experiment (oak bark with strong visual edges).

Surprisingly, the precise mechanism in which 'complexity' impedes target detection is unknown, and is often assumed to be caused by a cognitive limitation (Merilaita, 2003). To explore the possible reasons, I constructed artificial grey-scale targets and backgrounds which were able to isolate and manipulate the normally covarying factors of visual 'complexity'. By using search tasks in humans, I was able to see what factors precisely caused the deleterious effect of 'complexity' on target detection. I found that neither increased information content (entropy) nor greater feature variance (feature congestion) explained the relationship found. It was instead a greater visual clutter which could be confused with the target which aided concealment, i.e. reducing the signal-to-noise ratio. This highlights important questions as to when the term 'complexity' should be used and what it should be used to define. This work also suggests that how confusing a background might be to viewers is linked to how they estimate the distribution of the background features. How viewers learn the nature of the background is an important area of study for future work.

Additionally, the findings of the experiment in both of these chapters have benefits which span beyond biology. The findings of the field experiment are relevant to understanding human visual search in natural settings, and they can be extended to apply to the psychology and ergonomics of more naturalistic tasks. The findings of the human-based research, again, are very beneficial to the ergonomics of displays. By mitigating the effects that a greater clutter which matched the target has on detection, salience of important displays can be increased. All of this, tied with the behavioural and evolutionary consequences of the findings, gives this work importance in our understanding of how visual complexity can affect the natural world and how we are able to mitigate its effects whilst designing displays.

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