

The Role of Edge Enhancement in Animal Colouration

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(Signature)

A handwritten signature in black ink, appearing to read 'Jodie Henderson', written over a light grey rectangular background.

## **Acknowledgements**

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## **Abstract**

Many animals exhibit contrasting shapes across their surface which are thought to help conceal them from potential predators. It has been suggested that these patterns, known as disruptive markings, function by creating false edges that break up the characteristic form of the animal. Some disruptive patterns are graded in tone so that light patches become lighter and dark patches become darker at the points where they converge. Whilst this type of edge enhancement has been shown to improve camouflage efficacy, it still remains unclear how these patterns are typically expressed within real animals and how they may function within a natural setting. In chapter 1, the strength of edge enhancement was quantified for a variety of British moth species through the use of calibrated digital photography. Across the different species, the level of edge enhancement was shown to be more pronounced near the outline of the moth compared to the centre of the wing, caused by a greater offset in the dark edge.

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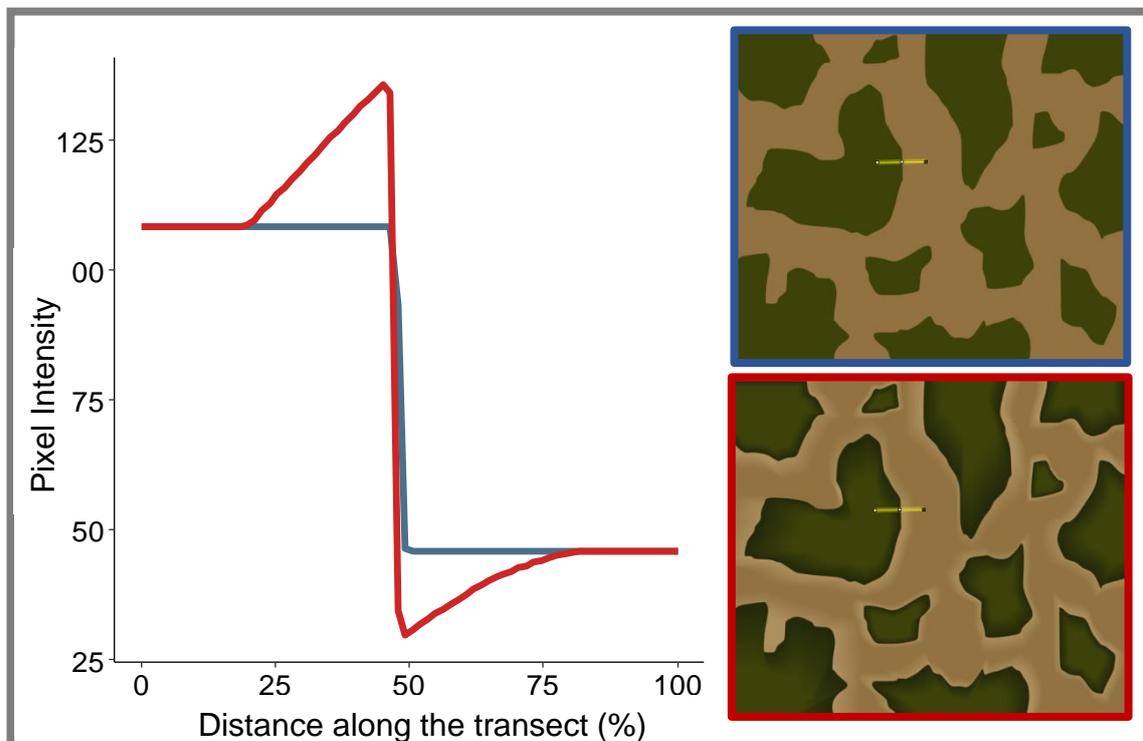
## Introduction

Camouflage is a protective strategy used by many animals to conceal their presence from the sight of a potential predator (Stevens & Merilaita 2008). Across the animal kingdom, camouflage can be achieved through a variety of behavioural and morphological adaptations, which are typically categorised according to how they prevent either detection or recognition (Stevens & Merilaita 2008). For any animal, the most effective strategy will depend not only on the visual characteristics of their environment (Merilaita 2003), but also on the sensory and cognitive abilities of their respective predator (Skelhorn & Rowe 2016). Camouflage form can therefore be seen as a product of the niche in which an animal exists.

One of the major forms of visual camouflage within the natural world is that of disruptive colouration. Unlike background matching patterns, which enhance concealment by closely resembling the colours and contours of their environment, disruptive camouflage comprises of contrasting patches which help to break up the characteristic form of the animal (Stevens & Merilaita 2009). The distinction between these two types of cryptic colouration was first made by Abbot Thayer in his book titled “Concealing-coloration in the animal kingdom” (Thayer 1909). When describing the disruptive form, Thayer noted that such patterns may be favoured in more visually heterogeneous environments where a replication of just one background type would increase conspicuousness amongst neighbouring habitats. However, it would not be until the turn of a new century that the adaptive benefit of disruptive patterns over background matching would be empirically demonstrated (Cuthill *et al.* 2005).

Following on from Thayer, the zoologist Hugh Cott described a variety of ways in which patterns could be structured to enhance their disruptive effect (Cott

1940). These ideas laid the framework for a variety of sub-principles which are still used today (Stevens & Merilaita 2009). Like Thayer before him, Cott combined his knowledge of artistic principles with his own field observations to understand how colour and tone may help disguise the characteristic form of an animal. One such principle was that of constructive shading, which has since become known as edge enhancement (Egan *et al.* 2016; Osorio & Srinivasan 1991). Cott used this term to describe a particular type of disruptive patterning where the contrasting patches were “graded in tone” so that light patches became progressively lighter and dark patches became progressively darker (figure 1).



**Figure 1**

An example of the difference between a stepwise edge and an enhanced edge, based on the patterning of the Australian grass frog (*Limnodynastes tasmaniensis*). The intensity values were gathered from transects across the patches, with the blue line representing the stepwise edge (top right) and the red line representing the enhanced edge (bottom right). The pattern graphics were created in Inkscape (2019) and were not intended to reflect any particular chromatic/achromatic values.

By displaying colour as a gradient as opposed to stepwise changes, the pattern mimics the appearance of light on naturally curved surfaces, which is thought to create a false sense of relief that disguises the true dimensions of the animal. Cott believed that this visual effect would be particularly beneficial for flat animals such as butterflies and moths whose form would appear conspicuous upon three-dimensionally complex backgrounds, such as bark and leaf matter. In addition to shape, edge enhancement may also create false depth information through the impression of cast shadows between pattern features (Cott 1940).

Whilst edge enhancement may improve camouflage through a false perception of relief, there are other perceptual processes which may be altered by the presence of high contrast borders between pattern features. Egan *et al.* (2016) proposed a second mechanism by which edge enhancement may improve disruptive camouflage, through the enhancement of false edges within a pattern. These false edges are thought to exploit edge detection processes within the visual system which register changes in tonal contrast as the boundary of an object against its background (Stevens & Cuthill 2006). Edge enhancement may therefore create a heightened response in edge detection algorithms which means the false edges within a disruptive pattern are processed more frequently as real edges. Whilst these two theories operate through different perceptual processes, and will be considered separately within this review, it does not necessarily mean that these two functions are mutually exclusive. In fact, Cott (1940) noted that the disruptive effect of edge enhancement would be most effective when pattern features were separated both in space, through the exploitation of edge detection, as well as in depth, through pictorial relief.

#### *Visual processing of edges*

In order to understand how edge enhancement may disrupt the detection of true edges, it is important to consider how this information is typically processed by the visual system. Through a series of experiments on the visual workings of domestic cats (*Felis catus*), the scientists Hubel and Wiesel (1959, 1961, 1962) were able to demonstrate how edge information is reconstructed at various interconnected points along the visual pathway. At its most basic level, the presence of edges was detected by specialised cells found within the lateral geniculate nucleus (LGN). Each of these cells had its own receptive field which corresponded to a specific part of the total visual scene. In line with previous findings by Kuffler (1953), they found that when light hit this area, photoreceptors within the receptive field would either enhance or diminish the neuronal response to the signal. These photoreceptors were grouped together in a centre-surround arrangement to form concentric regions of excitation and inhibition. These cells were most responsive to areas of high tonal contrast where variation in luminance caused one region to be activated more than the other. This resulted in either an increase or reduction in the neuronal firing rate depending on which region experienced the greatest stimulation. When light hit both the regions equally, the two actions cancelled each other out, leading to a nominal response from the neuron.

Further up the visual pathway, Hubel and Wiesel identified two distinct types of cells within the visual cortex which they referred to as simple and complex cells. The simple cells, in contrast to those found in the LGN, displayed receptive fields with regions of excitation and inhibition adjacent to one another. These cells responded best when edges of high tonal contrast aligned with the partition between these two regions. For each part of the visual scene, there were several corresponding simple cells each attuned to a slightly different direction,

allowing the cell to distinguish the orientation of the edges. In contrast, the receptive fields of the complex cells could not be mapped to specific regions but instead responded to edge information at various locations across the visual scene. Hubel and Wiesel proposed that all of these stages were connected through a hierarchical structure; complex cells were generated from the input of multiple simple cells which were in turn formed by the alignment of LGN cells. Whilst the findings of Hubel and Wiesel were restricted to the cat visual system, recent experimental work suggests that similar receptive field patterns are present in a variety of other mammalian groups (Scholl *et al.* 2013) as well as in homologous structures within the avian visual system (Li *et al.* 2006).

The effect of edge enhancement on edge detection processes may be felt at several stages within the visual pathway. Initially, edge enhancement will increase the tonal contrast across the receptive fields found in the LGN and simple cells, leading to an increased response in neuronal firing rate. At higher stages, due to the summation of edge information from neighbouring cells, strong edge enhancement in one area of the visual scene may be able to inhibit weaker signals nearby. In particular, strong edge enhanced internal edges may inhibit weaker boundary edges which provide the receiver with important visual cues with which to identify potential prey items (Troscianko 2009).

### *Creating false edges*

One way to test whether enhanced edges are perceived as real edges by potential predators is through the use of computer modelling, which can reconstruct the visual processes that underpin edge detection in real animals. Osorio and Srinivasan (1991) used this technique to compare the efficacy of edge enhancement in the Australian grass frog (*Limnodynastes tasmaniensis*) against three different edge-detecting algorithms. These models were based on the

different receptive fields found within the visual system, with one model replicating the centre-surround arrangement seen in the retinal ganglion cells and a second model using the antisymmetric arrangement seen in the simple cells. A third model incorporated the outputs from both types of receptive field. All of these models were shown to correctly detect the presence of the enhanced edge, with the first two models exhibiting a greater response when compared to a stepwise control. Osorio and Srinivasan noted that such an effect would enable predators to distinguish between enhanced edges and real edges within a visual scene. However, variation in illumination and the formation of cast shadows can lead to graded edges within nature (Gilchrist 2015), meaning predators may be unable to evolve ways to distinguish between the two types of edge information.

Later, Stevens and Cuthill (2006) were able to demonstrate how the appearance of false edges may enhance crypsis. Again, through the use of computer modelling, they were able to demonstrate how disruptive markings contained false edges which were registered as real edges by the algorithm. They were then able to demonstrate how this affected higher stages of edge reconstruction, resulting in the correct outline of disruptive targets being detected less frequently than targets with only internal-based markings. Higher contrasts between pattern elements was also shown to reduce the effectiveness of edge detection even further. These results matched the authors' previous experimental work demonstrating that disruptive patterns could confer increased survival against avian predators (Cuthill *et al.* 2005). These findings demonstrate that both the arrangement of pattern features as well as the levels of contrast can affect the edge disrupting abilities of a pattern.

*Creating pictorial relief*

As previously mentioned, another mechanism by which edge enhancement may improve camouflage function is through the appearance of false relief across an animal's surface. For this to be possible, the viewer must be sufficiently deceived that the graded tones found within edge enhancement are true representations of shape and depth information. As such, edge enhancement can be seen as a form of visual illusion (Kelley & Kelley 2014). In order to test the viability of this theory, it is important to establish whether animals are able to reconstruct 3D information from 2D visual scenes.

#### *Disguising three-dimensional cues*

When describing edge enhancement, Cott (1940) recognised the parallels between his own ideas and previous work by Abbott Thayer (1896) regarding countershading, which in many ways can be thought of as analogous to edge enhancement. Whilst both forms of colouration are about disguising the surface features of an animal, edge enhancement operates through the creation of false relief whilst countershading acts to obliterate such depth cues. Thayer believed that by expressing dark pigments on areas of the body where light is strongest and light pigment in the areas of greatest shadow, animals are able to cancel out the natural fall of light which can reveal the shape and dimensions of their surface. This may affect concealment through two mechanisms, by the removal of lighting effects which may reduce the effectiveness of background matching, or by the removal of depth cues which render a three-dimensional animal as optically flat (Rowland 2009). Whilst the precise function of countershading is still debated, these patterns are able to positively affect survival (Rowland *et al* 2008).

#### *Inferring shape from shading*

For edge enhancement to produce an effect of false relief, animals must use shading to recognise 3D information within their environment. In humans, depth can be interpreted through both binocular and monocular cues. Binocular cues help visualise depth by creating two images of the scene from slightly different perspectives, with the disparity between these two images providing depth information (Goldstein 2010). In contrast, monocular cues provide 3D information from only one image, meaning humans are able to perceive 3D depth upon a 2D surface (Goldstein 2010). A wide variety of monocular cues exist, including occlusion, texture patterns and shading (Norman *et al.* 2004).

Evidence for shape from shading was shown experimentally in humans presented with a range of computer-generated circles (Kleffner & Ramachandran 1992). These circles were shaded in a vertical gradient, with some fading from light to dark whilst others faded from dark to light. As the human visual system infers that both circles are being illuminated by the same light source, the circles will appear as either convex or concave in shape. During a set of trials, participants were asked to locate the odd one out, which could be either convex or concave in appearance. The trials were repeated with circles that were horizontally shaded. Whilst people were able to locate the vertically shaded circles independent of the number of distractors that were present, this was not the case for horizontally shaded circles. The fact that the same response was not found between the two targets suggests that the participants were not simply responding to colour gradient, but that the vertically shaded circles were in fact being perceived as 3D, allowing them to be identified quicker among a noisy environment. The authors suggested the preference for the vertically shaded circles may represent a fixed response within human visual processing that assumes that light always comes from overhead.

The same experiment was carried out with chimpanzees (*Pan troglodytes*) to identify how shape from shading would differ in non-human test subjects (Tomonaga 1998). Like humans, chimpanzees were able to distinguish between the two circle designs that only varied in shading orientation. Their quick response times also suggest that they were perceiving 3D form, making the targets “pop out” from their background. However, throughout the trials the chimpanzees exhibited the opposite response to humans, reacting quickest to horizontally shaded objects over vertically shaded ones. It was suggested this may be due to a greater sensitivity in chimpanzees to their orientation and the direction of light, as an adaptation to an arboreal lifestyle. Whilst this work provided some of the first experimental evidence of shape from shading, it also highlighted the variation that may exist in perceiving 3D form among even closely related organisms in response to different ecological pressures.

Following this, Reid and Spetch (1998) tested 3D perception in domesticated pigeons (*Columba livia*). To separate shading cues from other potential cues of 3D form, photographs of different shaped objects were edited with computer software to remove shading cues by filling the object with a uniform colour. Pigeons that had previously been trained to peck at the photographs of the 3D images were then provided with a choice between the photograph and the computer-generated image. Despite the only noticeable difference between the two images being the presence of shading cues, the pigeons showed a significant preference for the original photographs, suggesting that they were able to perceive shape from shading. The experiment was repeated with novel objects that the pigeons hadn't seen before to ensure that they were not exhibiting a learned response to the images. The same behavioural response was shown when the pigeons were presented with novel objects, showing that the pigeons

were responding to the cues available rather than displaying a learned response to the original images.

Following on from this work, more experiments were carried out to further understand how pigeons were using shading as a cue for 3D form (Cook *et al.* 2012). Through computer imaging, the authors created a dome and a trough shape. The birds quickly learned to distinguish the two stimuli and could be trained to respond to either of the shapes by pecking to receive a reward. They continued to exhibit this same response even when the perspective was skewed so that the dome or trough was being observed from a different perspective. This demonstrated that the pigeons were not simply learning the exact shape of the original stimuli, but that they were able to perceive the 3D form of the image and make the correct choice. They continued to select the correct image when the shape of the dome or trough was altered into different peaks. Recently, this work was replicated with starlings (*Sturnus vulgaris*), a species which originates from a different evolutionary lineage to pigeons (Qadri *et al.* 2014). The results strongly replicated those previously found with pigeons, suggesting that shape from shading could be a common feature within avian visual processing.

Whilst there is evidence to suggest that animals use shading to reconstruct 3D information, it is less clear how this visual process is exploited by animal camouflage. One animal that appears to exploit sensory processes involving 3D form for concealment purposes is the European cuttlefish (*Sepia officinalis*). Cuttlefish, as well as other cephalopods, are a popular study subject for animal colouration due to their ability to rapidly change colour and pattern according to their environmental substrate. Cephalopod colouration is typically classified into three distinct categories: uniform, mottle and disruptive (Hanlon 2007). Disruptive patterns are typically comprised of block shapes and triggered when the animal

is resting on pebbles. In European cuttlefish, the disruptive pattern often exhibits a large white square on its dorsal side, which may help to break up the outline whilst resembling the pebble background (Hanlon 2007). Cuttlefish can recognise real pebbles from photographs of pebbles (Kelman *et al.* 2008), which results in a stronger response in their disruptive colouration, demonstrating that the cuttlefish's perception of their 3D environment impacts their camouflage patterning. They also presented the cuttlefish with a checkerboard that was separated so that the white squares were on a higher plane (i.e. closer to the cuttlefish) than the black squares. Not only did the cuttlefish recognise the depth within the checkerboard, but they only showed a response in their colouration when the white squares were above the black. The authors suggest that highlights and shadows may play a role in cuttlefish 3D perception. Later work by Zylinski (2016) appears to corroborate these earlier findings. In their experiment, they presented cuttlefish with computer-generated circles which were either uniform in colour or shaded. They also presented some of the cuttlefish with 3D hemispheres as a control as well as circles with stepwise changes in tone to account for shading differences. Not only did they find that shading influenced the display of disruptive colouration, but that it also influenced the physical appearance of the disruptive markings. In particular, the white square on the dorsal surface varied in tone across the different trials, leading to asymmetry in colour. This is a form of pictorial relief, with the dark tones mimicking natural shadows and creating a sense of depth on the flat surface of the cuttlefish. The white square showed greatest pictorial relief when presented with shaded circles as opposed to uniform white circles. Stepwise circles also failed to induce pictorial relief patterning, suggesting that shading as opposed to two tone colours is important in recognising 3D information within the environment. Whilst it does

appear that cuttlefish are able to recognise the 3D information from their environment, and even incorporate that information in the form of pictorial relief on their surface, it is unknown if this actually provides adaptive benefits through increased survival from predation. Whilst the white square appears 3D to our vision, this is not necessarily the case for cuttlefish predators and the white square may perform another function we are not aware of.

### *Experimental tests of edge enhancement*

To date, there have only been four experimental tests on the effect of edge enhancement on camouflage function. The first of these was carried out by Egan *et al.* (2016), who used computer generated search tasks to compare the detectability of various disruptively patterned targets. Their results showed that human participants took longer to locate edge enhanced targets than disruptive controls. When questioned, participants also reported perceiving edge enhanced targets as having a greater sense of depth in relation to their background. The combination of these results provided the first support for the idea that edge enhancement not only improves crypsis but that it may do so through a disruption of real depth cues.

Following on from this, Sharman *et al.* (2018) used a similar experimental procedure to test whether edge enhancement may also alter the identification of targets beyond initial detection. For this, participants were asked to locate a series of camouflaged targets that resembled animal shapes before identifying them as either predator or prey. In keeping with Egan *et al.*, they found that edge enhanced targets took longer both to locate as well as to identify. When placed on a highly contrasting background which offered no opportunity for concealment, edge enhanced targets still took longer to identify suggesting that these features can still provide camouflage benefits regardless of detection probability. Further

work carried out by Sharman and Lovell (2019) suggested that identification may be reduced in edge enhanced targets through a disruption of the outline which prevents discrimination of the true shape.

The most recent work on edge enhancement was carried out by Adams (2019), who discovered that the camouflage benefits of edge enhancement are diminished in the presence of binocular depth cues. This suggests that edge enhancement may disguise the true shape of an animal through pictorial relief, but that when combined with more accurate measures of depth, edge enhancement no longer provides camouflage benefits above and beyond other disruptive patterns.

All of these experimental tests support the previously held idea that edge enhancement improves camouflage function through a false perception of relief which is able to disguise the true shape and outline of the animal. The next stage in investigating these types of patterns is to determine how they operate within a more ecologically relevant setting. To do this, I first quantified the strength of edge enhancement across a variety of species of British moth through the use of calibrated digital photography. The purpose of this was to identify whether there were any general patterns in how edge enhancement was typically expressed, both between species and within individual patterns.

## Chapter 1: What does edge enhancement look like?

### Introduction

Despite a growing body of evidence suggesting that edge enhancement can improve camouflage efficacy (Adams *et al.* 2019; Sharman & Lovell 2019; Sharman *et al.* 2018; Egan *et al.* 2016), it still remains unclear how these features are typically expressed within real animal patterns. To date, our understanding of edge enhancement has largely been shaped by anecdotal observations in lieu of more objective forms of quantitative analysis. This has led to a lack of clarity regarding the precise spectral properties that constitute an enhanced edge.

In order to make direct comparisons between different patterns, it is crucial to collect objective values of reflectance data. One way to gather such information is through the use of digital photography, which can be calibrated to produce normalised and linear outputs from a visual scene (Stevens *et al.* 2007). Whilst this process was traditionally carried out through a number of discrete stages, the development of integrated software has made digital photography an even more accessible tool in the analysis of animal patterning (van den Berg *et al.* 2019; Troscianko & Stevens 2015).

To date, edge enhancement has been reported in a range of different taxa, including, snakes, frogs and felids (Egan *et al.* 2016) but has yet to be compared across closely related species. Thus, it is unclear how much variation there is in the form of enhanced edges. I used digital photography of museum specimens of moths to quantify enhanced edges both within individuals and across species.

Moths make an ideal study subject for evaluating cryptic colouration. As most moths communicate through pheromones (Löfstedt 1997), their patterning is unlikely to have evolved for conspecific communication and is instead more

likely to be an anti-predator adaptation. This is particularly relevant for the majority of moths which have no form of chemical defence and are particularly vulnerable to predation from visually hunting predators during the day when they are at rest on trees or leaf matter (Endler 1984). In addition, both the quantity and accessibility of public collections of Lepidoptera means that accessing specimens for pattern analysis is comparatively easier than for other taxonomic groups.

After gathering calibrated images of the various moth species, the strength of edge enhancement was quantified by two separate metrics: intensity and offset. Intensity represented the maximum reflectance difference across the enhanced edge whilst offset measured the change in reflectance leading up to both the light and dark edge respectively. For each species, edge enhancement was compared at two points between the centre of the wing and near the outline. The purpose of this was to establish whether edge enhancement is limited to particular areas of an animal's surface, which may provide clues as to the adaptive significance of these features. For example, if edge enhancement is greater near the outline of the moth, this may suggest that edge enhancement provides camouflage benefits by disrupting the detection of true edges.

## **Methods**

### *Image Acquisition*

Moth species with edge enhancement were visually selected from a photographic guide of British Lepidoptera (Manley 2008). Edge enhancement was identified by the presence of discrete patches which became progressively lighter and darker at the points where they converged. A total of 50 species of moth from 9 different families were selected from a total of 2147 examples of both macro and micro moths. This excluded any species containing combinations of red, yellow or black

which are typically associated with aposematic colouration in insects (Joron 2009). When a species exhibited sexual dimorphism in its patterning, the sex with the most obvious edge enhancement was selected.

Specimens of each species were then located within the collections held at the Royal Albert Memorial Museum in Exeter, UK. 16 species were not part of the collection and were therefore excluded from analysis. Following an ad hoc inspection of the museum cabinets, nine more species were included which had not previously been identified from the photographic guide. This resulted in a total of 43 species being photographed from the collection.

One specimen of each species was then photographed using a Sony a7 camera converted to full spectrum sensitivity (Advanced Camera Services Limited, Norfolk, UK) with a Nikkor EL 80mm lens. Two photographs were taken per specimen, one in the human visible spectrum (400-680nm) using a Baader UV-IR filter (Baader Planetarium, Mammendorf, Germany) and one in the UV spectrum (320-280nm) using a Baader UV pass filter. Specimens were photographed indoors under a UV/white broad emission spectrum lightbulb simulating D65 illumination (Iwasaki Eye Colour arc lamp). The camera was held in position with a tripod and a custom-made lens slider was used to allow the changing of filters without altering the position of the camera. Photographs were taken in RAW mode using a fixed aperture (F8) and contained two grey standards of 7% and 93% reflectance (SphereOptics Zenith Polymer) and a scale bar.

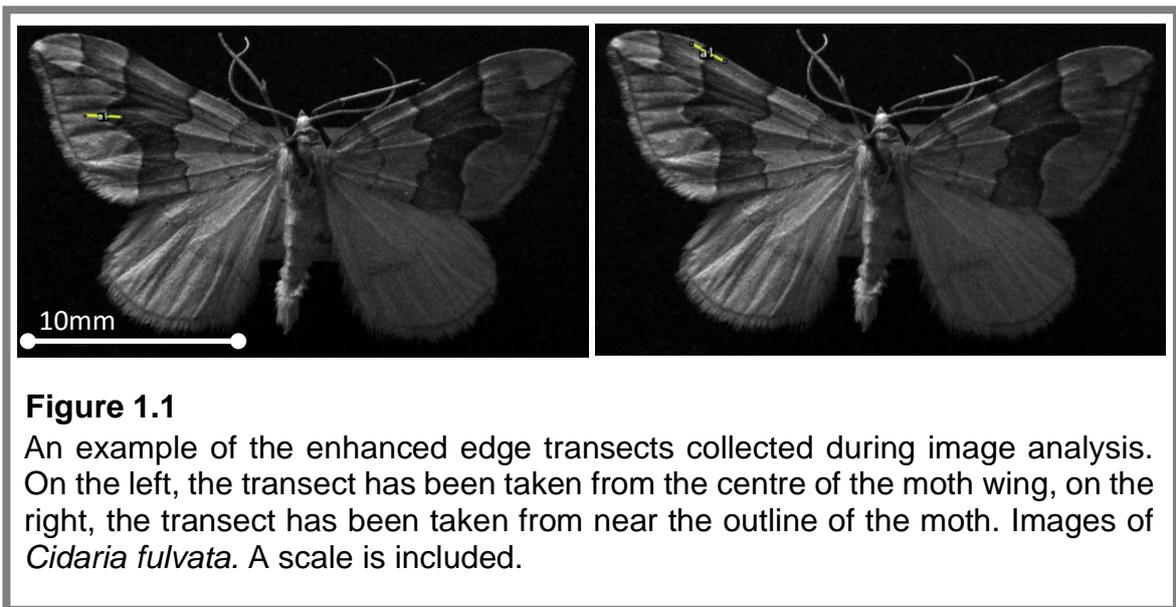
### *Image Analysis*

Following image acquisition, analysis was restricted to those species which exhibited enhanced edges that intersected their whole surface, as opposed to those containing enhanced edges only on internal pattern features. This was

done as edge disruption and surface disruption are generally considered as separate camouflage principles (Stevens & Merilaita 2009) and may therefore interact differently with edge enhancement. For an experimental test on the effect of edge enhancement between edge-intersecting and internal-based patterns, see chapter 2. This resulted in a total 23 species being included for image analysis purposes.

The visible and UV photographs for each specimen were checked for suitable exposure levels and then combined using the MICA toolbox in Image J (van den Berg *et al.* 2019; Troscianko & Stevens 2015) to produce a multispectral image with linear values of reflectance relative to the grey standards. A Gaussian blur was applied to reduce noise with a radius of 5 and a standard deviation of 0.61.

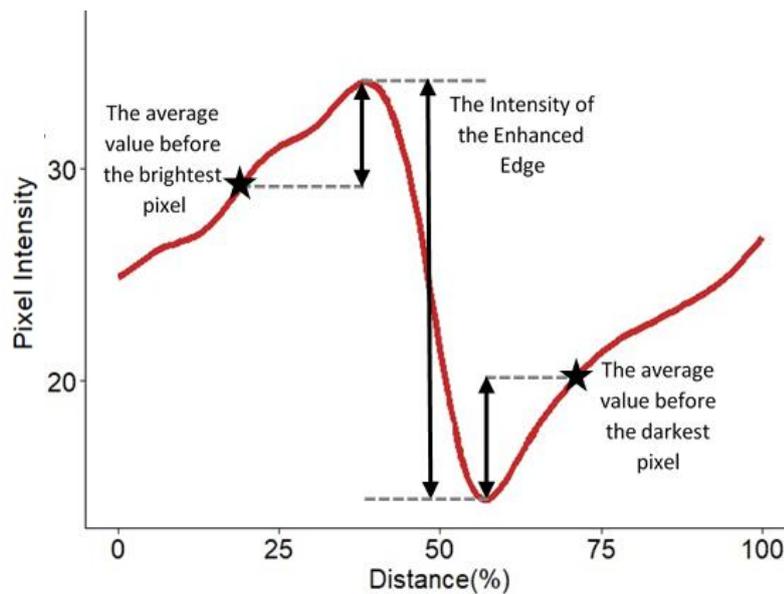
Objective reflectance values were then measured from transects running perpendicular to the enhanced edge using the line tool and plot profile function. Transects were fractionally longer than the enhanced edge to record the baseline values within the pattern. Each transect was 7 pixels wide, providing an average value of reflectance for each point. Within the multispectral image, measurements were taken from the visible green channel as studies have shown that the photoreceptors responsible for detecting luminance information are most sensitive to wavelengths within this range (Osorio & Vorobyev 2005). To compare the profile of the enhanced edge within the same pattern, two transects were established per moth along the same enhanced edge, with one near the outline and one near the centre of the wing (figure 1.1). Both transects were of the same length.



### *Statistical Analysis*

The reflectance values from the image transects were then plotted and analysed using R 3.6.2 (R core Team 2019). Edge enhancement was quantified by two separate metrics; the intensity and the offset. The intensity of the enhanced edge was calculated by measuring the reflectance difference between the brightest pixel in the light edge and the darkest pixel in the dark edge. The high offset was calculated by taking the average pixel value before the brightest pixel and recording the difference. The low offset was similarly calculated as the difference between the darkest pixel and the average value after this point (see figure 1.2).

The intensity of the enhanced edge was then compared between the centre of the moth and near the outline. As the data were not normally distributed, a Wilcoxon matched-pairs signed rank test was used to compare the intensity difference of the enhanced edge between the outline and the centre of the moth wing.



**Figure 1.2**

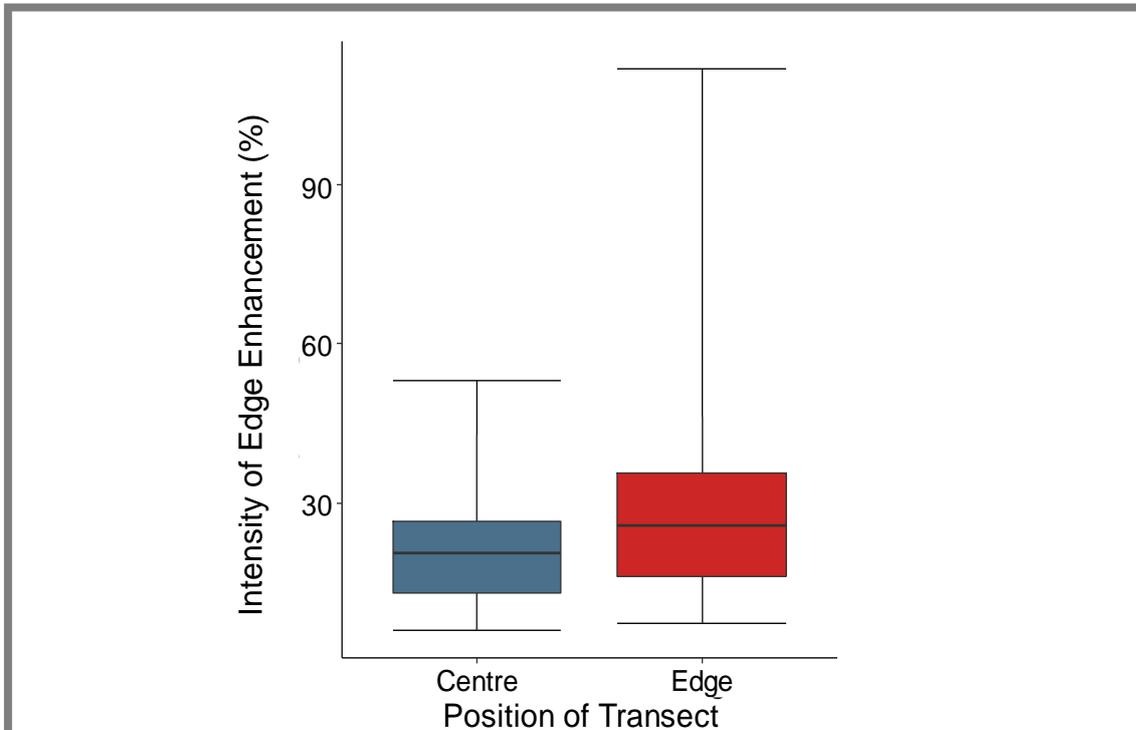
A diagram illustrating the various ways in which edge enhancement was quantified across the moth species. The red line represents a typical reflectance output across an enhanced edge, with the arrows marking the measurements of intensity and offset which were used for image analysis.

## Results

Across the 23 species of moth, the intensity of edge enhancement was shown to vary between 6.04% and 111.91% relative to the grey standards with a median of 23.79% (IQR = 16.65%). Figure 1.3 shows the intensity of edge enhancement for each species according to its location on the wing. There was found to be no statistically significant difference in the intensity of edge enhancement near the centre and near the outline of the wing (Wilcoxon matched-pairs signed rank test:  $N = 23$ ,  $V = 85$ ,  $p\text{-value} = 0.111$ ).

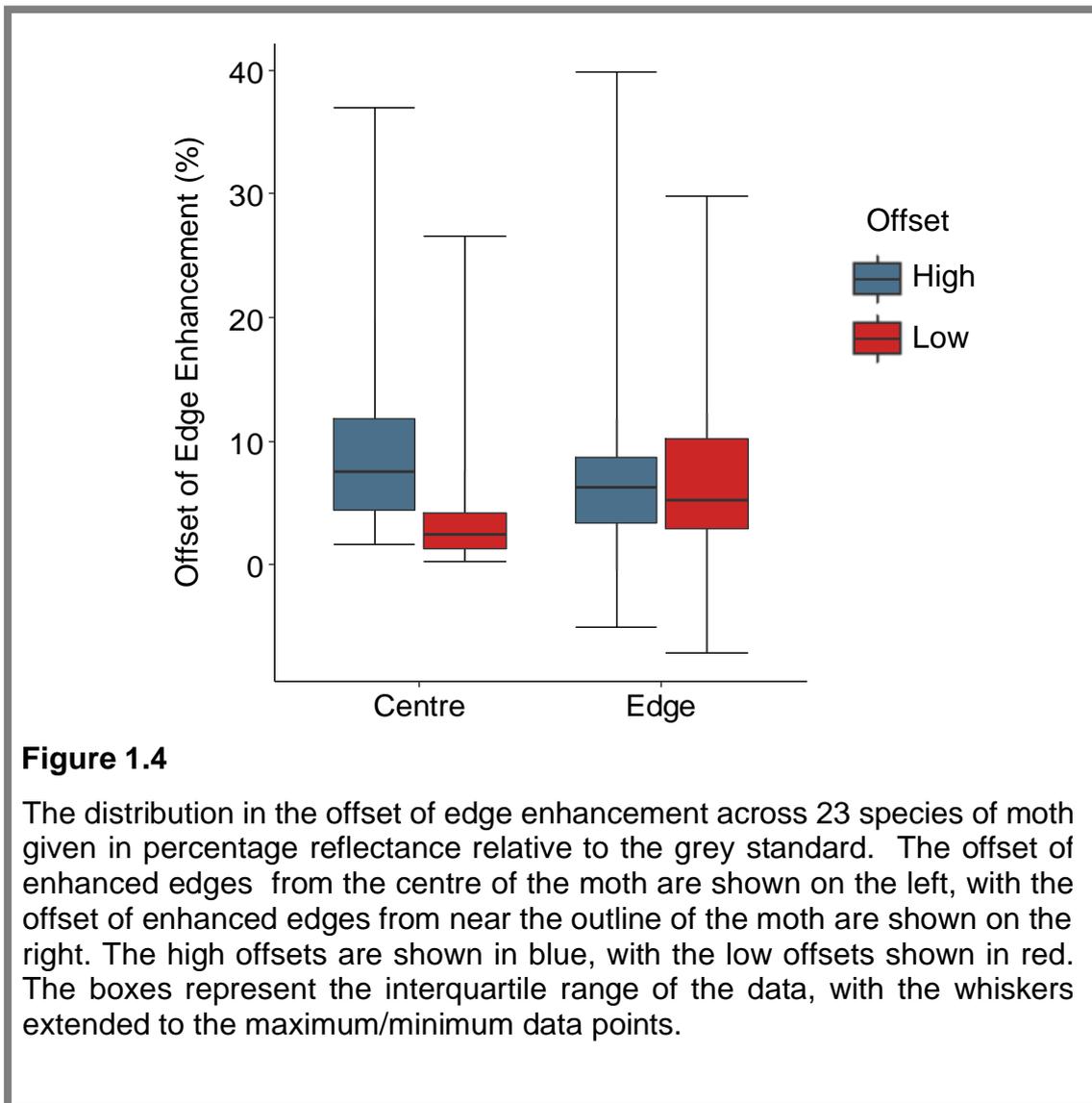
Across the 23 species of moth, the offset was shown to vary across the wing (figure 1.4). Within the centre, the difference between the high and low offset was shown to be statistically significant ( $N = 23$ ,  $V = 248$ ,  $p\text{-value} = <0.001$ ), with a median high offset of 7.4% (IQR = 7.34) against a median low offset of 2.4% relative to the grey standard (IQR = 2.88%). In contrast, near the outline of the moth, the offsets were found to not differ significantly from one another ( $N = 23$ ,

V = 131, p-value = 0.846), with a median high offset of 6.28% (IQR = 5.24%) against a median low offset of 5.20% (IQR = 7.27%).



**Figure 1.3**

The distribution in the intensity of edge enhancement across 23 species of moth given in percentage reflectance relative to the grey standard. The intensity of enhanced edges from the centre of the wing are shown in blue, whilst the intensity of enhanced edges from near the outline of the wing are shown in red. The boxes represent the interquartile range of the data, with the whiskers extended to the maximum/minimum data points.



**Figure 1.4**

The distribution in the offset of edge enhancement across 23 species of moth given in percentage reflectance relative to the grey standard. The offset of enhanced edges from the centre of the moth are shown on the left, with the offset of enhanced edges from near the outline of the moth are shown on the right. The high offsets are shown in blue, with the low offsets shown in red. The boxes represent the interquartile range of the data, with the whiskers extended to the maximum/minimum data points.

## Discussion

Our results represent the first attempt to quantify the variation in edge enhanced patterns across closely related species. Across the 23 species of moth, the intensity of the enhanced edge was fairly consistent and was skewed towards the lower values. This was true for both sets of transects, showing that the intensity of the enhanced edge was similar between the centre and near the outline of the wing. This consistency within the intensity of edge enhancement suggests these features may be optimised at a particular achromatic contrast in order to achieve maximum crypsis. Within the literature, there has been much debate as to the

level of contrast that disruptive camouflage works best at (Stevens & Merilaita 2009). Stevens *et al.* (2006) found that high contrast disruptive markings were able to reduce detection, but that they were most effective when they used luminance values that were found in the background. Troscianko *et al.* (2013) observed a similar effect, with high contrast markings reducing detectability apart from when the disruptive contrast represented the extreme achromatic values found in the background. However, in addition to this, they also found that high contrast patterns were learnt quicker than low contrast markings by participants who were viewing the targets over successive attempts. Whilst these results suggest some cost to high levels of contrast, they were carried out with patterns comprised of two-tone shapes with stepwise transitions as opposed to edge enhancement. It is possible that edge enhancement is an adaptation that allows the presence of high contrast markings but only in locations where they provide maximum disruptive effect (i.e. at false edges). By keeping high contrast markings to a smaller space, edge enhancement may reduce the ability for predators to form search images which they can use to locate such patterns when they are encountered a second time.

Whilst the intensity of the enhanced edge was consistent across the wing, the offset values showed variation. At the edge of the moth, the high and low offsets were statistically similar, whereas the high offsets were significantly greater than the low offsets in the centre of the wing. The adaptive function of this feature will depend upon the precise mechanisms by which edge enhancement achieves camouflage.

The fact that the offsets were greater at the edges suggests that edge enhancement plays some role in edge disruption. However, the precise mechanisms it does this may be altered in different ways. By displaying an

enhanced edge perpendicular from the real outline, the enhanced edge may act to inhibit the detection of the true edge through a visual process known as summation (Troscianko *et al.* 2009). This process may also be why the low offset is reduced in the centre of the wing, in order to maximise the edge disruption value. Previous experiments on edge enhancement have found that edge enhancement can reduce identification, possibly through disguising the shape of the outline (Sharman & Lovell 2019; Sharman *et al.* 2018).

It is also possible that the profile of edge enhancement is greater at the edges where it creates a greater sense of pictorial relief. In terms of pictorial relief, the light and dark edges can be thought of as both the highlights and the shadows of depth perception. Shadows are particularly important in establishing depth between two objects, so that one appears to be visually raised in front of another (Mamassian *et al.* 1998). Whilst it seems as though pictorial relief should remain consistent across a pattern to ensure the whole of the surface is effectively broken up into visual planes, this makes the assumption that the animal's surface is level. However in many moths, the centre of the moth is raised slightly by the body, with the wings sloping down at either side. In order to truly disguise the characteristic 3D shape of the moth, the depth relief should be greater at the edges to account for this difference in height. The shadows are therefore stronger at the edges to create this effect.

The findings from this chapter demonstrate how edge enhancement is not a fixed trait but shows variation both between species and even within individual patterning. In particular, the strength of edge enhancement was found to be greater near the outline of the moth compared to the centre of the wing. Previously, models of edge enhancement have been based on the assumption that these features are expressed equally across a pattern, however edge

enhancement may be optimised at locations where it creates the greatest camouflage effect.

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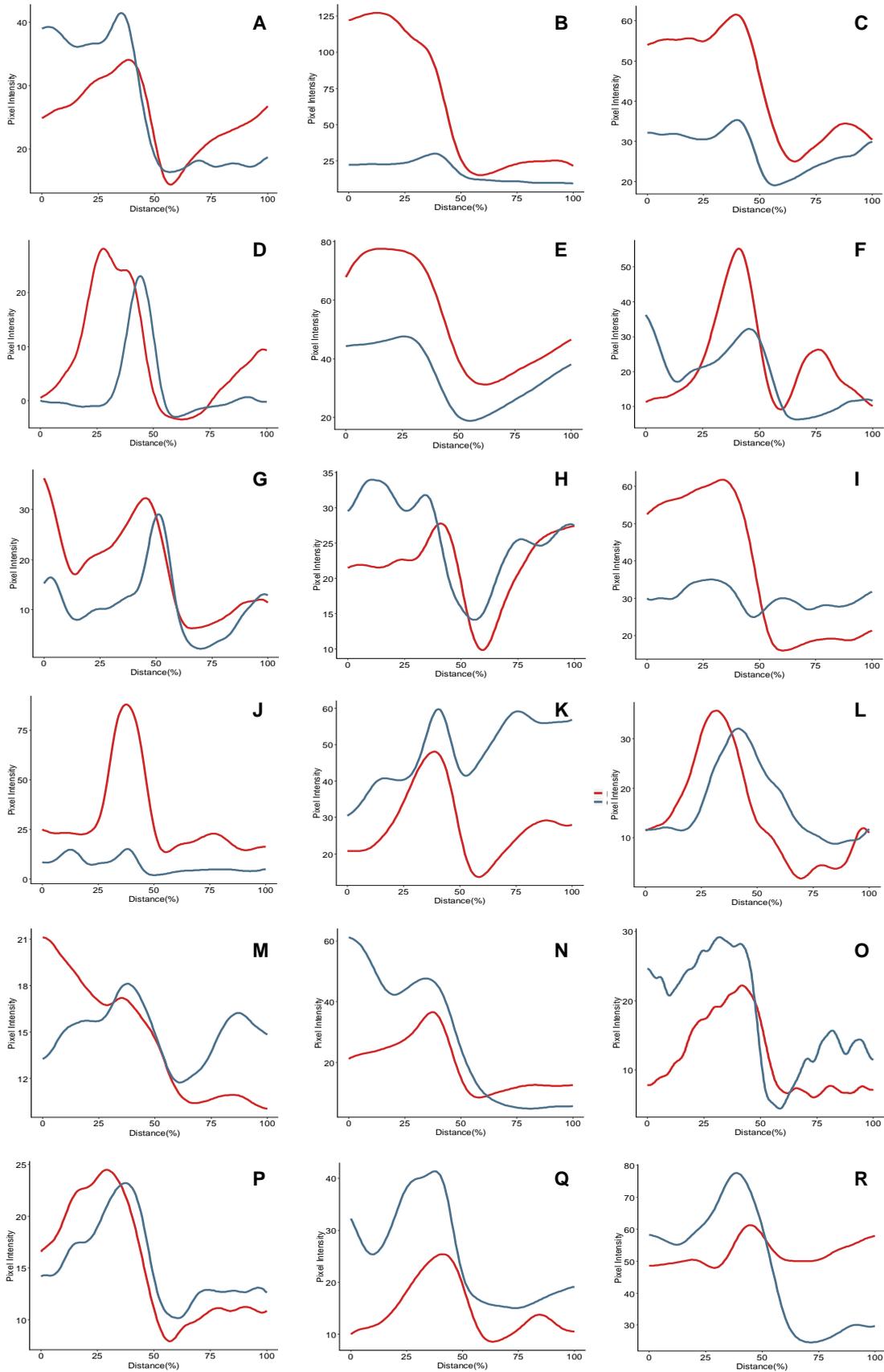
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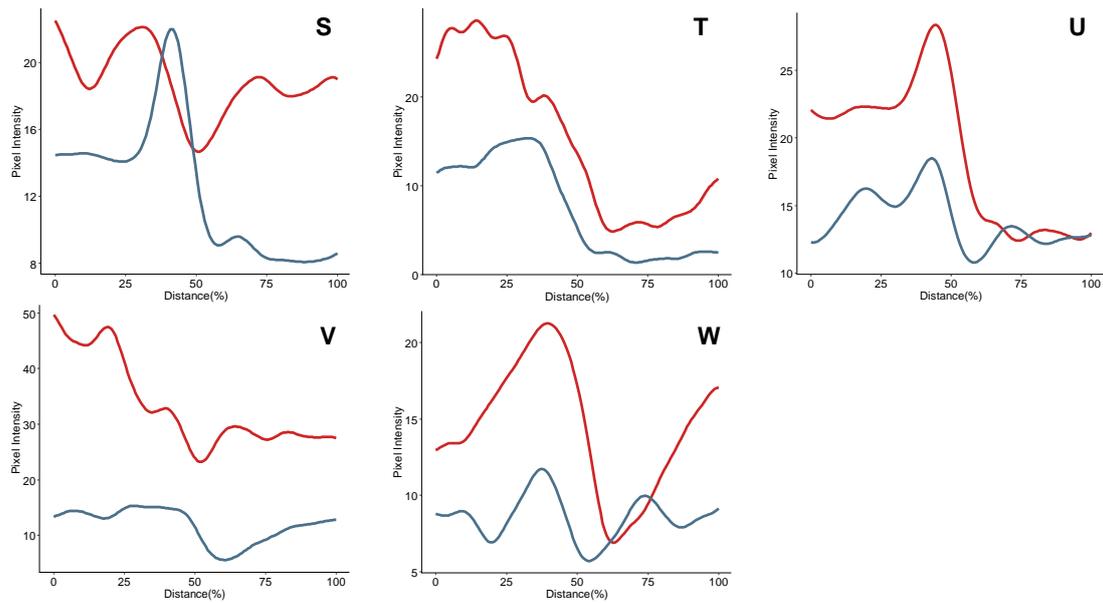
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## Supplementary materials

A) The plot profiles from all 23 species of moth included within image analysis in chapter 1.





The pixel intensity of an enhanced edge in 23 moth species. The two lines represent separate transects along the same enhanced edge, one near the outline of the wing (red), and one at the centre of the wing (blue). The moth species shown are: A) *Cidaria fulvata*, B) *Cosmia diffinis*, C) *Cosmia trapezina*, D) *Endromis versicolora*, E) *Eublemma parva*, F) *Euclidia glyphica*, G) *Euclidia mi*, H) *Eulithis mellinata*, I) *Eulithis populata*, J) *Eulithis prunata*, K) *Eulithis testata*, L) *Habrosyne pyritoides*, M) *Hylaea fasciaria*, N) *Hypena crassalis*, O) *Lasiocampa quercus*, P) *Malacosoma neustria*, Q) *Pelurga comitata*, R) *Petrophora chlorosata*, S) *Phlogophora meticulosa*, T) *Proserpinus proserpina*, U) *Pyralis farinalis*, V) *Scotopteryx mucronata*, W) *Smerinthus ocellata*.