

**Camouflage through behavior in moths: the role of background matching and disruptive coloration**

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Camouflage can be attained via mechanisms such as background matching (resembling the general background) and disruptive coloration (hiding the detection of an animal’s outline). However, despite much conceptual work with artificial stimuli there have to date been few studies of how such camouflage types work in real animals in their natural environments. Here, using avian vision models and image analysis, we tested which concealing mechanisms operate to provide camouflage during behavioral choice of a resting position in 2 bark-resting moths, *Hypomecis roboraria* and *Jankowskia fuscaria*. Our results suggest that both species reinforced their crypticity in terms of both background matching and disruptive coloration. However, the detailed mechanisms (such as achromatic/chromatic matching or pattern direction matching) that each species exploits differed between the 2 species. Our results demonstrate that an appropriate behavioral choice of background and body orientation is important to improve camouflage against natural predators, and highlight the mechanisms that confer camouflage to cryptic animals in their natural habitats.

*Key words*: background matching, behavior, camouflage, crypsis, disruptive coloration, predator–prey

**INTRODUCTION**

Predation is a prevalent selection pressure across animal taxa and many animals have evolved defensive coloration as a primary defense against predators (Poulton 1890; Cott 1940; Edmonds 1974; Ruxton et al. 2004). A common example of defensive coloration is camouflage (Stevens and Merilaita 2011). Visual camouflage deceives the perceptual mechanisms of predators and protects prey by preventing detection (crypsis) or recognition (e.g., masquerade) against the background substrate or environment (Stevens and Merilaita 2009a). A range of concealing mechanisms has been proposed for effective camouflage, including background matching and disruptive coloration (Thayer 1918; Cott 1940; Stevens and Merilaita 2009a, 2011).

Background matching prevents detection by possessing body colors and patterns that resemble those in the neighboring background (Endler 1984). The importance of background matching in avoiding predation has been demonstrated in a range of predation experiments (e.g., Kettlewell 1955; Johannesson and Ekendahl 2002; Cook et al. 2012). Disruptive coloration, recognized by Thayer (1918) and further developed by Cott (1940), breaks up the shape of an animal against the background and conceals the outline. Disruptive coloration works by hindering the detection, or recognition of an animal’s true outline and shape (Stevens and Merilaita 2009b). The efficacy of and mechanisms underlying disruptive coloration have been studied in some detail and demonstrated recently, mostly using artificial prey (e.g., Cuthill et al. 2005; Merilaita & Lind 2005; Schaefer and Stobbe 2006; Stevens and Cuthill 2006; Fraser et al. 2007; Webster et al. 2013). Another means by which concealment could be attained is by staying near visually complex backgrounds (Merilaita 2003), because these should increase the visual information that needs be processed, making search tasks more challenging, as well as potentially making it difficult for the viewer to identify the shape of an animal (Dimitrova and Merilaita 2010, 2012). Although the effectiveness of these concealing mechanisms has been explored in various recent studies, the vast majority of work has been conducted with
artificial prey or under laboratory conditions, and it remains poorly understood how real cryptic animals exploit these mechanisms to avoid predators in nature.

In studying animal coloration, various methods, such as spectrometry (e.g., Stuart-Fox et al. 2004) or photography (e.g., Lovell et al. 2013; Stevens et al. 2014), have been used for the quantification of the colors of animals. There are several advantages of using digital photography over the other methods (Endler and Mielke 2005; Stevens et al. 2007), most notably that it can capture and analyze entire color patterns of animals along with the surrounding background, and can employ powerful image analysis tools, such as edge-detection algorithms. Another useful application of photography in camouflage studies is that it can determine the contribution of different concealing mechanisms (such as background matching or disruptive coloration) separately in contributing to the degree of camouflage of animals.

Stevens and Cuthill (2006) tested the mechanism by which disruptively patterned prey conceal their contours, in terms of how it may exploit early visual processing mechanisms of vertebrate (e.g., avian) predators by using photographs of moth-like prey models on natural tree trunks. They modeled avian vision and employed edge-detection algorithms to quantify the effectiveness of disruptively colored and non-disruptive background matching prey in concealing their contours, and found that disruption reduced the amount of information left corresponding to the target edges. Recently, Lovell et al. (2013) identified the role of egg-laying behavior and substrate choice by quail in concealing their eggs. They performed background choice experiments using differently colored artificial substrates and tested whether quail lay their eggs on the background that provides the best camouflage. Furthermore, they quantified the degree of background color matching and disruptive camouflage of each egg against different backgrounds using photographs and image analysis. Their findings suggest that animals in the wild may be able to choose resting backgrounds that specifically optimize either background matching or disruptive coloration, or both. These 2 studies employed image analysis techniques using tightly controlled backgrounds or prey. However, to date, only a few studies have analyzed the appearances and camouflage of real animals from their natural environments (e.g., Endler 1984; Merilaita 1998). There has also been very little work into the role of behavioral choice to identify the concealing mechanisms that animals employ. In this study, we used bark-resting moths on their natural background to test how moths’ behavioral choice of resting positions mediates the degree of camouflage, and which concealing mechanisms moths exploit.

Bark-resting moths are known for their behavioral background selection for camouflage; they prefer to stay near backgrounds that exhibit colors or brightness similar to their own wing color (Sargent 1966; Grant and Howlett 1988), and adopt adaptive resting orientations that reinforce their crypticity (Pietrewicz and Kamil 1977; Webster et al. 2009). Recent studies revealed that some bark-resting moths can actively seek out cryptic resting positions and body orientations elaborately after landing on tree trunks by re-positioning (Kang et al. 2012), and they are more likely to do so when the crypticity conferred at the initial landing position is low (Kang et al. 2013a). However, previous evidence for this adaptive behavior of moths was based on detection data from non-real predators of moths (humans) and disregarded the specific mechanistic explanations that provided the moths with better camouflage. Here, we use image analysis and avian vision models to identify the concealing mechanisms that are involved in this adaptive behavior of moths.

METHODS

We used Hypomecis roboraia and Jankowskia fuscaria for testing (Figure 1). Both species are nocturnal and relatively common in East Asia. Adult moths appear from June to September and usually rest on various tree trunks during daytime. These species are chosen because previous studies show that they are known to actively search for new cryptic resting positions (by re-positioning) after landing on tree trunks (Kang et al. 2012). For both species, the experimental procedures were identical except that Hypomecis roboraia have 3 treatment groups (Initial, Final, and Stay, see below) whereas Jankowskia fuscaria have only 2 treatment groups (Initial and Final).

Acquisition of moth images

During June–September, 2012–2013, we collected moths near black lights that we setup in the study site (Mt. Baekwoon, South Korea; N35°01’54.30”; E127°36’22.30”). The moths were individually kept in small plastic containers with sugar-moistened tissue. Next

Figure 1
Typical resting postures of (a) H. roboraia and (b) J. fuscaria.
morning, we released the moths by letting them fly to nearby tree trunks (Pinus taeda). We then photographed the moths (with manual white balancing and exposure setting) in their initial landing positions, waited for 1 h until they re-positioned their bodies, and photographed the same moths again in their final resting positions (the distance between the camera lens and moths was roughly 40 cm). When photographing, we positioned the camera lens at the same height as moths and used slightly under-exposure setting to avoid saturation (Stevens et al. 2007). To avoid back-lighting, we included only the moths and nearby tree bark within the camera’s field of view and put a Macbeth color checker chart within the view for later image calibration. All photographs were obtained in the shade (by forest canopy or clouds) to minimize the effect of different light conditions on photographs. We used a Nikon D80 fitted with Nikkor 18–55 mm lens in 2012, Sony α65 fitted with 18–55 mm SAM lens in 2013 (focal length of the lens was set to F5.6, shutter speed varied depending on the light conditions). Photographs were saved as RAW image type and converted to 8-bit TIFF by the converting programs from each manufacturer (View NX2 for Nikon, Image Data Converter for Sony camera). In total 203 moths were successfully photographed and used for the analysis (103 H. roboraria and 100 J. fuscaria).

Image calibration

First, each image was linearized and equalized using gray references of the color checker (Stevens et al. 2007). Next, we cropped a 7 cm × 7 cm area of each image by putting the moth target in the center (wingspan of both moths ranged from 3 to 5 cm) and re-sized (always reduced) the images to 560 pixels × 560 pixels using bicubic interpolation. Then we transformed the camera’s red, green, and blue channel pixel values to a bird-specific color space (predicted photon catches for each cone cell type) using a polynomial mapping method (Párraga et al. 2002; Westland and Ripamonti 2004; Stevens et al. 2007, 2014) by a custom-built MATLAB program. Camera sensor sensitivities were obtained using quadratic programming methods (Pike 2011).

There exist a number of predators of bark-resting moths, but we considered birds as main predators that prey on the moths during daytime and drive the evolution of the camouflage of bark-resting moths (Cook et al. 2012). Although the color vision of birds show species-specific spectral sensitivities of cone cells (Hart and Vorobyev 2005), they can be generally categorized into 2 types: ultraviolet (UV) sensitive color vision and violet sensitive color vision (Odeen et al. 2011), with the latter being less sensitive to ultraviolet wavelengths. We used the blue tit (Cyanistes caeruleus) as a model species with ultraviolet sensitive color vision, and peafowl (Pavo cristatus) as a model species with violet-sensitive color vision (Hart and Vorobyev 2005). For each pixel, we calculated long wave sensitive (LWS), medium wave sensitive (MWS), and short wave sensitive (SWS) cone photon catches of each model species, and double cone photon catches (LUM) of blue tit model. This double cone data gave rise to our achromatic estimates, as luminance (perceived lightness) because double cones are widely considered to detect and process the lightness of visual signals (Osorio and Vorobyev 2005). We regarded that the fourth cone type in birds (ultraviolet/violet sensitive) would play a negligible role in detecting moths on tree bark in this instance, because both the moths and background tree bark reflect similar and low levels of UV (Kang et al. 2012). Thus, we did not include these cone types into analysis and used trichromatic color analysis (Stevens et al. 2007).

Identifying concealing mechanisms

For each image, we divided it into 3 regions (see Supplementary Figure S1): moth region (internal area of moth body and wings), contour region (contour of moth), and background region (nearby bark). We manually selected these regions using “polygon selection” and “band selection” tools in ImageJ 1.46r. The width of the contour region was set as 4 pixels.

The images of moths were divided into 3 groups: Initial (the initial landing positions of moths that subsequently re-positioned their bodies), Final (the final resting positions of moths that re-positioned their bodies), and Stay (the resting positions of moths that stayed put on their initial landing positions) (Kang et al. 2013a). About 77% of H. roboraria (79/103) re-positioned their bodies, which resulted in the sample size of 79 for both Initial and Final group and 24 for Stay group. In contrast, most of the J. fuscaria re-positioned their bodies (94%; 94/100), which resulted in extremely unbalanced sample sizes between treatments. Thus, we used and analyzed only Initial and Final (N = 94 for each) group for J. fuscara. Then, to investigate the mechanisms by which moths acquire better crypsis after re-positioning, we compared the effectiveness of several concealing mechanisms between treatments by extracting variables from each image, each of which represents a specific aspect of concealment.

Comparing the degree of background color matching

One way of conferring a cryptic effect is by staying near a background that exhibits similar colors to the animal. To test this hypothesis, for each image, we estimated mean photon catches of both moth and background region for each color channel, and calculated the color distance between the moth and background region using log-linear form of color discrimination model, which assumes that visual discrimination is limited by receptor noise (Vorobyev and Osorio 1998; Vorobyev et al. 2001). This model predicts both chromatic (signal inputs from single cones; termed HueDist) and achromatic (double cones; termed LumDist) signal discriminability as a unit of “just noticeable difference” (JND), where 2 colors cannot be discriminated when JND < 1. For the calculation of signal to noise ratio to derive JNDS, we assumed photoreceptor (Weber) noise (σi) for LWS photoreceptors = 0.05 (Vorobyev et al. 1998), and the ratio of the number of SWS, MWS, LWS cone cells (ni) were set as 1.9:2.7:2.7 in blue tit, 1.9:2.2:2.1 in peafowl model (Hart 2001). Then we compared the color discrimination values, in terms of both HueDist and LumDist, between treatments.

Comparing the degree of background pattern direction matching

Another background matching method by which crypsis can be achieved in bark-resting moths is aligning the direction of patterns between moth wings and background tree bark (Wang and Schaefer 2012; Kang et al. 2013b). Like many bark-resting moths, wing patterns of both H. roboraria and J. fuscara are directional, and are assumed to be adaptive in providing alignment between the direction of wing patterns and those of tree bark patterns. Therefore, we quantitatively measured the degree of pattern direction alignment between moths’ wings and background tree barks and compared them between treatments.

One of the ways to define the patterns of color in animal body is following the boundary lines between 2 or more distinguishable color patches. In image processing, these boundary lines can be extracted through “edge detection” algorithms (Marr and Hildreth 1980). These have been successfully employed for animal
camouflage studies (Stevens and Cuthill 2006; Lovell et al. 2013), and their application is supported by behavioral data (Cuthill et al. 2005; Stevens and Cuthill 2006). Previous studies point out that, in animal vision, edge information is likely to be primarily perceived and obtained using achromatic signals (most likely via the double cone photon catches in birds) (Osorio et al. 1999; Stevens and Cuthill 2006). Therefore, we used double cone photon catches of the blue tit model (LUM images) whenever edge detection algorithm was employed.

To detect/define the location of patterns in each image, we employed Canny-Deriche edge detection algorithm (Canny 1986; Deriche 1987) ($\alpha = 1$; smaller $\alpha$ results in more smoothing of an image before detecting edges; the value $1$ is recommended for most cases; “edge detection by canny-deriche filtering” plugin in ImageJ) and applied hysteresis thresholding method (low threshold of the gradient value = 20, high threshold = 60); these values are chosen because preliminary testing with several images yielded similar results to adaptive thresholding methods such as Otsu’s method (Otsu 1975) which searches for the thresholding that minimizes intra-class variance) to create binary image and define edge pixels. Then we calculated the direction angle of each edge pixel (between $-90^\circ$ to $90^\circ$; $0^\circ$ for the edge pixels from a vertical line, $-90^\circ$ or $90^\circ$ for the edge pixels from a horizontal line) and made a frequency table of edge pixel angles (using binned data for every $10^\circ$) for moth region and background region separately. The edge direction angle could be calculated at each pixel location because the edge is not computed on a single pixel basis, but a calculation of edge direction for each pixel takes into account neighboring pixels using the gradient in $x$ and $y$ axis (Canny 1986; Deriche 1987). From these gradient values, the direction angle at each pixel was computed (Canny 1986). The frequency table indicates the overall directionality of detected edges in a given region. Then we standardized the frequencies (dividing the frequency of each bin by sum of all frequencies) and calculated the difference in directionality between moth and background region using earth mover’s distance (EMD) for each image. EMD is a measure of distance between 2 probability distributions and is usually used to measure the dissimilarity between 2 histograms (Rubner et al. 2000). Two distributions are considered to be more similar when EMD is closer to 0. Then we compared the EMD values between treatments.

**Comparing the degree of pattern complexity**

Another means by which camouflage can be achieved is staying on heterogeneous backgrounds where complex patterns in the backgrounds conceal the presence of the animal (Merilaita 2003; Dimitrova and Merilaita 2014). Theories of background matching predict that animals are expected to benefit by this mechanism when the degree of pattern complexity in the animals’ body is similar to those of their adjacent backgrounds. To test whether this mechanism works during the re-positioning, we measured the proportion of detected edge pixels (the number of edge pixels inside the moth body/the number of all pixels representing the moth body) inside moth region (MothEdge), and the proportion of detected edge pixels inside background region (BgEdge) and calculated the ratio between MothEdge and BgEdge (MothEdge/BgEdge; hereafter Complexity ratio; CompRat). This ratio compares the degree of pattern complexity, represented as the number of detected edges, between moth wings and the background. A CompRat value closer to one indicates better complexity matching.

We additionally compared the complexity of background (BgEdge) directly between treatment groups because background complexity in terms of density of pattern elements can provide camouflage effect against avian predators independently of prey background matching (Dimitrova and Merilaita 2014).

**Comparing disruptive effects**

Although a major component of disruptive coloration will be determined by the color patterns animal has, behavioral choice of an appropriate backgrounds could also provide disruptive effects by blending color patches of animals into the background (“differential blending”) (Stevens and Merilaita 2009b; Lovell et al. 2013). For a simple measure of the degree of differential blending, we calculated the number of detected edge pixels within the contour region for each image. The thin contour region width (4 pixels) ensured that if edges were detected within the contour region, they were likely to come from the actual outline of the moths and not from patterns of tree bark or internal moth patterns. Because the areas of the contour region varied between images, we divided the number of detected edge pixels in contour region by the total area of contour region (in pixels) for each image (termed ContEdge) to control for the effect of differences in contour areas between images.

In addition to differential blending, theories, and empirical evidence of disruptive coloration suggest that it works not only by concealing the contour of animal body, but it also does so by having contrasting internal patterns that mask the real outline of animals (Cott 1940; Cuthill et al. 2005; Stevens and Merilaita 2009b; Stevens et al. 2009). Thus, to take this mechanism into account, we calculated the ratio between ContEdge and MothEdge (termed disruptive ratio; DisRat). DisRat shows how well the contours of moths were concealed relative to the patterns inside moths (i.e., concealing only contours of the moths’ wings whereas patterns inside the moths were still visible would give rise to a lower DisRat and a higher disruptive effect).

Finally, we compared ContEdge and DisRat values between treatments. We excluded some moths from the disruptive analysis if part of their wing contour was masked by bark structure.

**Statistical analysis**

We used 1-way analysis of variance (ANOVA) for the comparison between treatments. However, the comparison between Initial and Final groups was essentially different from other comparisons because these groups were derived from the images of the same moth and were not independent from each other. In order to account for this lack of independence, in accordance with Crawley (2012), we set individual moth’s identity as a random factor. Then we adjusted $P$-values using the Holm’s method (Holm 1979) to control for the family-wise error rates. To meet the assumptions of statistical tests, we transformed some variables using square root transformation (HueDist and EMD). Outliers were visually inspected and removed before analyzing. All the statistical analyses were performed in R 3.0.2. We reported mean ± standard error (SE) values for each variable for each treatment in Supplementary Table S1. Figures were drawn by using non-transformed original data.

**RESULTS**

**Background matching in terms of color and luminance**

We found that the level of either chromatic matching or achromatic matching between moth and background increased after re-positioning behavior. In *H. roboraria*, we found no difference in HueDist between treatments in blue tit model (Initial–Final: $F_{1,76} = 3.83$, $P_{adj} = 0.16$; Initial–Stay: $F_{1,101} = 0.02$, $P_{adj} = 1$, Final–Stay:...
$F_{1,101} = 0.26, P_{adj} = 1$; Figure 2a) as well as in peafowl model (Initial–Final: $F_{1,78} = 3.67, P_{adj} = 0.18$; Initial–Stay: $F_{1,101} = 2.13, P_{adj} = 0.30$; Final–Stay: $F_{1,101} = 0.54, P_{adj} = 0.47$; Figure 2c). LumDist was lower in Final group than Initial group in blue tit model ($F_{1,78} = 7.74, P_{adj} = 0.02$; Figure 2e), but we found no difference in LumDist between Initial–Stay ($F_{1,101} = 0.001, P_{adj} = 0.98$) and Final–Stay groups ($F_{1,101} = 1.90, P_{adj} = 0.34$). These results suggest that $H. roboraria$ re-positioned themselves to a location where their wing brightness match better with the background.

In $J. fuscaria$, HueDist was lower in the Final group than Initial group in blue tit model ($F_{1,93} = 22.84, P < 0.001$; Figure 2b) as well as in peafowl model ($F_{1,93} = 31.49, P < 0.001$; Figure 2d). There was no difference in LumDist between Initial and Final group ($F_{1,93} = 0.36, P = 0.55$; Figure 2f). These results suggest that

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**Figure 2**

Chromatic/achromatic color contrast for each treatment. Each subplot shows (a, b) chromatic color contrast (derived from single cone information of blue tit model; HueDist), (c, d) chromatic color contrast (from peafowl model; HueDist), (e, f) achromatic color contrast (from blue tit double cone model; LumDist) between background and moth regions for each treatment for each species. The unit of y-axis is JND (<1 means 2 colors were indistinguishable). The graphs in the left column show the results from $H. roboraria$ (a, c, e; $N = 79, 79, 24$ for each treatment), The graphs on the right column show the results from $J. fuscaria$ (b, d, f; $N = 94$ for each treatment). We plotted barplot with error bars (mean ± SE) for normally distributed data, plotted notched box-whisker plots (median–95% confidence interval notches–interquartiles–min/max/outliers) for non-normal data (for these variables statistics was calculated after transformations as described in the methods).
*J. fuscara* re-positioned themselves to a patch where their wing color was matched better to the background.

**Background matching in terms of pattern direction**

In *H. roboraria*, the degree of pattern direction alignment (EMD) was similar between treatments (Initial–Final: $F_{1,78} = 1.18$, $P_{adj} = 0.56$; Initial–Stay: $F_{1,101} = 3.49$, $P_{adj} = 0.19$, Final–Stay: $F_{1,101} = 1.13$, $P_{adj} = 0.56$; Figure 3a). In *J. fuscara*, pattern direction aligned better (lower EMD values) in Final group than Initial group ($F_{1,91} = 45.81$, $P < 0.001$; Figure 3b).

**Comparison of background-moth pattern complexity**

The patterns in moth wings were generally more complex than the patterns in background (CompRat value > 1 for all groups in both species). Therefore, lower CompRat value indicates better complexity matching. In *H. roboraria*, the complexity between moth wings and background was more similar (i.e., lower CompRat) in Stay group than the other 2 groups (Initial–Stay: $F_{1,90} = 9.55$, $P_{adj} = 0.008$; Final–Stay: $F_{1,90} = 6.26$, $P_{adj} = 0.03$; Figure 4a). We found no significant difference in CompRat between Initial and Final groups ($F_{1,87} = 2.82$, $P_{adj} = 0.10$). In *J. fuscara*, pattern complexity was more similar in Final group than Initial group ($F_{1,90} = 7.07$, $P = 0.009$; Figure 4b).

Direct comparison of background complexity shows that in *H. roboraria*, moths in Stay group were on a more complex patterned background than the other 2 groups (Initial–Stay: $F_{1,88} = 14.94$, $P_{adj} = 0.001$; Final–Stay: $F_{1,88} = 21.66$, $P_{adj} < 0.001$; Figure 4c). We found no significant difference between Initial and Final groups in background complexity ($F_{1,87} = 1.97$, $P_{adj} = 0.17$). In *J. fuscara*, we found no difference in background complexity between Initial and Final group ($F_{1,81} = 2.48$, $P = 0.12$; Figure 4d).

**Comparison of disruptive effects**

Both species of moth concealed their outlines better after re-positioning. In *H. roboraria*, ContEdge was lower in Final group than Initial group ($F_{1,67} = 20.33$, $P_{adj} < 0.001$; Figure 5a) suggesting that moth body contours were less visible after moth’s re-positioning. In *J. fuscara*, ContEdge was lower in Final group than Initial group ($F_{1,67} = 29.33$, $P < 0.001$; Figure 5b) suggesting that the repositioning behavior made the moths’ contour line less visible. However, we found no difference in DisRat between Initial and Final group ($F_{1,81} = 0.80$, $P = 0.37$; Figure 5d). These 2 results imply that both the outline of moth wings and the internal patterns of moth wings became less visible concurrently after re-positioning.

**DISCUSSION**

Our results suggest that, overall, both species of moths became better camouflaged against avian predators after re-positioning their bodies; the estimates of concealment were always lower in Final group than the Initial group whenever estimates of concealing mechanisms showed significant differences. Additionally, in *H. roboraria*, individuals in the Stay group performed better for some of the concealing mechanisms compared with those in the Initial group. These support previous studies on the adaptive value of re-positioning of moths, which employed humans for the detection task (Kang et al. 2012, 2013a). However, the analysis suggests that the mechanisms responsible for concealment in *H. roboraria* and *J. fuscara* differed in some aspects.

In *H. roboraria*, achromatic color matching (variable LumDist) contributed to the improvements in the degree of background matching. However, the difference in mean JND between Initial and Final group was low (0.31; Supplementary Table S1), which suggests that the actual difference that predators can perceive may not be strong. In terms of pattern direction matching, the results show no difference in pattern direction alignment between
Considering that pattern direction alignment is mostly determined by the body orientations of moths, this non-significant result may account for the fact that *H. roboraria* tend to orient their bodies in an adaptive manner (toward left or right side) already at landing, regardless of whether they re-position or not (Kang et al. 2013a). This behavioral trait should result in similar body orientations between treatments, thereby yielding no difference in pattern direction alignment. In terms of background complexity, the moths in Stay group seem to use the potential benefits of resting on more complex/heterogeneous background, which potentially can lead to an improvement in crypticity (Dimitrova and Merilaita 2014). This raises the possibility that background complexity might be involved in triggering the re-positioning behavior of *H. roboraria* and the moths may be less likely to re-position their bodies when nearby furrow structure is complex. This possibility was supported by our data (see Supplementary Figure S2 for the relationship between background complexity and re-positioning behavior; moths were less likely to re-position their bodies when background was more complex), but we did not include this result as main results because our experiments were not designed to explore this specific aspect. In terms of disruptive coloration, *H. roboraria* became better at in concealing contours in terms of both ContEdge and DisRat after re-positioning their bodies. This indicates that the concealment of contour of wings may be one of the main mechanisms that reinforce the crypticity of moths after re-positioning.

In *J. fuscaria*, chromatic color matching (variable HueDist) contributed to the improvements in crypticity in both blue tit and peafowl model, whereas achromatic color matching did not. Unlike in *H. roboraria*, pattern direction aligned better after re-positioning which can be explained by the fact that *J. fuscaria* usually modify their body orientations during the process of re-positioning (Kang et al. 2012). Like *H.roboraria*, *J. fuscaria* generally concealed their contours better after re-positioning in terms of lower ContEdge. But unlike *H. roboraria*, DisRat did not differ between treatments. Considering DisRat compares how much the internal patterns of moths were noticeable relative to the contours of moths, this indicates that for *J. fuscaria*, the internal patterns became less visible as the moths' contours became more blended into the background. One possible reason for this result is that *J. fuscaria* moved to the position where their overall body luminance became darker which makes both the contour and internal patterns hard to recognize (see Supplementary Figure S3 for supporting statistics that *J. fuscaria* became darker after re-positioning). Although the patterns in moth wings do not change, the contrast of internal wing patterns can be changed/reduced from the point of view of both predators and image analysis through behavioral mechanisms such as moving to a more shadowy area, which may result in better background luminance matching through darkening of the whole wing color.

For crypsis, color matching is definitely an important factor, but the relative importance between chromatic and achromatic

**Figure 4**
Degree of background matching in terms of background complexity. Each subplot shows (a, b) the ratio of the pattern complexity within moths to those within background (MothEdge/BgEdge; Complexity ratio), and (c, d) the background pattern complexity (BgEdge) for each treatment. Moths are thought to attain camouflage effect when complexity ratio is low, or background pattern complexity is higher (see Methods section). The graphs in the left column show the results from *H. roboraria* (*N* = 68, 68, 22 for each group), and the other graphs show the results from *J. fuscaria* (*N* = 84 for each group). We plotted barplot with error bars (mean ± SE).
signal in preventing detection of real predators is still unclear; there exists evidence for the importance of both chromatic (Stuart-Fox et al. 2004; Schaefer and Stobbe 2006) and achromatic (Stevens et al. 2006) color matching. In our study, *H. roboraria* became better at achromatic matching after re-positioning, whereas *J. fuscaria* were better at chromatic matching. One possible explanation for the chromatic contrast results is that because *H. roboraria* has lower chromatic contrast than *J. fuscaria* regardless of whether it repositioned or not (Figure 1), the necessity to improve chromatic contrast for *H. roboraria* may not be as strong as for *J. fuscaria*. Although this difference in concealing mechanism between the 2 species is difficult to explain (and it is likely that both properties are important to become camouflaged against natural predators), the degree of chromatic matching and achromatic matching were highly correlated with each other in both species (Pearson correlation test, $r = 0.475$, $P < 0.001$ for *H. roboraria*; $r = 0.355$, $P < 0.001$ for *J. fuscaria*). This implies that, although the 2 types of color matching are different and the role of this information on predator perception may differ (Osorio et al. 1999), chromatic and achromatic matching will co-vary in real prey and provide cryptic effects harmoniously.

It should be noted that the results of color/luminance matching analysis should be interpreted with a degree of caution because our method of averaging whole pixels within a region ignores the patterns within moth and background. That is, this averaging approach could miss individual matching of specific patches. However, the difficulty of incorporating the color/luminance matching for specific color patches is hard to overcome because we used natural tree trunks for the experiments. Even though moth wing patterns broadly exhibit 2-tone color patches, tree trunks usually show heterogeneous color patterns, which in our study makes it difficult to employ color matching analyses between specific color patches, such as done by Lovell et al. (2013) in which the experimenters used controlled artificial background substrates. Furthermore, in complex natural backgrounds it can be hard to determine objectively which patches on the animal match different patches in the background. Our results of color matching analysis would be more relevant for a situation where a predator is finding the moths from a distance because the color patches within animals and background blend each other and exhibit broadly averaged colors when viewed from a distance (Marshall 2000), and overall match to the background should be important. ContEdge can also be interpreted as an indirect index of the color/luminance matching because the better color/luminance matching between 1 of color patches in moths and the nearest background color should result in differential blending effect (Stevens and Merilaita 2009b; Lovell et al. 2013). Based on the ContEdge results, which showed lower values after re-positioning, we suggest that 1 of the 2 color patches of moths (most probably darker patches because tree barks are usually darker than moths) have matched better to the nearest color of the background after re-positioning.

Collectively, our results suggest that camouflage effect may be attained not by a single mechanism but several mechanisms that

![Figure 5](image-url)

*Figure 5* Degree of disruptive effects for each treatment. Each subplot shows (a, b) the proportion of detected moth contours (ContEdge), (c, d) the degree of disruptive effects (DisRat; (number of detected edges in contour region)/(number of detected edges in moth region), see methods) for each treatment. The graphs in the left column show the results from *H. roboraria* (a, c, e; $N = 68, 68, 22$ for each treatment), The graphs on the right column show the results from *J. fuscaria* (b, d, f; $N = 84$ for each treatment). We plotted barplot with error bars (mean ± SE).
operate as a whole to reinforce the moths’ crypticity. Specifically, the disruptive effect and differential blending seem to play a pivotal role in both species. Moths also became more similar to the background on average in terms of either color or luminance matching. Finally, the pattern direction of moths aligned more precisely with the tree furrow direction after re-positioning (see Figure 3, although the difference was statistically non-significant in H. saburaria), which should lead to an improved camouflage effect (Webster et al. 2009, Wang and Schaefer 2012). Considering that pattern direction matching is mainly attained via modification of body orientation, our results suggest that the selection of an appropriate resting spot is crucial to attain background color/luminance matching and a disruptive effect, whereas the selection of a resting orientation is crucial to attain background pattern direction matching.

An interesting point in our results is that moths’ outlines were less visible after repositioning despite both species lacking typical disruptive color patterns (clear high contrast marginal patterns) on their wings. In conjunction with previous evidence of the importance of behavior on the degree of disruptive effect (Lovell et al. 2013), these results suggest that cryptic animals can enjoy the benefits of multiple concealing mechanisms through behavioral background choice even though their appearance is fixed.

In summary, in addition to previous studies on camouflage of moths (Kang et al. 2012, 2013a), this study provides compelling evidence for the adaptive significance of the interplay between animal color pattern and behavior for producing effective camouflage against natural predators and the mechanistic explanations behind this. Our results highlight that the behavioral choice of background in the wild plays a major role in causing camouflage against natural predators, and the different types of camouflage that exist in nature. We encourage future studies on animal camouflage (or signaling) to consider behavioral elements of animals (such as Kang et al. 2012; Kjernsmo and Merilaita 2012; Lovell et al. 2013) in natural circumstances in order to properly understand the adaptive value of color signals and evolution of animal color patterns.

**SUPPLEMENTARY MATERIAL**

Supplementary material can be found at [http://www.beheco.oxfordjournals.org/](http://www.beheco.oxfordjournals.org/)

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