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Moths on tree trunks seek out more cryptic positions when their current crypticity is low

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Many animals use camouflage to avoid predation. Their crypticity, that is, the degree of a visual match between the animal's body and the background, affects their survival. Therefore, they may develop the ability to choose an appropriate background, which matches the animal's own colour pattern. We have previously shown that moths, *Hypomecis roboraria*, have the ability to increase their crypticity by repositioning their bodies from the initial landing position to the final, more cryptic, position. However, this repositioning behaviour is not always performed: some moths stay put on the initial landing position. We hypothesized that the moth's decision whether or not to reposition itself is related to its crypticity at the landing spot. We determined the crypticity from a detection task experiment, in which 'human foragers' searched for the moths in photos of moths at their landing spots. Moths that landed on the less cryptic positions were more likely to reposition themselves to the more cryptic positions. In contrast, moths that had already landed on substantially cryptic positions were less likely to reposition themselves. We suggest that the tactile cues received by moths from furrows and crevices, the elements of bark structure responsible for the colour pattern of the bark, may play a role in mediating this adaptive behaviour that results in improving the moths' visual crypticity.

Camouflage decreases the probability of an animal being detected or recognized and it is one of the most prevalent evolutionary outcomes of predator–prey arms races (Poulton 1890; Thayer 1918; Cott 1940; Stevens & Merilaita 2011). Visual camouflage can be achieved through a range of concealing mechanisms such as background matching, disruptive coloration or countershading (Endler 1978, 1984; Cuthill et al. 2005; Endler 2006; Fraser et al. 2007; Rowland et al. 2008; Stevens & Merilaita 2011) and depends on the visual patterns on the animal's body in relation to the characteristics of its background. Because the concealment of animals is strongly dependent on background, many animals have developed the ability to choose appropriate backgrounds and background choice often reinforces the crypticity of animals (Cott 1940; Kettlewell 1955; Kang et al. 2012).

While the degree of concealment depends on background choice behaviours, it may also affect other behaviours. For example, the degree of crypticity may affect behaviour of prey animals (Martin & Lopez 2000; Cuadrado et al. 2001; Briffa et al. 2008; Cooper & Sherbrooke 2010; Briffa & Twyman 2011; Kjernsmo & Merilaita 2012). Although this effect of crypticity may be related to the animal's awareness of its own conspicuousness as suggested in hermit crabs (Briffa & Twyman 2011), the actual perception and awareness of an animal's own crypticity in other prey species that adaptively modify their antipredator behaviour according to their crypticity (e.g. fleeing/immobility of reptiles and finding a matching/complex background of killifish in response to predators' presence) has not been examined, and may not be needed. Recent studies on cuttlefish suggest that these animals are able to modify their body pattern and colour in response to specific visual properties of the background (Chiao & Hanlon 2001; Barbosa et al. 2008, 2011; Allen et al. 2010). Although these behaviours result in higher visual crypticity as perceived by a potential predator (or prey), the underlying sensory processes appear to rely on simple responses to specific elements in the background (Chiao & Hanlon 2001; Barbosa et al. 2008; Allen et al. 2010) rather than on comparison and awareness of the animal's own versus its background visual patterns.

Here, we ask whether similar behavioural adjustments according to degree of crypticity may exist in an insect, a geometrid moth, the great oak beauty, *Hypomecis roboraria*, and we discuss hypothetical sensory mechanisms that may be responsible for the observed behaviours. Moths actively select a resting substrate,

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location and body orientation, all of which contribute to the match between the colour patterns of the moths' wings and those of the background (Kettlewell 1955; Sargent 1966, 1973; Boardman et al. 1974; Kettlewell & Conn 1977; Pietrewicz & Kamil 1977; Webster et al. 2009; Kang et al. 2012; Wang & Schaefer 2012). We have recently shown that, after landing on tree bark, two species of geometrid moths, including *H. roboraria*, perform 'repositioning behaviour' by walking on the tree bark in search of a final resting position that precisely matches its wing patterns with those on the bark (Kang et al. 2012; see Supplementary video).

In our previous study, only half of the *H. roboraria* individuals repositioned their bodies (from the initial landing position to the final resting position) soon after landing (Kang et al. 2012). The other half remained at their initial positions. The individuals that repositioned themselves chose the spot and body orientation that provided a better match between the background and the moth's wings than before repositioning. However, it is still unclear why some individuals stayed put at their initial landing position without repositioning themselves. Here, we ask the follow-up question of whether their decision to reposition or not is related to the degree of crypticity in their initial (landing) position. If moths behave in an adaptive manner and if they improve their crypticity only when the current crypticity is low, we predicted that the landing positions of moths that did not decide to reposition their bodies (fixed positions) would be characterized by higher crypticity than the landing positions (initial positions) of moths that later decided to reposition themselves to the final positions. We also predicted that the probability of repositioning would be higher for moths that landed at positions of low crypticity.

METHODS

Comparison of Crypticity with Human Predators

Experimental design

We used *H. roboraria* (Figs 1, 2) to test our hypothesis. This is a monomorphic species which has a colour pattern resembling tree bark. After landing on a tree bark, the species is known to perform repositioning behaviour, which reinforces its visual crypticity (Kang et al. 2012). The repositioning behaviour (choosing a new position defined as a combination of location and body orientation) usually occurs a few times within 1 h after landing. In our previous study, only 51% of *H. roboraria* repositioned their bodies after landing on tree bark while the others stayed put on the initial landing spots (Kang et al. 2012). We compared the crypticity of moths in three situations (treatments): Fixed, Initial and Final position. Fixed position is the position of a moth that did not reposition its body and remained at the landing spot and in the original body orientation assumed at landing. Initial position is the position of a moth just after landing for only those moths that later repositioned their bodies. Final position is the position of a moth after the repositioning behaviour has taken place (only for those moths that repositioned themselves).

Although we compared crypticity between the Initial and Final groups in our previous paper (Kang et al. 2012), we included the two groups in the present experiment so that we could provide a direct comparison between Fixed–Initial and Fixed–Final groups. To measure the degree of crypticity of moths quantitatively, we used our previous method (Kang et al. 2012), which employs photographs of moths presented to humans as visual 'foragers' (Kang et al. 2012).

Moths were collected at night near black lights, kept individually in small containers and tested the next morning. We released the moths in a forest (near the collection site) one by one and followed each moth until it landed on its initial landing position. All the tested moths landed on tree trunks of *Pinus taeda* (which comprised more than 95% of tree species near our release site). The choice of the landing tree and landing position was totally dependent on the moths. Then we took photographs of each moth twice using a Canon Powershot S5IS with an interval of 1 h, which is sufficient time for the moths to reposition. From the photographs, we categorized the moths into three groups: Initial, Final and Fixed (see above for the description of each group). We successfully tracked and took photographs of 63 moths (32 moths that repositioned their bodies and 31 moths that remained in their landing position). We discarded some photos where a part of the moth wing was concealed by furrow structure or photos were blurred. Then we resized the photos so that moths were of similar size in each. We cropped each photo to the size of 750 × 1000 pixels (corresponds to 21 × 28 cm on the monitor screen). While cropping, we randomized the position of the moth shape in each photo (i.e. the spatial position of the moth shape in each cropped image was predetermined by the generation of random x, y coordinates) to neutralize any effect of spatial position of moths on the monitor screen on their detectability. The size of the moth shape (length of the longest axis of the moth's body) was set to 125 pixels (corresponds to 35 mm on the monitor screen).

We used the custom-built pictorial puzzle program (previously used in Kang et al. 2012) to measure the performance of humans in detecting the moths in prepared photos on a monitor screen (24 inches LG widescreen LCD monitor with 1920 × 1080 resolution setting). This program presents the photos on the monitor in a designated order, and if a human participant clicks the target or does not click within a certain time, it presents the next photo. Each human participant, who was totally unaware of our experimental purpose, was asked to find a moth in each photo, and to click on it within 10 s. If participants clicked the wrong area or failed to click within 10 s, the next photo was presented and the moth was considered to have survived. Before real testing, all participants went through a training session to get used to the test system.

In each photo, we measured (the program automatically recorded) the latency to the detection (clicking) of a moth (continuous response variable) and whether the moth was detected or not within 10 s (binary response). A total of 49 real photos from 32 moths (15 moths at fixed position, and 17 moths at initial and final positions) were shown to 30 human participants. All participants were presented with all 49 photos. The presentation order of the photos was randomized and was always different between participants. Therefore, although it is likely that the participants became better able to detect moth targets towards the end of the series of images (owing to search image formation), the effect of presentation order, if any, should not vary between treatment groups. All the photographs were taken in August–September 2010 at Choosan field station, Mt Baekwoon, South Korea (35°,01′,54.30′N, 127°,36′,22.30′E).

Because a difference in photographing conditions between treatments may influence moth detection by human subjects, we first confirmed that colours in photos did not differ between treatment groups. For each photo, we used the RGB values extracted from the pixels of each colour channel to compare the colour and intensity of photos. We randomly selected 100 points in each photo and extracted RGB values for each pixel. Then we averaged the RGB values of the 100 selected pixels (each channel separately) and this averaged value was used as the mean RGB value of each photo. These values of images in each treatment group were compared by multivariate analysis of variance (MANOVA; the mean RGB values as response variables, treatment groups as an explanatory variable). We found no difference in RGB values between treatment groups (MANOVA: Wilks's lambda $= 0.94$, approximate $F_{6,88} = 0.43$, $P = 0.86$). Therefore we considered that there was no