

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.

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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 counter-shading (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; Kjærnsmo & 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 Choo-san 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

perceptual difference in colour properties between treatment groups. ImageJ 1.44p (National Institutes of Health, Bethesda, MD, U.S.A.) was used for pixel selection and RGB value extraction.

Although humans are not natural predators of moths, human predators have been successfully used in detection task experiments (Fraser et al. 2007; Cuthill & Szekely 2009; Webster et al. 2009; Tsurui et al. 2010; Bohlin et al. 2012; Kang et al. 2012). There are several advantages of using human predators over real predators: control of the factors that can influence the behaviour of real predators (previous experience, hunger level or the degree of tameness to experimental condition), and the wide applicability of various experimental designs. Furthermore, the results of detection task experiments using human predators are congruent with those using natural predators (Beatty et al. 2005; Fraser et al. 2007; Cuthill & Szekely 2009). The most problematic issue of using humans over natural predators is that the visual sensory system of humans is different from those of natural predators, mainly the lack of UV detection (Cuthill et al. 2000). In this experiment, both tree bark and wings of *H. roboraria* reflect low levels of UV (less than 7% throughout the whole UV spectrum range) and we consider that UV contributes insignificantly to the crypticity of moths.

Statistical analysis

We used R 2.14.0 (<http://www.r-project.org>) for all statistical analysis. We employed generalized linear mixed models (GLMMs; using 'glmer' function in 'lme4' package) to compare the two response variables (the binary response of whether a moth was detected or not within 10 s, and the latency to the detection of a moth in each photo if the moth was detected) between treatment groups. However, comparison of the three treatment groups (Fixed, Initial and Final) in one analysis is statistically invalid because Initial and Final groups are paired photographs of the same moth whereas photographs at fixed positions are from different moths. For comparison between Initial and Final positions, we set human subject ID and moth ID as random factors. For the comparison between Fixed and Initial and between Fixed and Final groups, we set human subject ID as a random factor. We transformed the latency by Box–Cox power transformation (Sokal & Rohlf 1995) to satisfy the assumptions of GLMMs ($\lambda = -0.70, -0.71, -0.36$ for Initial–Final, Initial–Fixed and Final–Fixed, respectively). *P* values were adjusted by Holm correction (Holm 1979) to control the familywise error rate.

We defined a moth's orientation as the angle between the direction in which its head points out and the direction indicated by the main axis of the tree trunk (mostly standing upright). Hence, the orientation of each moth was measured as an angle from 0 to 360 degrees which runs in the clockwise direction. For example, 0 degrees indicates a moth headed upwards and 90 degrees indicates a moth headed towards the right side. Since the angular data did not follow the assumptions of parametric tests (von Mises circular normal distribution), we performed Watson's two-sample test for homogeneity (nonparametric circular statistics) to compare three groups of angles (Zar 1999). We present approximated *P* values for Watson's two-sample test because exact *P* values cannot be calculated by currently existing critical U^2 statistical tables (Zar 1999).

All the field experiments were conducted within a 2.5 h period (1000–1230 hours), and we assumed that the effect of the time of the test on moths' behaviour was negligible. All the statistical tests were two tailed.

Initial Crypticity and Probability of Repositioning

To test directly whether the occurrence of repositioning behaviour is related to the crypticity in the initial position, we

initially used the original two variables obtained from each test (the binary response variable indicating whether the moth was detected or not within 10 s, and the latency to the detection of a moth in each photo if the moth was detected within 10 s) to calculate two new variables for each moth image: the proportion of humans who detected the moth and the mean latency to detect the moth if detected in 10 s. Because these two new variables measured only slightly different aspects of crypticity and were correlated with each other (Pearson product–moment correlation test: $t_{30} = 6.24, r = 0.75, P < 0.001$) we used principal component analysis (PCA) to create a principal component (PC1) as a composite crypticity index. This initial crypticity index (PC1_{10 s}) explained 88% of total variance in the data (eigenvalue = 1.76), and correlated positively with the original two variables (Pearson product–moment correlation test: PC1_{10 s}–mean latency: $t_{30} = 14.55, r = 0.94, P < 0.001$; PC1_{10 s}–proportion undetected: $t_{30} = 14.55, r = 0.94, P < 0.001$). However, it did not differentiate the moths well.

Many moths were located in the lower range of values of crypticity and they differed little from each other in this respect: only 13% of data (four of 32) were located within the upper 50% of the range of the crypticity values (Appendix Fig. A1c). This was due to the skewed distributions of the two contributing variables (Appendix Fig. A1a, b), and especially the proportion of humans who detected the moth within 10 s (>0.4 for only three of 32 moths). Hence, the power of testing the relationship over the upper range of crypticity was expected to be low.

By shortening the time basis from 10 s to 8 s, followed by shortening it to 6 s and then to 4 s, we devised a new index of crypticity that used less skewed variables (Appendix Fig. A1d, e) and resulted in a more even distribution over the whole range of crypticity and in a better differentiation between moths in their crypticity values (Appendix Fig. A1f). We also tried a PC extracted from the proportion of detection during 4 s and the original latency until detection (measured between 0 and 10 s). Hence, we decided to use all latencies, including those larger than 4 s. However, the resulting PC also had a skewed distribution (Appendix Fig. A2; only five moths were in the upper range of crypticity values).

All these analyses resulted in similar outcomes and we present them in Appendix Figs A1 and A2, but only the PC1_{4 s} had a low degree of skewness of the distribution. Hence, for the main analysis, we used the principal component from two variables: proportion of humans who detected a moth within 4 s, and the average latency to detect for those subjects who detected a moth within 4 s. The PC1_{4 s} explained 78% of total variance of the data (eigenvalue = 1.58), and correlated positively with the two original variables (Pearson product–moment correlation test: PC1_{4 s}–mean latency: $t_{30} = 10.41, r = 0.89, P < 0.001$; PC1_{4 s}–proportion undetected: $t_{30} = 10.41, r = 0.89, P < 0.001$). Then, we used generalized linear models (GLMs) with binomial errors and logit link to determine the effect of the crypticity index (the PC1_{4 s}) on the binary variable that indicates whether a moth repositioned itself or not (1 = a moth repositioned itself after landing; 0 = a moth did not reposition itself after landing).

RESULTS

Comparison of Crypticity with Human Predators

The detection probability of the moths that did not reposition themselves and remained in their landing positions (Fixed group) was significantly lower than the detection probability at landing positions (Initial group) for those moths that later repositioned themselves (GLMMs: $\chi^2_1 = 9.60, \text{adjusted } P = 0.004$), but significantly higher than the detection probability of these moths in their final positions (Final group), after they repositioned themselves

(GLMMs: $\chi^2_1 = 5.53$, adjusted $P = 0.02$; Fig. 1a). The latency to detection of the moths in the Fixed group was significantly longer than that of the moths in the Initial group (GLMMs: $\chi^2_1 = 13.62$, adjusted $P < 0.001$) but shorter than that of the moths in the Final group (GLMMs: $\chi^2_1 = 10.75$, adjusted $P = 0.001$; Fig. 1b). After

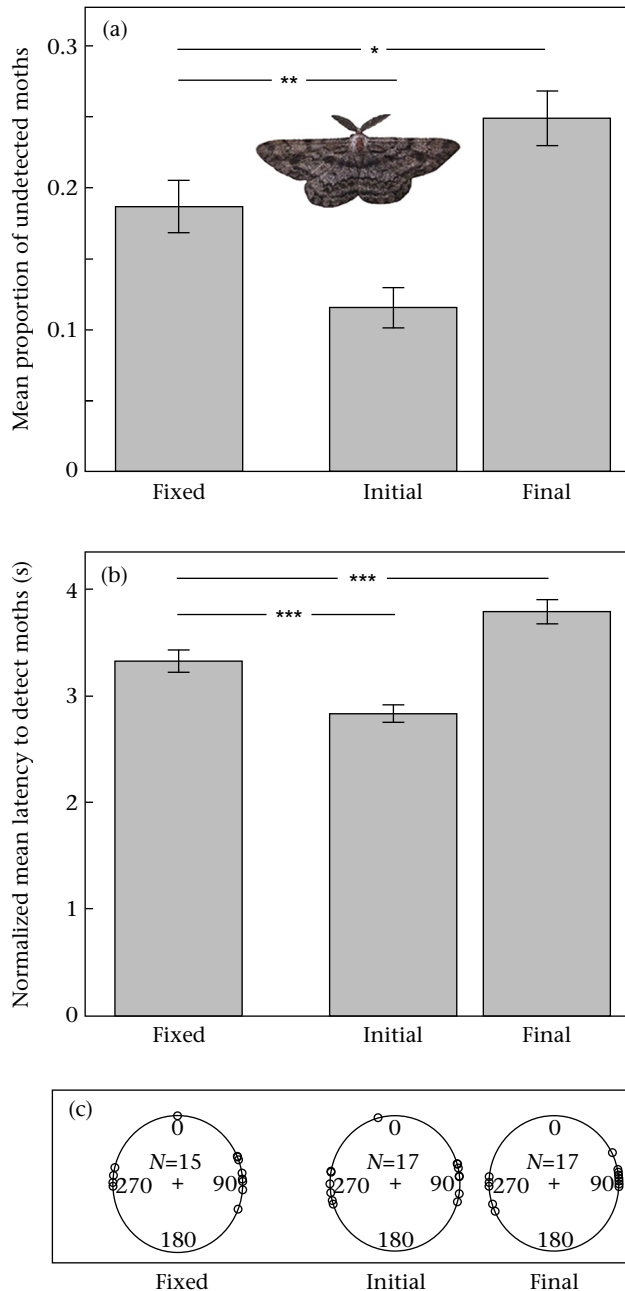


Figure 1. Comparisons between three types of moth, *H. roboraria*, locations with respect to (a) the proportion of undetected moths, (b) the latency to the detection and (c) the angular distributions of body orientations. Types of locations: 'Fixed': locations of moths that did not reposition themselves after landing; 'Initial': landing locations of moths that later repositioned themselves to the 'Final' positions. The latency to the detection in (b) is transformed by Box-Cox transformation (see Methods). The columns and error bars indicate mean and SEM, respectively. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. A photo of *H. roboraria* is inserted within (a). In (c), black circles indicate the orientation of the head relative to the vertical upward orientation. Almost all moths in the three treatment groups orient their heads towards the side (towards 90 and 270 degrees in the graphs).

repositioning, the detection probability decreased (comparison between Initial and Final: GLMMs: $\chi^2_1 = 42.31$, adjusted $P < 0.001$; Fig. 1a), and the latency to detection increased (GLMMs: $\chi^2_1 = 81.96$, adjusted $P < 0.001$; Fig. 1b). Orientations of moths did not differ between the groups (Watson's two-sample test for homogeneity: Initial–Final: $U^2 = 0.07$, $N_1 = N_2 = 17$, $P \approx 0.50$; Initial–Fixed: $U^2 = 0.11$, $N_1 = 15$, $N_2 = 17$, $P \approx 0.20$; Final–Fixed: $U^2 = 0.11$, $N_1 = 15$, $N_2 = 17$, $P \approx 0.20$; Fig. 1c). These results suggest that the repositioning behaviour involves changing resting positions rather than changing body orientation, and that those moths that were already in relatively cryptic positions rarely repositioned themselves, even though repositioning would still increase their crypticity.

Initial Crypticity and Probability of Repositioning

The probability of repositioning decreased when the crypticity at the initial landing spot increased (Fig. 2; GLMs: $\chi^2_1 = 4.42$, $P = 0.04$). This tendency was also present when we used different crypticity indices for the analysis (see Appendix Figs A1 and A2). Seventy per cent of moths (12 of 17) that were at the lower crypticity landing positions ($PC1_{4s} < 0$) repositioned their bodies, whereas only 14% (one of seven) of those at the higher crypticity positions ($PC1_{4s} > 1$) repositioned their bodies.

DISCUSSION

We have shown here that cryptically patterned moths adaptively adjust their behaviour to their current level of crypticity: the moths that achieved substantial crypticity right after landing tended to stay put while the moths that landed on positions that offered low crypticity repositioned themselves and eventually achieved better camouflage at the new position. While our current findings do not provide information to determine the sensory mechanisms of these adaptive behavioural decisions by moths, together with our previous study (Kang et al. 2012) they indicate not only that moths are able to find a cryptic spot soon after landing (Kang et al. 2012), but also that they are more likely to do so when their current crypticity is low.

While the sensory mechanisms that underlie this adaptive behavioural decision by moths are unknown, moths need not be aware of their own pattern in relation to the pattern of the bark. Although moths perform subtle wing-lifting movements (see Supplementary video) that may potentially allow for visual comparison between patterns on wings and on the nearby tree bark, it would be difficult or impossible for moths to recognize detailed visual patterns considering the location and resolution of moths' eyes (Land & Nilsson 2002). Previous experiments on moths have indicated that vision is used to choose a landing substrate according to its general reflectance (Kettlewell 1955; Sargent 1966, 1968; Kettlewell & Conn 1977; Grant & Howlett 1988), and that some moths, once they have landed on the substrate, have a general preference for an edge between dark and light substrates (Lees 1975). However, our recent study on another geometrid indicates that these general visual stimuli are not crucial in choosing the resting spot via repositioning behaviour (unpublished data).

Our direct experimental evidence for the importance of tactile stimuli from the bark structure in finding a cryptic spot by geometrids (unpublished data) suggests that tactile stimuli may be important in triggering the decision to reposition and in finding the new resting position. For example, it is possible that a specific set of tactile stimuli, typically associated in this monomorphic species with poorer crypticity on the bark of their preferred tree species, may trigger the repositioning behaviour while a different set of tactile stimuli, typically associated in this species with good

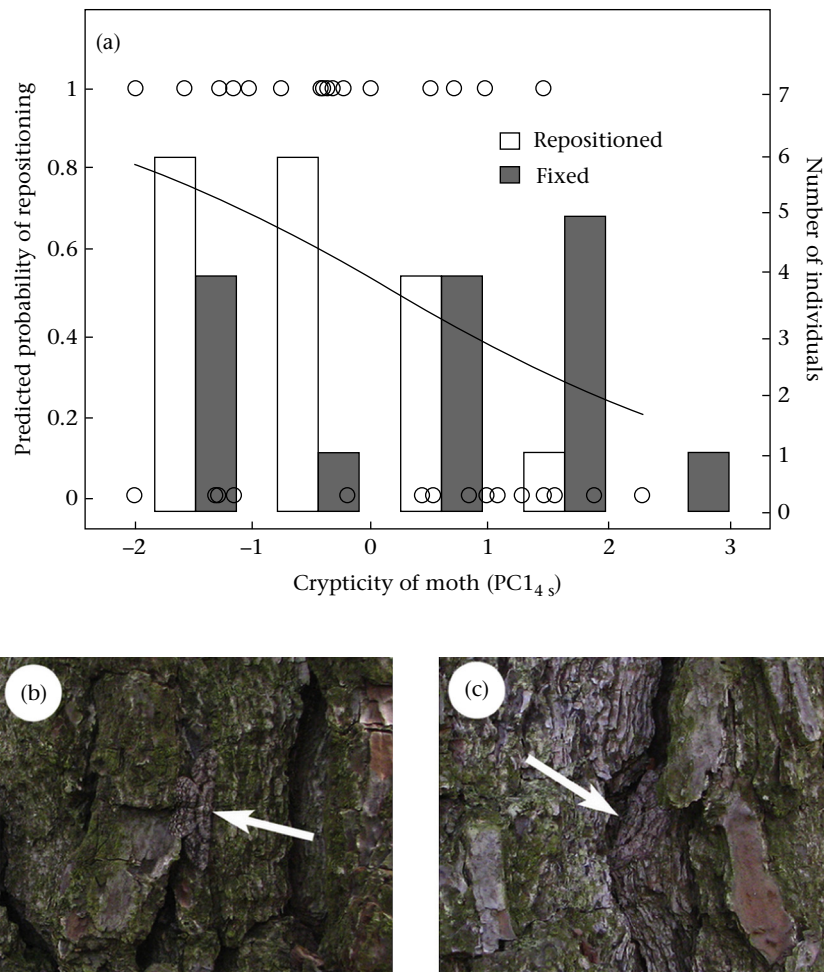


Figure 2. The effect of crypticity on the decision of moths to reposition. (a) The predicted probability of repositioning (the black line, left vertical axis) as a function of crypticity index. This relationship is derived from behaviour of $N = 32$ moths (each circle represents one moth; 0 represents moths that did not reposition themselves, and 1 represents moths that repositioned themselves). Y-axis on the left shows whether a moth repositioned itself or not. The bar histogram, and the corresponding Y-axis on the right, shows the number of individuals that did ($N = 17$) and those that did not ($N = 15$) reposition their bodies in each class of crypticity values. (b) An example of a moth with low crypticity. (c) An example of a moth with high crypticity.

crypticity, may promote staying put at the landing spot. The importance of tactile stimuli has also been suggested in experiments on artificial substrates (Sargent 1969) and from observations of moths on natural substrates (Steward 1976). Therefore, we suspect that predation-mediated selection on monomorphic geometrid moths led to the evolution of moth sensitivity to a species-specific set of tactile cues from the bark structure and that the resulting decisions to reposition based on these tactile stimuli produce the species-specific resting positions that increase the species-specific visual crypticity of moths on their preferred tree species.

Specifically, we hypothesize that *H. roboraria* moths find a cryptic spot on a bark by finding a body position at which the frontal edge of their forewings ‘touches’ an edge of a furrow in the bark, as can be seen in the [Supplementary video](#). This may lead to concealment of the frontal outline of the moth body (which is ‘hidden’ in the furrow or aligns with the furrow outline), and the degree of this ‘touching’ may also be correlated, on average, with the degree of matching between the visual pattern on the wing and that on the bark. Whether this mechanism of repositioning evolved after or before the evolution of body patterns that match patterns on bark is currently unknown.

Repositioning behaviour does not seem to be performed only by particular individuals, because in an additional field test (repeated observations on the same individuals; see Appendix Table A1, Fig. A3), there was no apparent within-individual consistency in the occurrence of repositioning behaviour. This may indicate that the occurrence of repositioning behaviour depends on the circumstances that vary among resting spots. Although in this additional field test we did not measure the degree of crypticity at each spot, we believe that the degree of matching between the bark and moth wings is one of the important characteristics that varies among consecutive landing spots of the same individual and affects moths’ decision to reposition.

Our results suggest that if certain crypticity was already achieved at the initial landing, the moths rarely repositioned themselves, even though repositioning would still improve their camouflage. We consider two adaptive hypotheses for this behaviour. First, an increase in predation risk during conspicuous movements on the bark while repositioning their bodies can be more costly for moths than the costs of remaining in this position at the intermediate level of crypticity for a day (maximally). Second, it is possible that above a certain threshold of matching between the wing and bark pattern, the probability of a bird detecting a moth

may be very low and further improvement in crypticity is not necessary. Saltatory search for prey by birds involves hops and pauses of species-specific durations (Anderson et al. 1997). Each hop brings a bird to a new spot where searching for prey lasts for the species-specific pause duration modelled as optimal giving-up time (Anderson 1981). Only during the pauses, lasting for a half to a few seconds (0.54 s for the painted redstart: Jablonski & Strausfeld 2000; 2.4 s for wood-gleaning warbler: Landres & MacMahon 1980), is the capacity of birds to scan their immediate surroundings maximized. Thus, our second adaptive hypothesis is that the probability of not being detected by birds during these short scans already reaches near certainty for the intermediate levels of our crypticity index and therefore those moths that achieved this level do not decide to reposition themselves.

In summary, we showed not only that moths are able to find a new cryptic spot (Kang et al. 2012), but also that they can change their behaviour adaptively depending on their current crypticity, even though they are apparently not able to evaluate the degree of visual match between their patterns and the patterns on the background directly. Our studies on moths (Kang et al. 2012, these results), along with studies on several other organisms (Chiao & Hanlon 2001; Barbosa et al. 2008; Allen et al. 2010; Barbosa et al. 2011; Briffa & Twyman 2011), provide opportunities to explore how prey animals respond to their own degree of crypticity by seeking highly cryptic sites in complex visual environments.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.06.014>.

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APPENDIX

The order of the presentation significantly influenced the detection probability. GLMMs analysis revealed that human subjects became better at detecting moth targets (Fixed–Final: $\chi^2_1 = 21.45$, adjusted $P < 0.001$; Fixed–Initial: $\chi^2_1 = 13.43$, adjusted $P < 0.001$; Initial–Final: $\chi^2_1 = 9.19$, adjusted $P = 0.002$) and took less time (Fixed–Final: $\chi^2_1 = 30.55$, adjusted $P < 0.001$;

Fixed–Initial: $\chi^2_1 = 23.97$, adjusted $P < 0.001$; Initial–Final: $\chi^2_1 = 35.27$, adjusted $P < 0.001$) to detect moths towards the end of the series of images.

After taking into account the order of the presentation in the analysis, we obtained results congruent with the results in our main text. The detection probability of the moths that did not reposition themselves and remained in their landing positions (fixed positions) was significantly lower than the detection probability at landing positions (initial positions) for those moths that later repositioned themselves (GLMMs: $\chi^2_1 = 12.08$, adjusted $P = 0.001$), but significantly higher than the detection probability of these moths in their final positions, after they repositioned themselves (GLMMs: $\chi^2_1 = 4.59$, adjusted $P = 0.03$). The latency to detection of the moths in the Fixed group was significantly longer than that of the moths in the Initial group (GLMMs: $\chi^2_1 = 29.22$, adjusted $P < 0.001$) but shorter than that of the moths in the Final group (GLMMs: $\chi^2_1 = 13.69$, adjusted $P < 0.001$). After repositioning, the detection probability decreased (comparison between Initial and Final; GLMMs: $\chi^2_1 = 39.72$, adjusted $P < 0.001$), and the latency to detection increased (GLMMs: $\chi^2_1 = 107.12$, adjusted $P < 0.001$).

Table A1

Results of consecutive tests on the same individual ($N = 36$ individuals used) released and observed after landing on a tree trunk

Moth ID	Consecutive trials on the same moth				
	First	Second	Third	Fourth	Fifth
1	Y	Y	Y	Y	Y
2	Y	Y	Y	Y	
3	N	Y	Y		
4	Y	Y			
5	Y	Y			
6	Y	Y			
7	Y	Y			
8	Y	N	N	Y	
9	Y	Y			
10	Y	Y			
11	Y	N	Y		
12	Y	Y			
13	Y	Y			
14	N	Y	Y		
15	N	Y	Y		
16	N	Y	Y		
17	Y	Y			
18	Y	Y			
19	Y	Y			
20	Y	Y			
21	Y	Y			
22	Y	N	Y		
23	Y	Y			
24	Y	Y			
25	N	Y	Y		
26	N	N	Y	Y	
27	N	Y	Y		
28	N	Y			
29	N	N	N	N	
30	N	N			
31	Y	N	N		
32	N	N			
33	N	Y			
34	N	N			
35	N	N	N		
36	Y	N			

'Y' indicates that repositioning behaviour was performed and 'N' indicates that the repositioning did not occur within 1 h from landing on a trunk. This behavioural test was conducted in summer 2011 without determining the degree of crypticity.

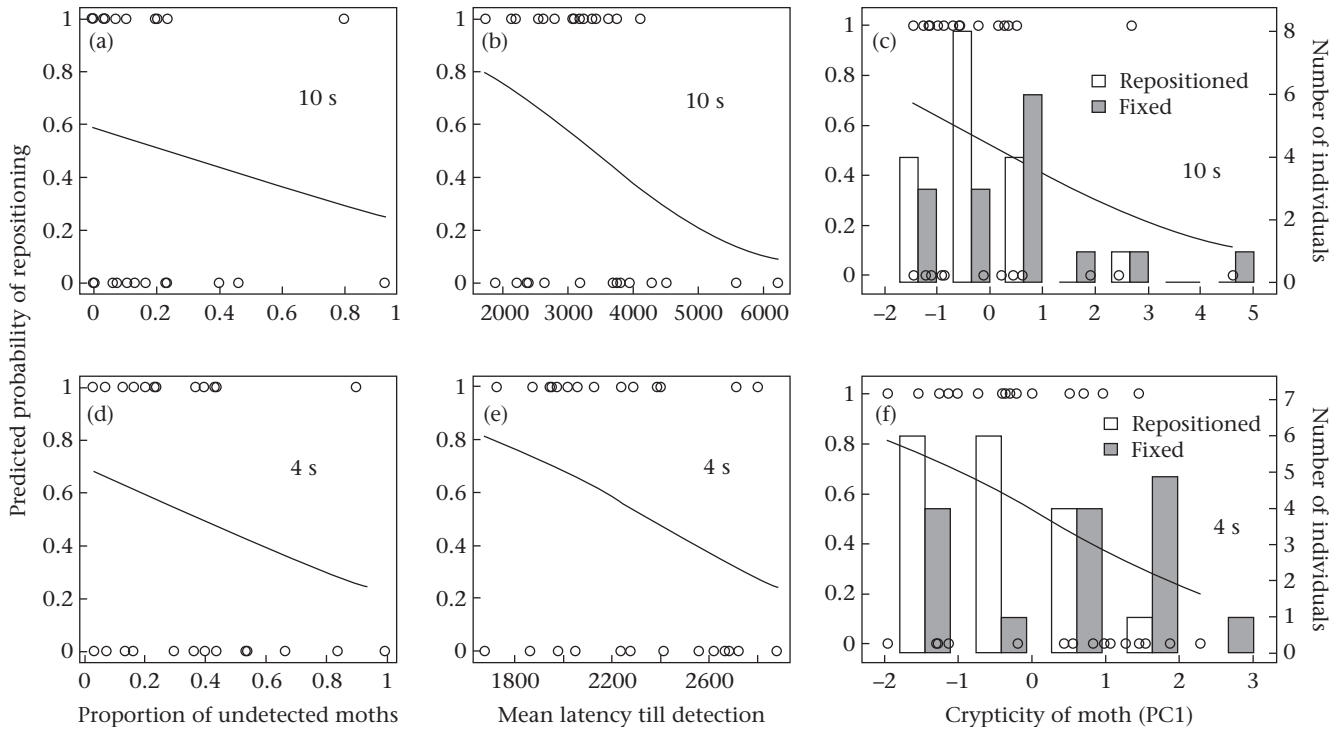


Figure A1. The predicted probability of repositioning (the black line) as a function of variables related to crypticity: the proportion of humans who did not detect a moth within (a) 10 s (GLMs: $\chi^2_1 = 0.85, P = 0.36$) or (d) 4 s (GLMs: $\chi^2_1 = 2.05, P = 0.15$), the average latency to detect for those human subjects who detected a moth within (b) 10 s (GLMs: $\chi^2_1 = 4.23, P = 0.04$) or (e) 4 s (GLMs: $\chi^2_1 = 3.61, P = 0.06$), and the principal component derived from these two variables separately for (c) 10 s (GLMs: $\chi^2_1 = 2.53, P = 0.11$) and (f) 4 s (GLMs: $\chi^2_1 = 4.42, P = 0.04$). Histogram in (c, f) shows the number of moths that repositioned (white) or did not reposition (grey) themselves within each of several classes on the X-axis.

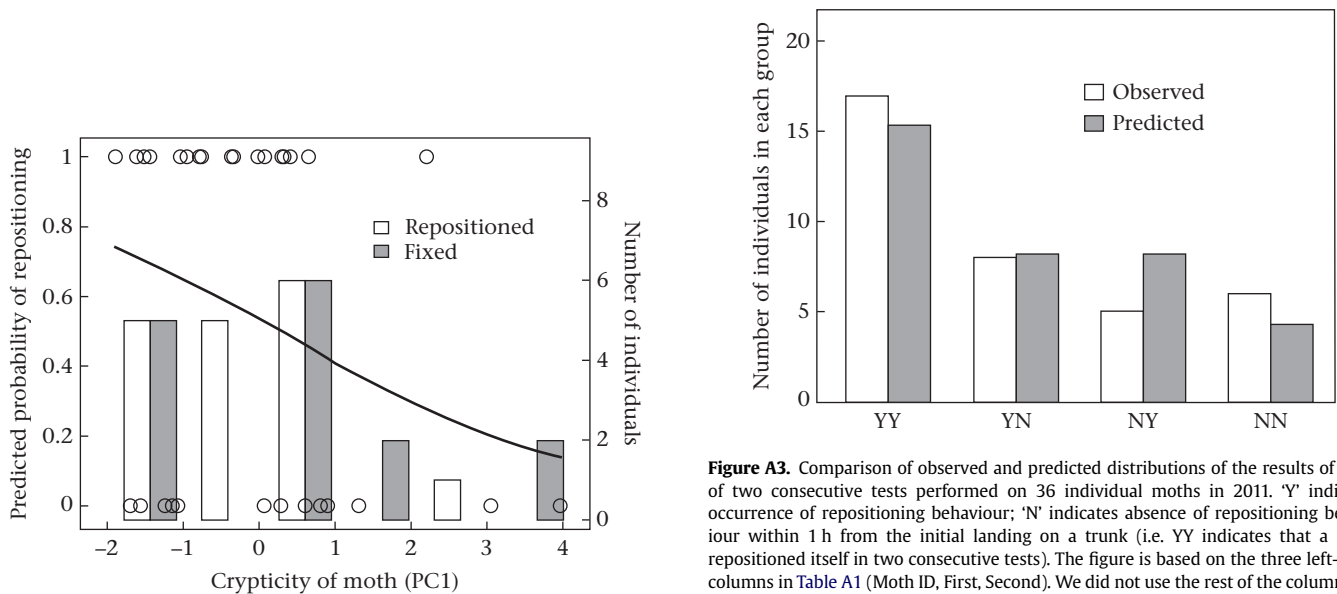


Figure A2. The predicted probability of repositioning (the black line) as a function of variables related to crypticity: the principal component derived from the two variables (the proportion of humans who did not detect a moth within 4 s and the average latency to detect for those human subjects who detected a moth within 10 s). This PC1 value explained 96% of the variance (eigenvalue = 1.93) and was highly correlated with the original two variables ($t_{30} = 28.12, r = 0.98, P < 0.001$ for both variables). GLM analysis revealed a marginally significant effect of crypticity (PC1) on the binary response variable indicating whether a moth repositioned itself or not ($\chi^2_1 = 3.14, P = 0.08$). Histogram shows the number of moths that repositioned (white) or did not reposition (grey) themselves within each of several classes of PC1 (on the X-axis).

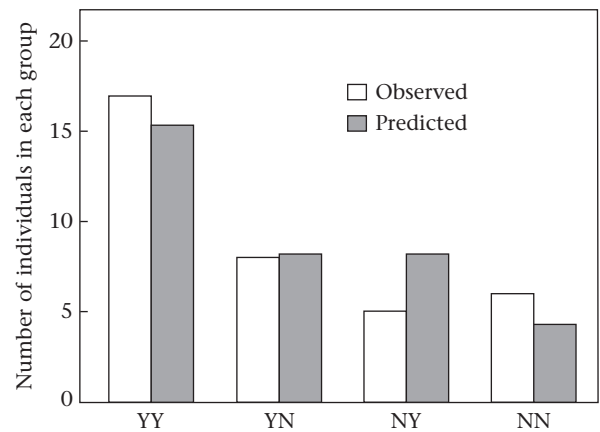


Figure A3. Comparison of observed and predicted distributions of the results of pairs of two consecutive tests performed on 36 individual moths in 2011. 'Y' indicates occurrence of repositioning behaviour; 'N' indicates absence of repositioning behaviour within 1 h from the initial landing on a trunk (i.e. YY indicates that a moth repositioned itself in two consecutive tests). The figure is based on the three left-most columns in Table A1 (Moth ID, First, Second). We did not use the rest of the columns for analysis to avoid biases from our data-collecting method; we tried to continue testing the same individual at least until one performed the repositioning behaviour twice, but we failed to recapture some individuals, which resulted in fewer tests than we intended. But all the individuals were tested at least twice and the data from the first two consecutive tests are used here. The predicted probability p of repositioning per trial is calculated as 'the number of trials with repositioning/total number of trials' in the two columns of Table A1: 'First' and 'Second'. The predicted probability of not repositioning is $q = 1 - p$. The predicted null probability of occurrence of each of the four pairs YY, YN, NY and NN is calculated from p and q (p^2 for YY; p^*q for YN; q^*p for NY; q^2 for NN). A chi-square test revealed no difference between the observed and the expected frequency ($\chi^2_3 = 2.041, P = 0.56$).