

## Camouflage through an active choice of a resting spot and body orientation in moths

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### Abstract

Cryptic colour patterns in prey are classical examples of adaptations to avoid predation, but we still know little about behaviours that reinforce the match between animal body and the background. For example, moths avoid predators by matching their colour patterns with the background. Active choice of a species-specific body orientation has been suggested as an important function of body positioning behaviour performed by moths after landing on the bark. However, the contribution of this behaviour to moths' crypticity has not been directly measured. From observations of geometrid moths, *Hypomecis roboraria* and *Jankowskia fuscaria*, we determined that the positioning behaviour, which consists of walking and turning the body while repeatedly lifting and lowering the wings, resulted in new resting spots and body orientations in *J. fuscaria* and in new resting spots in *H. roboraria*. The body positioning behaviour of the two species significantly decreased the probability of visual detection by humans, who viewed photographs of the moths taken before and after the positioning behaviour. This implies that body positioning significantly increases the camouflage effect provided by moth's cryptic colour pattern regardless of whether the behaviour involves a new body orientation or not. Our study demonstrates that the evolution of morphological adaptations, such as colour pattern of moths, cannot be fully understood without taking into account a behavioural phenotype that coevolved with the morphology for increasing the adaptive value of the morphological trait.

### Introduction

Evolution of adaptations through natural selection is the central theory in biology (Darwin, 1859; Fisher, 1930), and crypticity of moths (morphological phenotype) has been the icon of morphological adaptations to avoid predation throughout the history of evolutionary biology (Thayer, 1909; Cott, 1940; Kettlewell, 1955a,b; Endler, 1984). Most nontoxic and nonmimetic moths are inconspicuous in their natural habitat due to colour patterns on their wings that provide camouflage when the moths rest in species-specific sites (Poulton, 1890; Thayer, 1909;

Cott, 1940; Endler, 1978, 1984). Whereas morphological aspects of crypsis such as disruptive colouration (Cuthill *et al.*, 2005; Fraser *et al.*, 2007; Cuthill & Székely, 2009) and background matching pattern (Sumner, 1934; Pietrewicz & Kamil, 1977; Stuart-Fox *et al.*, 2004) have attracted the attention of researchers, some crucial aspects of behavioural adaptations are poorly understood. The importance of previously unexplored aspect of behaviour in moth crypticity has become apparent in recent discussions (Majerus, 1998; Wells, 2000) of Kettlewell's classic research (Kettlewell, 1955a,b), as well as in popular attempts to criticize the evolution as a scientific discipline (Wells, 2000; Hooper, 2003).

Although the preference of moths for landing on substrates that generally resemble the moth's colour has been well studied (Sargent, 1966, 1973; Steward, 1976; Kettlewell & Conn, 1977; Endler, 1984), it alone cannot

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explain how the final cryptic match between the patterns on the moth wings and the patterns on the background such as tree bark is achieved. This is because the landing spots and body orientations at the moment of, and immediately after, landing on a trunk are different from the spots and body orientations in which the moths finally rest on a substrate. The final resting positions and orientations, which result from body positioning behaviours after landing (Sargent, 1969), are species specific (Endler, 1978) and have been hypothesized to be the key adaptation to achieve crypticity (Sargent & Keiper, 1969). The positioning behaviour is more crucial than the general preference for trunk colouration, because even if a moth landed on a bark with a colouration or a pattern different from its own, the behavioural positioning may in principle lead to considerable crypsis through disruptive colouration or matching between the wing and background patterns. Therefore, the positioning behaviours performed by moths after landing are essential to account for the almost perfect match between the pattern on the moth wing and the pattern of the bark. However, the body positioning behaviour has only been approached from the proximal perspective (Sargent, 1969), and no direct test of adaptive role of this behaviour has been conducted.

The effect of final resting orientation (resulting from the body positioning behaviour) on crypsis has been experimentally confirmed by Pietrewicz & Kamil (1977), Webster *et al.* (2009), Wang & Schaefer (2012). Pietrewicz & Kamil (1977) showed that the camouflage effect of species-specific body orientation is the largest on a bark of tree species that provides the typical species-specific resting sites for the moths. Researchers interested in more general principles of crypsis also confirmed that the orientation of patterns in artificial prey models relative to the orientation of patterns in the background has strong effect on the degree of crypsis (Wang & Schaefer, 2012). However, the adaptive role of behavioural adjustments of a resting spot by moths after landing has been largely neglected.

Although, in his classical experiment, Kettlewell (1955b); but see also Majerus, 2005) used wild birds to measure the detectability of live moths after the moths landed on natural substrates, the experimental paradigm that has been employed over the last 50 years can be summarized as 'an experimenter arranges the prey – a predator attempts to detect it'. Researchers used specimens pinned on a tree bark (or photographs of thereof), or images copy-pasted onto a tree bark image, in body orientations chosen by the experimenter based on the knowledge on how the moths position their bodies (Pietrewicz & Kamil, 1977; Webster *et al.*, 2009; Wang & Schaefer, 2012). This paradigm ignores that moths may choose landing spots on a bark differently than humans do. This paradigm also ignores that the moths after landing actively search for a 'suitable' resting spot and that the body orientation in nature functions as

adaptation for camouflage only when matched with the natural behaviour to seek the resting spot. An additional consequence of this typical experimental paradigm was inability to realistically imitate the variation in body orientations of the moths and in the choice of the resting spot.

We decided to switch back to the experimental paradigm originally proposed by Kettlewell (1955b): *a moth positions itself – a predator attempts to detect it*. We focused on measuring the direct consequences of moth behaviour in their natural habitat. Rather than artificially arranging moths in positions that are believed to imitate their naturally achieved resting spot and orientation, we allowed the moths to do this for us. To determine whether moths' positioning behaviour after landing increases their crypticity, we studied two geometrid moths, *Hypomecis roboraria* (Denis & Schiffermüller 1775) and *Jankowskia fuscaria* (Leech, 1891), with wings that resemble colour patterns of a tree bark (Figs 1 and 2).

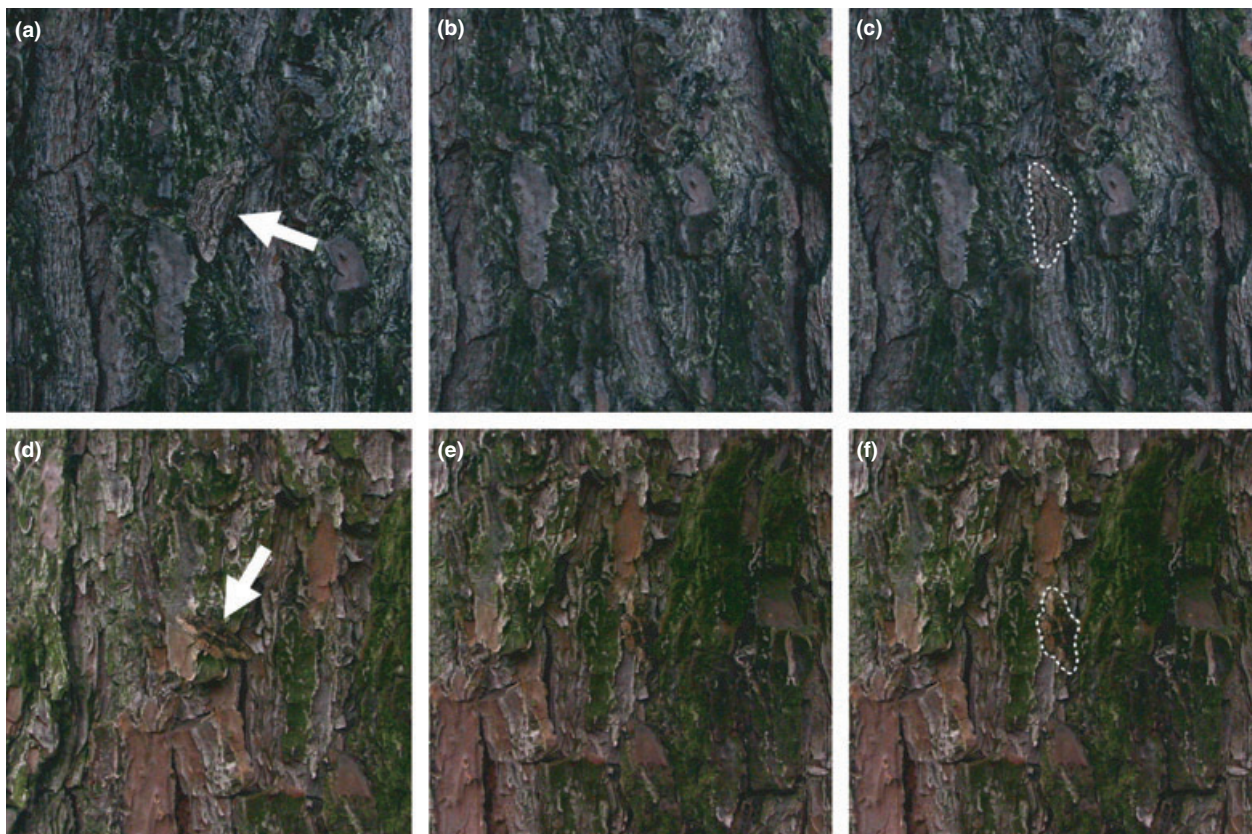
## Materials and methods

### Field observations

We studied two geometrid moths, *H. roboraria* and *J. fuscaria*, with wings that resemble colour patterns of a tree bark (Figs 1 and 2). The observations were conducted in August–September 2010 at Mt. Baekwoon, South Korea (N35°01'54.30'; E127°36'22.30'). Moths were collected at night with a black light, kept at 4 °C in plastic containers and released one by one in the next morning after waiting at least 30 min for their bodies to warm up to ambient temperature. The moths were released in the same forest habitat in which they were captured comprising mostly pine trees (more than 95% trees were *Pinus taeda*). The release point was surrounded by at least several trees so that the moths could actively choose a tree to which they fly. We watched the behaviour of moths in response to being released from containers during daylight hours. The species-specific resting sites and postures of moths after such a disturbance do not differ from the postures of undisturbed moths found naturally in the same habitat (C.-K. Kang, pers. obs.; Sargent & Keiper, 1969). Most of the released moths (except few which fell down to the ground) landed on *Pinus taeda*, and the trunk of this tree was used as the background in the subsequent experiments. The exact location of release site varied among the moths.

### Preparation of moth images

We used humans as experimental predators of the moths in digital photographs taken at the study site. As the moth landed, we took photographs of the trunk with a moth at the moth's initial position (*real initial*, i.e. photograph before positioning) from 60 cm away using



**Fig. 1** Examples of moths on a bark of *Pinus taeda* before (a,d) and after (b,c,e,f) body positioning behaviours. *Hypomecis roboraria* is presented in (a–d). *Jankowskia fuscaria* is presented in (d–f). Arrows in (a) and (d) point to the head of a resting moth. Contour lines in (c) and (f) are drawn to make detection of the moth in the final position easier. Original, unmarked versions of (c) and (f) are in (b) and (e).

a camera (Canon Powershot S5IS; ISO400, F3.2, 1/125s–1/250s shutter speed and 3264 × 2448 resolution). After 1 h, which is sufficient for the moth to finish positioning, we took photographs of the same moth again at the final position (*real final*, i.e. photograph after positioning) and collected the moth. Immediately after each moth has been collected, the tree bark area containing both the initial and final location of a moth was photographed again to obtain photograph of exactly the same illumination as the photograph of the moth in the final position. These three photographs (moth on a bark in initial position, moth on a bark in final position and the bark only containing both spots of the initial and the final position) were used to generate *control* images (see below). We photographed 63 *H. roboraria* and 32 *J. fuscaria*. Among them, 32 *H. roboraria* (51%) and 25 *J. fuscaria* (78%) changed their resting position from the initial spot where they landed to a new one. We excluded the photographs where part of the moths' wing was concealed by tree bark. We additionally excluded the moths for which the initial and final positions cannot be included in one background image either because the moth moved over especially long distance or because it

moved to another side of the tree trunk. In these cases, we were unable to create *control* image because we were unable to overlay the two positions (*initial* and *final*) of the moths on the same background photographs. For the experiment, we used photographs of 14 individuals of *H. roboraria* and 16 individuals of *J. fuscaria* at both initial and final positions. All photographs were taken under a thick canopy of forest between 0900 and 1400 h, and there is no reason to believe that differences in lighting conditions between *initial* and *final* photographs were biased. However, because moth detection by humans can also be influenced by the difference in light conditions between the *initial* and *final* photographs, we created a pair of photographs that differed only in the position and body orientation of a moth, but not in the lighting conditions. Using Photoshop 10.0 CS3 (Adobe, San Jose, CA, USA), we manually cut out the image of a moth from the *real final* photograph, saved it as a PNG file and overlaid it onto a separate bark-only photograph of the same area of a trunk (taken after moth collection) at the initial (*control initial* photograph) and, in a separate file, at the final (*control final* photograph) site/body orientations (see below for examples of photographs). Thus, in these

*control* photographs, *initial* and *final* photographs represented similar brightness.

To randomize the position of a moth within the screen presented to the observer, and to include only the bark surface in each photograph, we cropped each photograph to the size  $750 \times 1000$  pixels. Cropping made the position of the moth within the screen, and the characteristics of the visible background, dissimilar among four photographs of the same individual (*real initial*, *real final*, *control initial* and *control final*). In this way, we avoided temporal memory retention (in the human subjects) of moth position on the screen that might have been observed if we used the same background for all four photographs (for each moth). Size of the moths was same in all photographs (lengths of the longest axis of moth body were 140 pixels for *H. roboraria* and 124 for *J. fuscaria*, which reflects the real size ratio of the two species: 4.24 and 3.75 cm (mean of wingspan of five females) for *H. roboraria* and *J. fuscaria*, respectively). IMAGEJ 1.43u (National Institute of Health, Bethesda, MD, USA) was used for cropping and resizing the photographs. Total 56 photographs of *H. roboraria* (14 moths  $\times$  4 images) and 64 *J. fuscaria* (16 moths  $\times$  4 images) were prepared.

### Human predator system

We developed a pictorial puzzle program in Java that presents the photographs on the monitor in a specific order and records the latency until the moth image is clicked. The program also presents the next photograph if a participant clicks or spends 10 s without any click. Sixty participants (30 for *H. roboraria* and 30 for *J. fuscaria*), who were unaware of our experimental purpose and design, were tested. Each participant was asked to find a moth in the photograph and click on it. A training session of six photographs, of additional six moths different from those used in the test, was given before the actual test to ensure that the volunteers were accustomed to the shape of the moth and to the testing system. Photographs were presented in a random order on the LG Flatron (LG, Seoul, South Korea) 24 widescreen LCD monitor ( $1920 \times 1080$  resolution that corresponded to the 16 : 9 ratio) at a distance of 60 cm from the subject's eyes. To prevent the formation of memory about the features of the background, which could affect the perceived crypticity of the moth, the photographs of the same moth (in different positions and orientations on the same trunk) were separated by at least four images of other moths.

### Statistical analyses

For each species separately, we used generalized linear mixed models (GLMMs) to examine the effects of two fixed factors, the position (*initial* vs. *final* position) and the type of photograph (*real* vs. *control*), as well as the interaction between them, on the probability of a moth

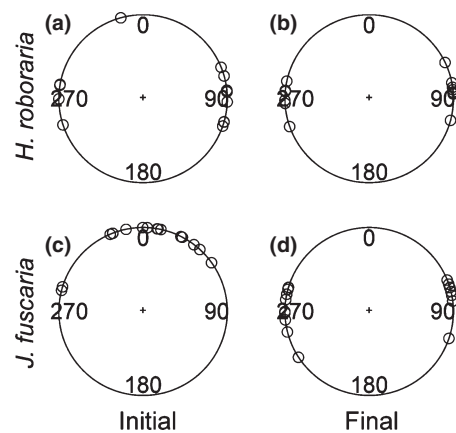
being detected (binary) and on the latency to the detection of those moths that have been detected in all four photographs (*real initial*, *real final*, *control initial* and *control final*). Identities of human participant and the moth were used as random factors. The latency to the detection of a moth was measured as the time from the beginning of a trial until the moment of moth image being clicked on. This variable was power-transformed to meet the assumptions of GLMMs (Sokal & Rohlf, 1995). The orientations of moths were measured as angle from 0 to  $360^\circ$  and nonparametric circular statistics [Watson's two-sample test for homogeneity (Zar, 1999); data did not follow the assumption of parametric test] was performed to compare two groups of angles (*initial* vs. *final*). R 2.12.0. (<http://www.r-project.org>) was used for all statistical analyses.

### Results

After a moth was released, it flew towards a neighbouring tree, landed on the bark and assumed the initial body orientation (Fig. 1a,d). Later, many of the moths repositioned themselves by walking and turning the body while repeatedly lifting and lowering their wings (see Movie S1, S2 in Supporting Information). The positioning behaviour started within several minutes after landing (for *H. roboraria*: 224 [98–317]s; median [lower–upper quartile],  $n = 12$ ; for *J. fuscaria*: 201 [167–241]s,  $n = 9$ ). After several attempts at repositioning (1–3 times, average 1.5 times for both species), the moth eventually (after 509 [234–739]s for *H. roboraria*; 208 [178–303]s for *J. fuscaria*) remained motionless in the final body position and orientation (Fig. 1b–e).

The final position was always different (within a distance of 50 cm) from the initial position. The final body orientation of *H. roboraria* (93% of moths oriented horizontally, within  $20^\circ$  from the horizontal plane; Fig. 2b) did not differ from the initial body orientation (85% horizontally;  $U_{14,14}^2 = 0.04$ ,  $P > 0.1$ ; Fig. 2a). The final body orientation of *J. fuscaria* significantly differed from the initial orientation (88% vs. 13% of individuals oriented horizontally;  $U_{16,16}^2 = 0.64$ ,  $P < 0.001$ ; Fig. 2c,d).

Once a moth repositioned itself, the probability of being detected significantly decreased (effect of position [*initial* or *final*]:  $\chi_1^2 = 31.69$ ,  $P < 0.001$  for *H. roboraria*;  $\chi_1^2 = 49.91$ ,  $P < 0.001$  for *J. fuscaria*; Fig. 3a,b) and the latency to moth detection increased (effect of position:  $\chi_1^2 = 11.96$ ,  $P < 0.001$  for *H. roboraria*;  $\chi_1^2 = 165.02$ ,  $P < 0.001$  for *J. fuscaria*; Fig. 3c,d). For *H. roboraria*, there was no effect of photograph type (*control* vs. *real*) on the probability of being detected (effect of photograph type:  $\chi_1^2 = 0.37$ ,  $P = 0.54$ ; interaction between photograph type and position:  $\chi_1^2 = 2.91$ ,  $P = 0.09$ ) or on the latency to the detection of the moth (effect of photograph type:  $\chi_1^2 = 1.36$ ,  $P = 0.24$ ; interaction between photograph type and position:  $\chi_1^2 = 0.01$ ,  $P = 0.93$ ).



**Fig. 2** Angular distribution of body orientations of *Hypomecis roboraria* (a,b) and *Jankowskia fuscaria* (c,d) at immediately after landing (initial position; a,c) and after positioning (final position; b,d). Black circles indicate the orientation of the head relative to the orientation of the upright tree. At final position, both moth species orient their heads nonrandomly but towards the side (towards 90 and 270° in the graphs).

Although in *J. fuscaria* the increase in crypticity due to positioning behaviour was stronger for real than for control photographs in both the probability of being detected (interaction between positioning and photograph type  $\chi^2_1 = 15.96$ ,  $P < 0.001$ ; effect of photograph type:  $\chi^2_1 = 4.31$ ,  $P = 0.04$ ) and the latency to moth detection (interaction between positioning and photograph type  $\chi^2_1 = 10.10$ ,  $P < 0.001$ ; effect of photograph type:  $\chi^2_1 = 17.11$ ,  $P < 0.001$ ), all the results clearly show that the body positioning behaviour resulted in better background matching than the initial position taken by a moth right after landing on the tree trunk.

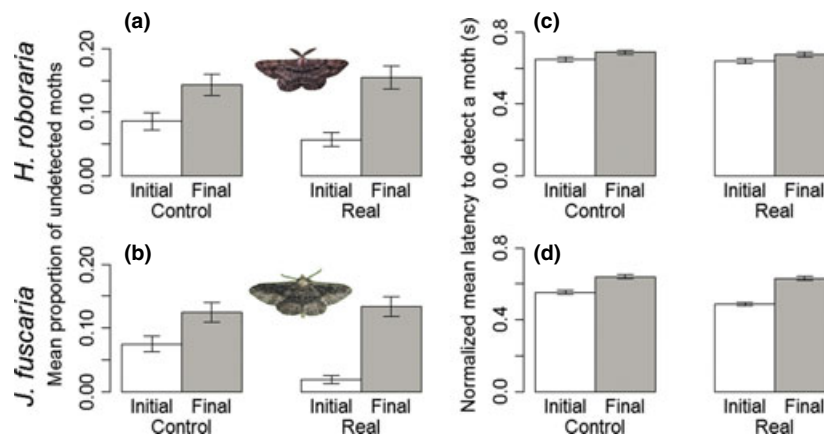
## Discussion

This is the first study that directly measures the detection of moths by visual predators before and after a moth performed the body positioning behaviour. The behaviour includes finding an appropriate spot on a bark after landing and, at least in some species, adjusting the body orientation. The results show that the natural body positioning behaviour, involving both the choice of spot on a bark and the choice of body orientation (*J. fuscaria*), or only the selection of the new resting spot (*H. roboraria*), will lead to even greater crypticity against typical substrates than previously shown in experiments using photographs of moths specimens on tree trunks (Pietrewicz & Kamil, 1977) or moth images (Webster *et al.*, 2009) placed by a researcher on a tree bark. This conclusion is valid for both the real photographs, where the natural variation in illumination is present, and control photographs, where the variation in general illumination of the background is artificially minimized

using the same photograph of a background similar to the final photograph of a moth. The moth silhouette in the initial control photograph originates from the final photograph where, due to a different body orientation between initial and final positions and perhaps due to different resting spot and time of picture taking, the moth wing pattern might have been illuminated in a different manner than the natural way expected at the initial position. This is especially crucial if initial and final body orientations differ (such like in *J. fuscaria*), and it might have led to lower crypticity of the initial than the final control photographs of *J. fuscaria*, as well as to the significant interaction between positioning and photograph type for *J. fuscaria*. Nevertheless, the effect of positioning was still clearly visible and significant even in those artificially designed photographs, indicating that behaviourally mediated change of resting spot (for both species) and body orientation (for *J. fuscaria*), rather than change of illumination, leads to a significant increase in crypticity at the final resting spots.

Although other studies of moth crypticity used both avian (Kettlewell, 1955b; Pietrewicz & Kamil, 1977; Cuthill & Székely, 2009; Wang & Schaefer, 2012) and human (Fraser *et al.*, 2007; Cuthill & Székely, 2009; Webster *et al.*, 2009) predators, the human predator model is more convenient for experiments (Fraser *et al.*, 2007; Cuthill & Székely, 2009; Webster *et al.*, 2009; Tsurui *et al.*, 2010). In studies with simple images on the monitor screen, results were consistent between human and avian predators (Beatty *et al.*, 2005; Fraser *et al.*, 2007; Cuthill & Székely, 2009). The main concerns for using humans as predators of colour images of insects presented on the computer screen may be the lack of UV sensitivity in humans [unlike in many birds (Cuthill *et al.*, 2000; Majerus *et al.*, 2000)] and unnatural spectral properties of monitor-generated images. However, based on spectrometric data obtained in natural habitats (see Supporting Information), we believe that UV contributes little to the general crypticity of the moths as perceived by UV-sensitive birds. Although the contrast between the moth and the bark in the range visible to humans (blue, green, yellow and red sections separately; see Supporting Information) in the monitor-generated image was lower than the natural contrast for *H. roboraria*, the contrast on the monitor closely imitated the natural contrast for *J. fuscaria* (see Supporting Information). Hence, our results indicate that the body positioning behaviour should significantly enhance the crypticity of the moths in natural situations.

The effect of body orientation on moth's crypticity has been already addressed in experiments where the moths (specimens or fairly naturalistic models) were presented at random locations on a tree bark to avian or human predators (Pietrewicz & Kamil, 1977; Webster *et al.*, 2009; Wang & Schaefer, 2012). Additionally, Wang & Schaefer (2012) reanalysed Endler's (1984) data set including information on moths' orientations at resting sites. These



**Fig. 3** Effect of body positioning behaviour on the detectability of moths (mean  $\pm$  SEM). Comparison of the proportions of undetected *Hypomecis roboraria* (a) and *Jankowskia fuscaria* (b), or the latency to the detection of *H. roboraria* (c) and *J. fuscaria* (d), between the *initial* position, at which the moth landed, and the *final* position, recorded after the moth performed body positioning and body orienting behaviours. Results from *control* and *real* photographs are shown separately. The latency to the detection of the moth was power-transformed ( $\lambda = -0.83$  for *H. roboraria*,  $-0.68$  for *J. fuscaria*) to comply with the normality assumption of the generalized linear mixed models.

studies suggested not only that moths orient nonrandomly in order to maximize their crypticity at resting spots (Pietrewicz & Kamil, 1977; Webster *et al.*, 2009; Wang & Schaefer, 2012), but also that the camouflage effect of species-specific body orientation is the largest on a bark of tree species that provides the typical species-specific resting sites for the moths. Our results are consistent with these studies: natural body positioning behaviour of *J. fuscaria*, which includes adjustments of body orientation, indeed increased moths' crypticity. However, we demonstrated that body positioning comprising only the selection of a new resting spot without significant changes in body orientation, like in *H. roboraria*, is sufficient to significantly increase the moth's crypticity. This suggests that not only a suitable body orientation, but also a choice of a cryptic spot critically reinforces moth crypticity. Although the ability of moths to find locally most cryptic spot is generally admitted, no study has formally confirmed that moths actually move towards a cryptic spot from the spot on which they initially land.

The body positioning that occurs soon after a moth lands on a tree trunk is a behavioural mechanism that significantly contributes to moth crypticity in a finer scale, after larger-scale processes of habitat choice (Endler, 1984) and the choice of tree trunks that match the moth's colour (Sargent, 1966, 1973; Steward, 1976; Kettlewell & Conn, 1977; Endler, 1984) have taken place. It appears that tactile stimuli from the tree bark, rather than vision, are used by the moths for choosing the final position and orientation (Sargent, 1969, 1973; Lees, 1975) in geometrid moths. Therefore, the positioning behaviour (choice of spot and body orientation) may not increase moth crypticity if both the colouration and the structure of furrows on the bark are not properly

combined in a manner which is a characteristic for the typical resting substrate of a moth species. Many classical studies of the moths' camouflage ignored the role of positioning behaviour. Our results suggest that some studies might have overestimated the contribution of moths' preferences for landing on a bark of a specific colour to the crypticity because the camouflage was measured after both the landing preferences and the positioning behaviour have been completed (e.g. Kettlewell, 1955b). In studies using moth specimens pinned at random spots on a tree bark in body orientations imitating the species-specific orientations (Pietrewicz & Kamil, 1977), the contribution of natural body positioning to crypticity might have been underestimated because resting spot selection has not been imitated. We suggest that in the future research the contribution of preferences for landing on a specific bark colour should be differentiated from the contribution of the subsequent positioning behaviours to the final crypticity of moths.

In summary, by using one of the iconic examples of evolution, we showed how a morphological adaptation cannot be fully understood without taking into account a full behavioural phenotype responsible in natural situation for increasing the adaptive function of the morphological trait. Our experimental approach to moth crypticity (*a moth positions itself – a predator attempts to detect it*) provides an unexplored method for testing hypotheses about behaviourally mediated morphological evolution (McPeck, 1995; Webster *et al.*, 2009) and about cospecialization between morphological and behavioural adaptations (Dewitt *et al.*, 1999). We expect that a quantitative comparative analysis of naturally observed body positioning behaviours among moths with various wing patterns, combined with tests of crypticity against

species-specific resting substrates, will illustrate an adaptive coevolution between cryptic morphology and the corresponding behaviours.

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### Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Methods and results of spectrometry.

**Movies S1, S2** Positioning behaviour of *H. roboraria* (S1) and *J. fuscaria* (S2) after landing on tree bark.

**Tables S1, S2** The statistics of the results of spectrometry analysis.

**Figures S1, S2** Example of photographs used in the experiment.

**Figure S3** Reflectance spectra of *H. roboraria*, *J. fuscaria* and background tree bark.

**Figures S4, S5** The contrasts between the moth and its background for moth images and for specimens in the field (S4 for *H. roboraria*, S5 for *J. fuscaria*).

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