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Overcoming the detectability costs of symmetrical coloration

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For camouflaged prey, enhanced conspicuousness due to bilaterally symmetrical coloration increases predation risk. The ubiquity of symmetrical body patterns in nature is therefore paradoxical, perhaps explicable through tight developmental constraints. Placing patterns that would be salient when symmetrical (e.g. high contrast markings) away from the axis of symmetry is one possible strategy to reduce the predation cost of symmetrical coloration. Artificial camouflaged prey with symmetrical patterns placed at different distances from the axis were used in both visual search tasks with humans and survival experiments with wild avian predators. Targets were less conspicuous when symmetrical patterning was placed outside a ‘critical zone’ near the midline. To assess whether real animals have evolved as predicted from these experiments, the saliency of features at different distances from the midline was measured in the cryptically coloured forewings of 36 Lepidopteran species. Saliency, both in absolute terms and relative to wing area, was greatest away from the axis of symmetry. Our work, therefore, demonstrates that prey morphologies may have evolved to exploit a loophole in the ability of mammalian and avian visual systems to spot symmetrical patterns.

1. Introduction

Camouflage is a ubiquitous visual defence strategy in the animal kingdom [1–3], but one seemingly paradoxical feature of concealing coloration is the presence of bilateral symmetry [4]. Experiments with avian predators in the field and laboratory have shown that symmetrically patterned camouflaged targets have lower survival rates than asymmetrical ones [5–7], consistent with earlier findings on symmetrical stimulus saliency in humans [8,9]. This is because most substrates where an animal might rest are asymmetrical, particularly at the spatial scale of the animal, making symmetry a salient Gestalt cue to a predator [10,11].

Evo-devo research on Lepidoptera suggests significant genetic and developmental constraints on the evolution of asymmetrical body patterns in this taxon [12–14]. Noteworthy exceptions in other insects demonstrate that these constraints are not absolute (e.g. [15]), but decoupling surface patterning from the symmetry of the underlying morphology may require many mutations. Assuming that genetic and developmental constraints are the main factor suppressing the evolution of asymmetrical coloration, one might ask whether animals have evolved ways of optimizing their surface patterning to mitigate the detectability costs of symmetrical appearance. One suggestion is that the positioning of body pattern elements relative to the axis of symmetry may be of significance [6,7].

Human visual systems are particularly sensitive to features within a narrow strip around the symmetry axis [8,9,16,17], presumably due to increased receiver attention at the point of fixation: symmetry is more likely to be detected if a saccade happens to alight on the axis of symmetry [7,8,17,18]. To date, there have been no studies to test the biological relevance of this phenomenon in non-human animals in the wild, but previous work on captive great tits, using abstract patterns, has indicated that this can affect detection [7]. For a



Figure 1. A selection of artificial targets created from one of the *Melanolophia* specimens, showing the five treatment groups when divisions were made by equal area (a) and equal width (b). From left to right: all-symmetrical (S), inside-only symmetrical (I), middle-only symmetrical (M), outside-only symmetrical (O), all-asymmetrical (A). (Online version in colour.)

cryptic animal with left and right elements visible simultaneously to the receiver, e.g. a moth on a substrate, one would expect camouflage elements, such as high-contrast disruptive markings, that might attract a saccade [19], to be placed away from the axis of symmetry [7]. This would constitute an evolutionary compromise, enhancing crypsis while retaining bilateral symmetry.

We investigated whether such a critical region about the axis of symmetry exists in camouflaged, artificial, moth-like prey, using human visual search and wild bird predation experiments. We also tested whether salient elements on the wings of real Lepidopteran species are, on average, positioned away from this critical region about the symmetry axis.

2. Material and methods

(a) Experiment 1: human visual search

(i) Stimuli

Artificial outlines were created based on the North American genus *Melanolophia* (family: Geometridae), a group with a typical moth shape when in their resting position [20], usually in forest habitats. Photographs of the bark of 180 oak trees (*Quercus robur*), were taken with a calibrated Nikon D80 (Nikon Corporation, Tokyo, Japan) at Leigh Woods National Nature Reserve (North Somerset, UK, 2°38.6' W, 51°27.8' N) to provide the surface patterning of the artificial prey and the backgrounds against which they would 'rest'.

To create the experimental treatments, each moth was divided into sixths: three each side of the midline [8]. Divisions were made by both equal area and equal width because moth shapes are not uniform in area along their width, and both area and distance from the midline could affect detectability. Five treatment groups (figure 1), for both division variants, were created by manipulating the mirror symmetry of the bark between the complementary sixths on each half of the target. The treatments were: S: Complete symmetry; I: Inner sixths symmetrical only; M: Middle sixths symmetrical only; O: Outer sixths symmetrical only; A: Complete asymmetry.

There were 18 replicates of each treatment \times division combination, giving a total of 180 stimuli. The targets were then placed, in the same vertical orientation, at random locations on their corresponding bark background, although never in the location where the background for the target was extracted. When displayed in the experiment, the visual angle occupied by the targets was 4.18°.

(ii) Procedure

The experiment was a visual search task programmed in MATLAB [21] using the Psychophysics Toolbox Version three extensions [22,23]. Twenty-five participants (52% female, aged 18–30) with normal or corrected-to-normal vision, and naive to the purpose of the experiment were briefed in line with the Declaration of Helsinki. The display was a linearized, 22", 1024 \times 768 pixel LaCie

Electron 22Blue CRT monitor (LaCie Ltd., London) (as in [24]). Subjects sat with their head level and within 1 m of the screen. They clicked on the moth in each of the images using a computer touchpad (MacBook Pro; Apple Inc., Cupertino, CA, USA). Five practice trials preceded the experiment.

The 180 stimuli were displayed in a different random order for each participant, with a black fixation cross on a mid-grey background shown for 0.5 s before each trial. There were six 30-image blocks, with the participant able to take a break after each block. Trials timed out after 30 s when the next image would be shown. Response time (RT), mouse click location and time-outs were recorded.

(iii) Analyses

RTs and residuals from fitted models were inspected visually and an inverse transform of the time (effectively response rate) was found to normalize residuals. Inverse RTs were analysed with a linear mixed model using the function `lmer` in the *lme4* package in R [25,26]. Symmetry treatment (five levels) and division variant (two levels) were treated as fixed effects, while subject, particular target and background were fitted as random effects.

A miss was defined as any click outside an invisible rectangle centred on the target which had dimensions that were 5% greater than those of the targets. Analyses of errors and time-outs were attempted using Generalized Linear Mixed Models with binomial errors (function `glmer` in *lme4*). However, owing to the low frequency of misses (5.9% of trials) and time-outs (0.8%), the fitted models did not converge (the maximum likelihood could not reliably be found). Because all the variation in participant performance is captured in RT, speed-accuracy trade-offs are not a concern.

(b) Experiment 2: avian predation in the field

(i) Procedure

The same 180 artificial prey from Experiment 1 were calibrated for passerine vision (using the techniques described in [24]) and printed onto waterproof paper (Rite-in-the-Rain, Tacoma WA, USA) to be used in the field experiment, which took place from February to March 2018. The targets were 3.5 cm by 2 cm and the experimental procedure followed similar previous work (e.g. [27]). Targets were pinned on to the bark of mature oak trees at the site the bark textures had been photographed (Leigh Woods National Nature Reserve). A dead mealworm (*Tenebrio molitor* larvae frozen at -80°C then thawed) was pinned underneath each target as bait. A total of 1350 individual targets were put out in 15 blocks of 90, giving eight repeats of moth shape replicates 1–9 and seven repeats of replicates 10–18. Each block of stimuli was placed in a different area of the wood, on different dates, in order to reduce the likelihood of predation by the same individual predators. Fresh targets were printed for each block.

Once an individual tree was selected, individual targets were chosen at random by blindly selecting from a bag. Checks were then made at 24, 48 and 72 h intervals. The 'survival' of each artificial moth was determined by the presence or absence of the mealworm, with the target still intact and attached to the tree.

127 Targets were marked as 'censored' in the survival analysis if they
 128 were lost, if they survived until the end of the trial (72 h) or if
 129 there was evidence of non-avian predation [24].

131 (ii) Analyses

132 A mixed-effects Cox regression was used to perform a survival
 133 analysis using the *coxme* function from the *coxme* R package
 134 [25,28]. Symmetry treatment and division variant were treated
 135 as fixed effects, with experimental block a random effect. The
 136 effect of treatment was tested using an analysis of deviance comparing
 137 the unexplained variation of a model with and without the
 138 factor in question, tested against a χ^2 distribution.

139 Experiments 1 and 2 investigate how the presence and position
 140 of bilateral symmetry affect the detectability of cryptic prey
 141 if all competing biological constraints which might preserve symmetrical
 142 coloration are removed. The following natural pattern analysis
 143 uses real, bilaterally symmetrical Lepidoptera specimens to ask
 144 whether real animals have evolved to follow the trends suggested
 145 by these human and avian predation experiments.

146 (c) Natural pattern analysis

148 (i) Photographing, editing and categorization of specimens

149 Dead British moth species were acquired from collections at the
 150 Bristol City Museum and Art Gallery (UK) and photographed
 151 under controlled lighting conditions (see electronic supplementary
 152 material). Scans were also taken from Sterry *et al.* [29], a
 153 photographic field guide which shows species in their natural
 154 resting positions. Museum and field guide specimens were
 155 then identified to family, genus and species level. Unlike the
 156 photographs taken personally, the colours in the field guide
 157 cannot be taken as accurate (even for human vision), but the
 158 rationale was that the within-wing distribution of salient features,
 159 with most of the pattern variation being in intensity not hue,
 160 would be correlated between uncalibrated photograph and
 161 avian-perceived colour. Because they are always visible when
 162 the moths are at rest, only the forewings (left and right) of
 163 the moth specimens were selected for the analysis. These were
 164 then cropped and edited on GIMP 2 (The GIMP Team, www.gimp.org)
 (see electronic supplementary material).

165 Moth species of interest were those with cryptic, discrete, high-contrast
 166 markings relative to the average colour and pattern of the wing.
 167 These criteria could include high-contrast disruptive markings,
 168 but with the exception of horizontal markings that transected
 169 the entire wing. To confirm whether a moth's coloration was
 170 cryptic, albeit subjectively, multiple photographs of the animal
 171 against its natural background were compared using Google Images.
 172 Only moths with such discrete markings would have had the
 173 evolutionary freedom to position pattern elements further or
 174 nearer from the axis of symmetry. Species with patterns conforming
 175 to these criteria were selected by an unbiased group of 20
 176 human participants (electronic supplementary material). A
 177 phylogenetically diverse spread of moths was selected for the
 178 analysis with the sample size consisting of 36 species, 31 genera
 179 and seven families. Of the 36 moths chosen, 9 were from the
 180 museum, while the remaining 27 were from the field guide.

181 (ii) Image analysis

182 A computer program for analysing the visual salience of the
 183 edited right and left forewings was written using MATLAB
 184 [21]. Saliency maps were generated by applying an avian-vision
 185 adaptation of a model created by Rosenholtz *et al.* [30,31].
 186 This is a model, used previously for investigating other aspects
 187 of animal camouflage [32], which analyses variation in three
 188 features based on low-level visual perception: luminance,
 189 colour and orientation contrast. These are then summed to get
 an overall measure of visual salience. A combined measure of

salience as a function of distance from the midline was obtained
 by summing values of each column of pixels from left to right
 (for a right forewing) or right to left (for a left forewing). In
 the absence of any data on the perceptual weightings of achromatic
 intensity, colour and edge orientations for birds, the empirically
 derived values for humans were used with the rationale that this
 should not affect within-wing differences in salience. Tests of the
 robustness of this assumption, and of whether the use of both
 museum specimens and book-sourced images affect the conclusions,
 are provided in the electronic supplementary material. Because
 wings are not equal in area across their width, we calculated
 relative salience which controlled for the width of the wing at
 a particular point (figure 2). Further details on the computer
 program and how salience was calculated are provided in the
 electronic supplementary material.

189 (iii) Statistical analysis

Thirds of equal width were created and the summed salience
 and wing area within each third was calculated. Wing area was
 used to determine the relative salience (absolute salience/wing
 area) of each third. Within-wing differences between the inner,
 middle and outer thirds were analysed with linear mixed models
 in R [25], using the modified *lmer* function from the *lmerTest*
 package [33]. Side and species were both treated as random
 effects, the null hypothesis being that the mean difference
 between wing thirds is zero.

There is no complete phylogeny of the species in our study
 but, to assess whether phylogeny could be a potential confounding
 factor, we reran analyses with moth family as an additional
 random effect.

3. Results

(a) Experiment 1

For the inverse response times, the symmetry treatment \times division
 variant interaction was significant ($\chi^2 = 13.69$, d.f. = 4, $p =$
 0.0084). The data were therefore split by stimuli divided by
 equal area or width, with linear mixed model analyses performed
 separately for each. A limited set of *a priori* custom contrasts
 was applied using the *glt* function in the *multcomp* package
 [34] using a Tukey-style procedure where treatments S and A
 were contrasted with all other treatment groups.

When the targets were divided into sixths by equal area, the
 effect of treatment was significant [$\chi^2 = 256.82$, d.f. = 4,
 $p < 0.0001$; figure 3a(i)]. There was no significant difference
 comparing S with I ($z = -0.361$, $p = 0.9880$). However, treatment
 S evoked a lower average RT than M ($z = 12.797$, $p < 0.0001$),
 O ($z = 3.404$, $p = 0.0035$) and A ($z = 12.813$, $p < 0.0001$).
 Treatment A had a significantly greater RT than I ($z = -4.345$,
 $p < 0.001$). No significant differences were found between A
 and M ($z = -1.343$, $p = 0.5259$) or O ($z = -0.587$,
 $p = 0.9422$).

When the targets were divided into sixths by equal width, the
 effect of treatment was also significant [$\chi^2 = 124.65$, d.f. =
 4.0, $p < 0.0001$; figure 3a(ii)]. As with targets divided by
 equal area, there was no significant difference between S and
 I ($z = 0.816$, $p = 0.8494$). Again, S had a significantly lower
 RT than M ($z = 9.705$, $p < 0.0001$), O ($z = 2.672$,
 $p = 0.0330$), and A ($z = 8.007$, $p < 0.0001$). No significant
 differences were found between A and I ($z = -1.526$,
 $p = 0.4072$), M ($z = 0.936$, $p = 0.7851$) and O
 ($z = 0.337$, $p = 0.9902$).

Overall, all-symmetrical and inside-only symmetrical
 patterns were most easily detected. Although there was an
 interaction between treatment and division variant, the
 treatment effects were the same, just slightly stronger in
 the width variant.

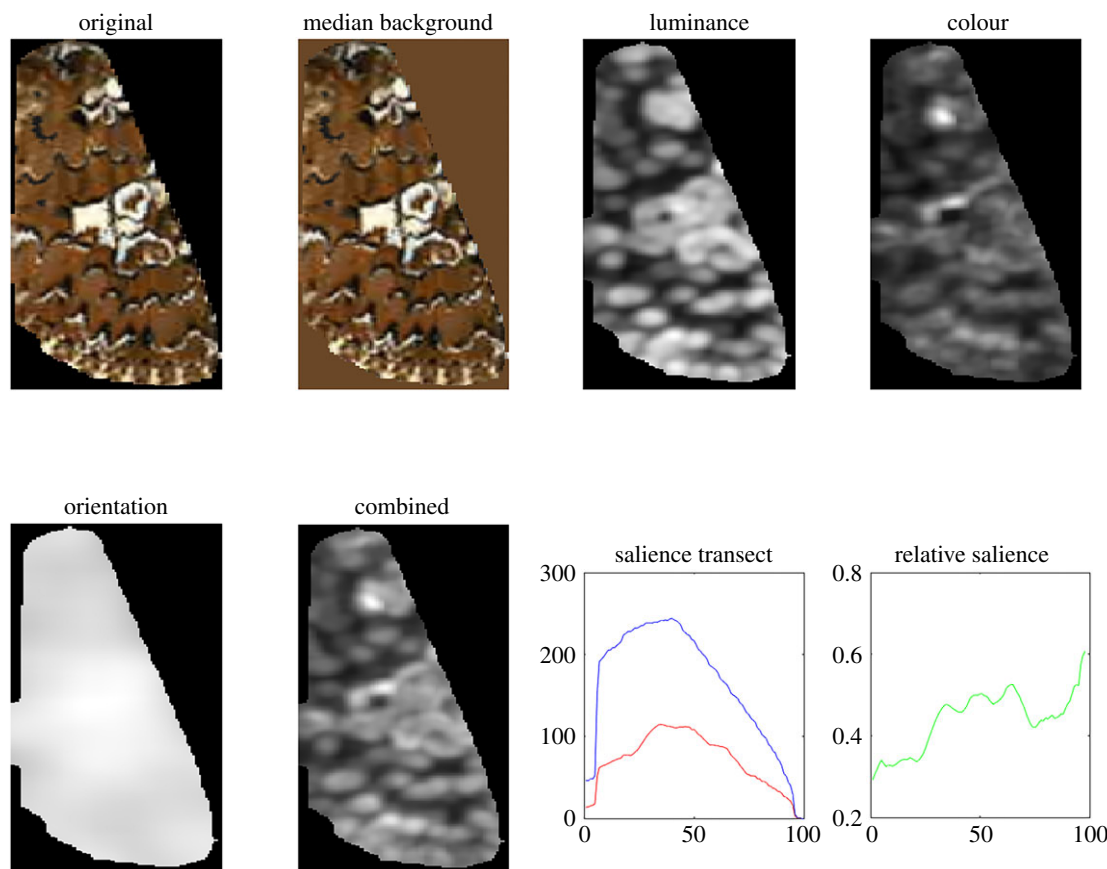


Figure 2. An example of the output from the wing salience computer program for the right wing of *Hadena albimacula*. From left to right: the original image file, the file with background set to the median colour of the wing, a salience map based on luminance contrast, a salience map based on colour contrast, a salience map based on orientation contrast, a combined salience map, a transect along the combined salience map, showing the sum of salience values (red line) and available wing area (blue line) in each vertical column when moving from left to right along the wing, a transect of the salience score relative to the available wing area Q3 when moving from left to right along the wing. (Online version in colour.)

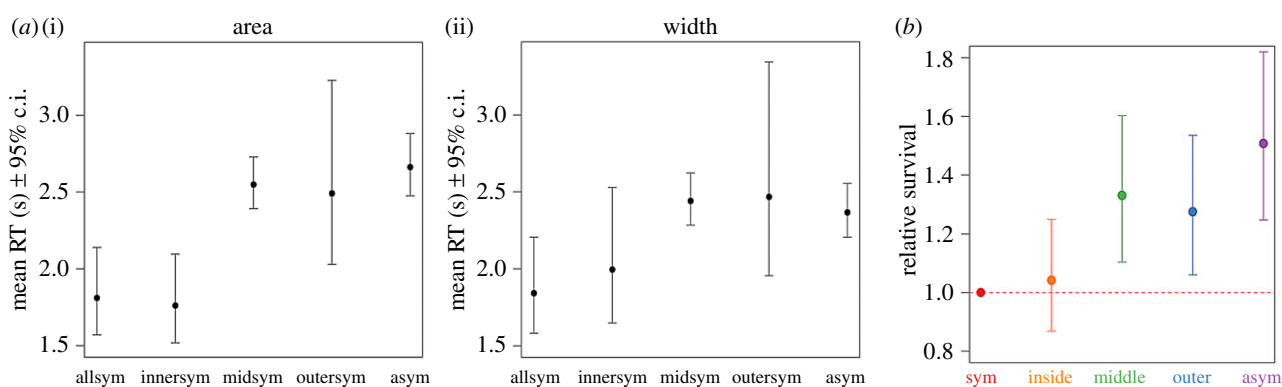


Figure 3. Experiment 1 (a) and 2 (b) results. (a) The mean response times with respect to all treatment groups when the targets were divided by equal area (i) and width (ii). Error bars represent 95% confidence intervals. (b) Odds of survival relative to complete symmetry, the treatment which received the lowest survival rate. Values and 95% confidence intervals are from the fitted survival model. (Online version in colour.)

(b) Experiment 2

In the mixed-effects Cox regression, the symmetry treatment \times division variant interaction ($\chi^2 = 4.8441$, d.f. = 4, $p = 0.3037$) and the main effect of division variant were not significant ($\chi^2 = 0.9559$, d.f. = 1, $p = 0.3282$), but the effect of symmetry treatment was significant ($\chi^2 = 25.626$, d.f. = 4, $p < 0.0001$; figure 3). A limited set of custom contrasts was then calculated, as in Experiment 1. There was no significant difference between S and I ($z = 0.438$, $p = 0.9889$). However, the survival rate was significantly lower for treatment S compared to M ($z = 2.994$, $p = 0.0168$), and A ($z = 4.259$, $p < 0.0001$). The difference between S and O was similar, but

not significant ($z = 2.576$, $p = 0.0567$). Treatment A had a significantly higher survival rate than I ($z = -3.831$, $p < 0.0001$), but not M ($z = -1.273$, $p = 0.6451$) or O ($z = -1.712$, $p = 0.3610$).

(c) Natural pattern analysis

The absolute salience of the middle third was significantly greater than that of the inner third ($t = 9.208$, d.f. = 27.2, $p < 0.001$). However, the inner third was significantly more salient than the outer third ($t = 9.687$, d.f. = 35.3, $p < 0.001$). By necessity, the difference in salience between the middle and outer thirds was also significant ($t = 11.45$, d.f. = 24.7, $p < 0.001$) (figure 4).

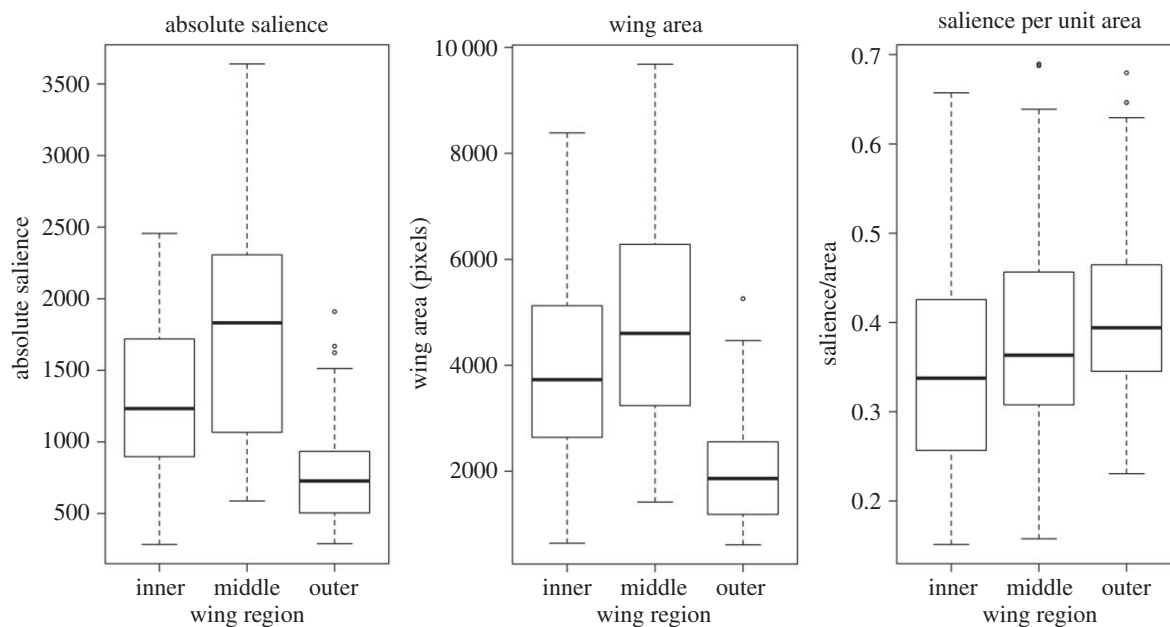


Figure 4. Boxplots displaying (from left to right) the absolute salience, wing area and relative salience for the inner (closest to the midline), middle and outer (furthest from the midline) thirds of the moth forewings (natural pattern analysis) when divided by equal width. Medians (thick horizontal bars), interquartile ranges (boxes), values within 1.5 interquartile ranges of the box edges (whiskers) and possible outliers (circles outside the whiskers) are plotted.

When the analysis was repeated using relative salience, both the middle third and the outer third had a significantly greater relative salience than the inner third ($t = 6.381$, $d.f. = 33.2$, $p < 0.0001$) ($t = 5.665$, $d.f. = 35.2$, $p < 0.0001$) (figure 4). The relative salience of the middle was also significantly lower than that of the outer third, although not as marked as the previous pairwise comparisons ($t = 2.95$, $d.f. = 35.3$, $p = 0.0060$).

To check for confounds due to phylogeny, we reran analyses with moth family as an additional random effect. The results for absolute salience remain highly significant (inner versus middle: $t = 4.154$, $d.f. = 5.133$, $p = 0.008$; inner versus outer: $t = 4.139$, $d.f. = 3.810$, $p = 0.016$; middle versus outer: $t = 4.806$, $d.f. = 5.309$, $p = 0.004$). The pattern of results for relative salience are unchanged but become non-significant (inner versus middle: $t = 2.326$, $d.f. = 5.611$, $p = 0.062$; inner versus outer: $t = 2.866$, $d.f. = 2.169$, $p = 0.060$; middle versus outer: $t = 1.137$, $d.f. = 4.624$, $p = 0.311$), the large loss of degrees of freedom being an obvious factor. That said, the variance estimates for the factor family in these two analyses have 95% confidence intervals of -0.04 to 0.04 and -0.06 to 0.06 , respectively. Therefore, the family did not explain significant variation, indicating that we can have confidence in the results from our analysis without including family as a factor.

4. Discussion

The results from Experiments 1 and 2 suggest that prey which are symmetrical only near their midline are just as salient as prey which display symmetry across their whole body. The RTs and predation rates of the middle-third-only and outer-third-only symmetrical treatments show that symmetry is relatively inconspicuous to both human and avian predators when placed outside this critical zone (figure 3). Jenkins [9] used dot textures to demonstrate that most symmetry information used by the human visual system is found within a strip 1.1° wide about the symmetry axis of the stimulus. The visual angle occupied by the inner pair of sixths in

Experiment 1 represented approximately 1.19° , making it comparable to Jenkins' stimuli and, by using more naturalistic stimuli, puts these findings into a biological context.

A symmetrical midline makes a target more salient to predators because symmetrical elements are closer together and therefore more easily compared by the receiver's visual system. Midline symmetry should also increase the accuracy of attack when a predator targets the centre of the prey. Mirror symmetry about the midline may also create abnormal patterns that are rarely present in the background [7]; although the complex oak bark texture of our targets is likely to have reduced these effects in comparison with the line element patterns used in [7]. In contrast to our data, Cuthill *et al.* [6] found no difference between midline and non-midline symmetry treatments; however, they placed their mealworm bait above the target which would have highlighted the axis of symmetry and therefore could have made any positioning effects of patterning undetectable during their analysis.

The relative cost of symmetry near the midline is likely to vary between camouflaged organisms, depending on their coloration, the nature of their respective backgrounds and the perspective from which they are viewed. Symmetrical patterns are not a cost for animals viewed from the side, but for moths, seen from above in plain view, they might be. The marginal costs of symmetry for species with homogeneous, low-contrast, background matching patterns are likely to be low, whereas species with discrete, highly contrasting cryptic markings will be under stronger selection pressure to position these pattern elements away from the midline. The nature of the background or camouflage strategy will determine how many variations of positioning surface pattern elements relative to the midline are possible. It is these discrete markings that we investigated in the comparative image analysis.

There was significantly higher salience in the middle third than in the inner third, but the salience of the inner third was significantly higher than that of the outer third (figure 4). This is primarily because there is less wing area in the outer third to contribute to the total salience score, and this

was demonstrated when the analysis was re-run using relative salience (figure 4). The shape of many moth wings therefore adds to the intrinsic cost of symmetrical coloration by virtue of there being more area near the midline. Even though the median wing area is greatest in the middle third, our results demonstrate that the saliency of pattern elements relative to wing area is still greater in the middle and outer thirds than in the inner third. Absolute values of saliency are ultimately more relevant in the context of the visual ecologies of predators searching for these prey items against their respective backgrounds. However, what emerges from the analysis of relative salience is that, despite the constraint of wing shape, animals have evolved to place a disproportionately high number of salient markings away from their body midline.

Given that the salient markings of interest included disruptive patterns that break the body outline, it is possible that these are more prevalent on the outer third to facilitate edge disruption rather than reduction of symmetry saliency. However, the relative salience of the middle third was also significantly greater than that of the inner third, despite the middle having less edge per unit area. This suggests that the positional bias of disruptive markings cannot be the sole explanation for the trends that emerge from the natural pattern analysis. In any case, consideration of the moth species chosen for the experiment (electronic supplementary material) shows that 18 of the 36 species do not have

disruptive markings near the wing edge. Our work, therefore, provides insights into how camouflaged prey have evolved to counter, at least in part, the predation cost due to symmetrical colour patterns.

Ethics. The human research had ethical approval from the Faculty of Science Research Ethics Committee and the bird experiments from the Animal Welfare & Ethical Review Body, both at the University of Bristol.

Data accessibility. All data are available from Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.0860t19> [35].

Authors' contribution. J.B.W. wrote the first draft of the manuscript, with subsequent significant contributions by all authors; carried out the laboratory experiment and edited the moth images for the natural pattern analysis. J.B.W. and I.C.C. carried out the field experiment; took photographs of the museum specimens and analysed all the data. N.E.S.-S. and I.C.C. wrote the visual search program; and devised the experiments and stimuli. I.C.C. wrote and ran the program for the natural pattern analysis.

Competing interests. We declare we have no competing interests.

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