

Butterfly wing patterns create powerful illusory motion cues

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The dazzling stripes found on zebras and snakes have long been thought to interfere with predator motion perception, but this hypothesis has received little empirical support to date. Butterflies demonstrate enormously diverse and high-contrast wing patterns, the function of which has inspired intense theoretical debate and research. Here we suggest that butterfly wing patterns work in tandem with flight dynamics to create visual illusions that confuse predators. We use multiple independent lines of enquiry with biologically inspired modelling to support this hypothesis: free-flight butterfly take-offs filmed at high speed demonstrate the creation of misleading motion cues; phylogenetically controlled analyses demonstrate that this is an evolutionarily widespread strategy; and *in silico* evolution experiments independently converge on butterfly-like wing patterns. Our results show that butterfly wing patterns and flight dynamics create powerful illusory motion effects, potentially representing one of the most successful and hitherto unknown visual defence strategies in moving animals.

Movement can break even the most effective camouflage¹⁻³, rendering almost any animal highly conspicuous. Animal markings have evolved to exploit limitations in the vision of their predators, and this principle should hold true for animals in motion, where patterns have long been thought to interfere with a predator's perception of the speed and direction of their prey^{4,5}. High-contrast stripes and patterns are known to create illusory motion^{3,6,7}, but studies testing their effects in animals such as zebras, snakes and lizards have been somewhat equivocal in their support⁸⁻¹². Importantly, these studies have exclusively used rigid prey, despite animal locomotion requiring limb movements that oppose the body's main direction of travel. Biological motion therefore introduces unexplored potential for visual interference that is potentially common in nature⁵.

The striking colouration of butterflies has captivated the attention of evolutionary biologists for well over a century, making them one of the most studied groups in terms of how their appearance is linked to their evolution and behaviour¹³. Research has focused on the adaptive significance of warning signals, mimicry, sexual signals, thermoregulation and camouflage, and the underlying genetics and evolution¹⁴. It is striking then that these fundamental adaptive visual strategies often fail to readily explain the high-contrast dorsal wing patterns seen in many butterflies. We propose another key function of butterfly wing patterns is anti-predator defence through creating illusory motion. There are multiple factors that suggest flight behaviour and wing patterning may interact to create

misleading motion cues in butterflies; many species have high-contrast patterns similar to those suggested to affect motion detection, as well as low wing beat frequencies that are resolvable by avian vision¹⁵. They also often display evasive flight behaviour, and features such as eyespots and hindwing tails can act to deflect predatory attacks^{16,17}. Furthermore, strikingly few predators have specialised on catching butterflies on the wing despite their extreme conspicuousness¹⁸. This is in contrast to nocturnal moths, which are targeted by a wide range of avian predators when in flight, and generally have lower-contrast patterns and high wingbeat frequencies that would likely produce too much motion blur to create illusory motion cues^{19,19–22}.

Results and Discussion

Motion confusion

We quantified motion detection in each video frame as the mean elementary motion detector (EMD) motion ‘energy’ in four cardinal directions (forwards, backwards, left and right)²³, and defined motion confusion in two directions: forwards-confusion (the Michelson contrast between forwards-energy and backwards-energy), and sideways confusion (the Michelson contrast between the mean left-right energy and forwards-energy). Forwards-confusion is likely to interfere with a predator’s estimation of speed (e.g. deflecting attacks behind a butterfly), while sideways confusion is likely to deflect attacks laterally.

Butterfly wing patterns create motion confusion during takeoff

First, we experimentally tested whether the natural wing patterns maximised illusory motion cues in free flight compared to unpatterned treatments. This was tested by filming butterfly take-offs at 1,000 frames-per-second, and segmenting the footage in order to manipulate and test how patterning affects early-stage motion detection (see Supplementary Video 1). Butterflies with real wing patterning created significantly more motion confusion than experimentally unpatterned treatments (Tukey post hoc comparisons for unpatterned treatments compared to patterned, forwards-confusion: average grey $\beta = 0.079$, $p < 0.001$; black $\beta = 0.078$, $p < 0.001$; white $\beta = 0.078$, $p < 0.001$; sideways-confusion: average grey $\beta = 0.044$, $p < 0.001$, black $\beta = 0.044$, $p < 0.001$, white $\beta = 0.044$, $p < 0.001$; see Figure 1 and Supplementary Tables 1 and 2). In line with predictions of EMDs, higher contrast (being lighter or darker against the background) resulted in higher estimates of speed. However, patterning influenced the ratio of energy in different directions, creating both forwards and sideways confusion effects.

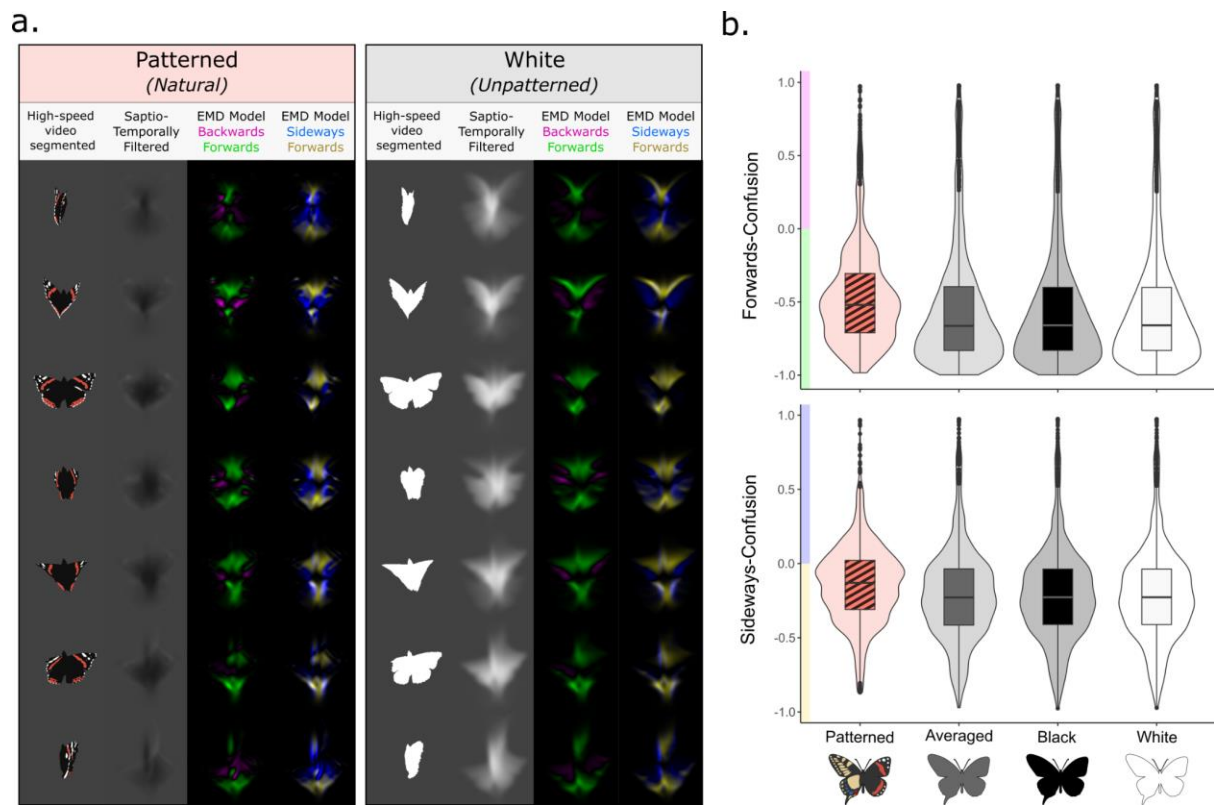


Fig.1 | EMD measures for butterfly slow motion take off. a. Example free-flight motion confusion analysis using a red admiral butterfly, *Vanessa atalanta*, with frames re-centred to match time, so spatial location is only approximate. From left to right, panels show the colour-segmented butterfly, the butterfly converted to avian double-cone vision with spatio-temporal filtering, the EMD model output for forward confusion, and then sideways confusion. This process is repeated for an unpatterned butterfly where the wing colouration has been replaced by white. **b.** Boxplots with violins for forward confusion (top), and for sideways confusion across all frames for all 7-butterfly wing morphotypes with patterning, and without patterning (averaged, black, and white).

Multiple character traits that are widespread in European butterflies maximise motion confusion

Next, we determined the properties of natural wing patterns that maximise motion confusion effects and explored whether they are evolutionarily widespread. We rendered the simulated flight of 757 unique butterfly morphotypes across 397 European species at 2,000 frames per second to achieve fluid motion (see Supplementary Video 2). European butterflies provide an ideal system because there are no major mimicry rings (comparatively few are chemically defended)²⁴, yet many have otherwise unexplained high-contrast markings, and there is a detailed phylogeny available^{25,26}.

Using random forest models we identified which pattern features best explained our motion confusion metrics (forwards-confusion: %var exp = 65, $R^2 = 0.002$; sideways-confusion: %var exp = 69, $R^2 = 0.002$; forwards-energy: %var exp = 90, $R^2 = 0.001$). During flapping flight, forwards-confusion was

most effectively maximised through (in order of importance, with all highly influential): increased forewing contrast; resolvable vertical stripes on the hindwing, uneven stripe distribution (generally meaning a single stripe, either relatively central across both fore and hindwing, or a contrasting edge), higher hindwing luminance, higher hindwing shape roughness (e.g. hindwing tails), and vertical stripes on the forewing. Sideways-confusion similarly increased with vertical patterning and hindwing tails but was less affected by contrast and also increased with butterfly size. As with our take-off analyses, being whiter increased forwards-energy (see supplementary material, random forests for motion confusion metrics, for a full table of results).

Natural butterflies were found to vary in their level of motion confusion with forwards and sideways confusion correlating with one another (linear model for forwards-confusion against sideways-confusion: $\beta = 0.518$, $p < 0.001$; fig 2a). Controlling for phylogenetic relatedness using principal coordinates showed that motion-confusing phenotypes are widespread among butterflies during flapping flight (Fig.2b), with Papilionidae demonstrating the highest overall motion confusion as a taxon, and Nymphalidae with a single vertical stripe extending across both wings achieving the highest overall forwards-confusion (Fig.2c and Fig.2d). Sideways-confusion was predominantly determined by resolvable vertical hindwing stripes, with higher hindwing luminance and wing shape roughness, i.e. “tails”, also showing important effects.

Comparisons between flapping and gliding flight showed that forwards-confusion can only be created by wing motion, whereas gliding flight is still able to generate powerful sideways confusion. This may explain why Papilionidae (a group that glides during flight) have wing patterns that maximise both forwards-confusion and sideways-confusion (Fig.2a).

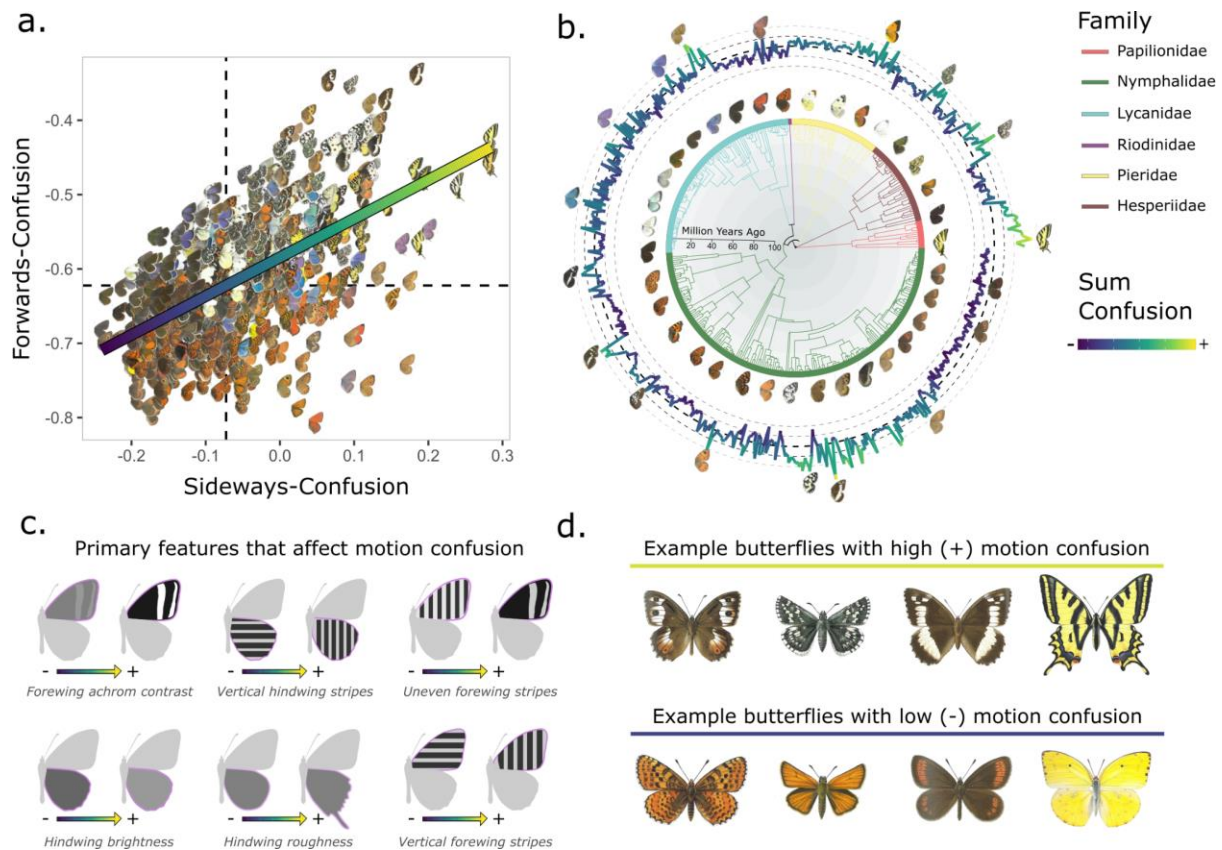


Fig.2 | Motion confusion across European butterflies. **a.** Correlation between forwards-confusion and sideways-confusion within European butterflies. Each image corresponds to the motion confusion measures for the shown butterfly. **b.** Phylogeny of European butterflies with the normalised sum of forwards-confusion and sideways-confusion across the phylogeny: the radius of each point corresponds to the level of motion confusion. The thick dashed line shows the mean, while the lighter dashed lines indicate 1x and 2x the standard deviation from the mean. Inner wing images show randomly selected butterflies at 10-degree intervals. Outer wing images show the butterfly with the highest motion confusion at 20-degree intervals. **c.** Features identified as increasing motion confusion using forest plots for forwards and sideways confusion. **d.** Examples of butterflies with high motion confusion (above) and with low motion confusion (below). Images of butterflies and their wing patterns for **a.**, **b.**, and **c.** were used from Collins Butterfly Guide with permission from artist Richard Lewington.

Artificially evolved butterflies selected for motion confusion alone mimic real butterflies

Finally, we used genetic algorithms to evolve 57,600 unique butterfly wing patterns *in silico*, selecting for maximal motion confusion, free from evolutionary and developmental constraints of true butterfly wing patterns¹³ (see Supplementary Video 3), and tested for pattern convergence with real butterfly wings. The genetic algorithm (GA) consistently evolved butterfly patterns that maximised either forwards-confusion, sideways confusion, or forwards energy (i.e. the absolute motion energy in the forwards direction), replicated across three wing shapes (Fig.3a). As with real butterflies, forwards and sideways-confusion significantly correlated (linear model for sideways-confusion against forwards-confusion for GA generated butterflies; sideways-confusion: $\beta = 0.733$, $p < 0.001$).

Analysis of the evolved phenotypes revealed convergence between GA-evolved wing patterns selected for forwards-confusion and those of European butterflies. Patterns that were effective at motion confusion possessed a lower pairwise euclidean distance of principal components (PC 1-2 explain cumulatively 29% of variance) from natural butterflies compared to butterflies randomly generated at the start (unevolved), butterflies evolved under random selection (drift), or even outlying butterfly species (Fig.3b, Tukey post hoc comparisons of natural butterflies to GA generated butterflies compared, unevolved: $\beta = -0.102$, $p < 0.001$; forwards-confusion: $\beta = 0.056$, $p < 0.001$; sideways-confusion: $\beta = 0.00$, $p = 0.999$; forwards-energy: $\beta = -0.122$, $p < 0.001$; random-selection: $\beta = -0.062$; see Supplementary Material for the full table). Selecting for forwards-energy resulted in immaculate white butterflies, consistent with the strategy adopted in the Pieridae ('whites'), although they were more different from natural butterflies than other treatments. This strategy would be expected to cause predators to under-estimate forward speed and over-shoot their attacks.

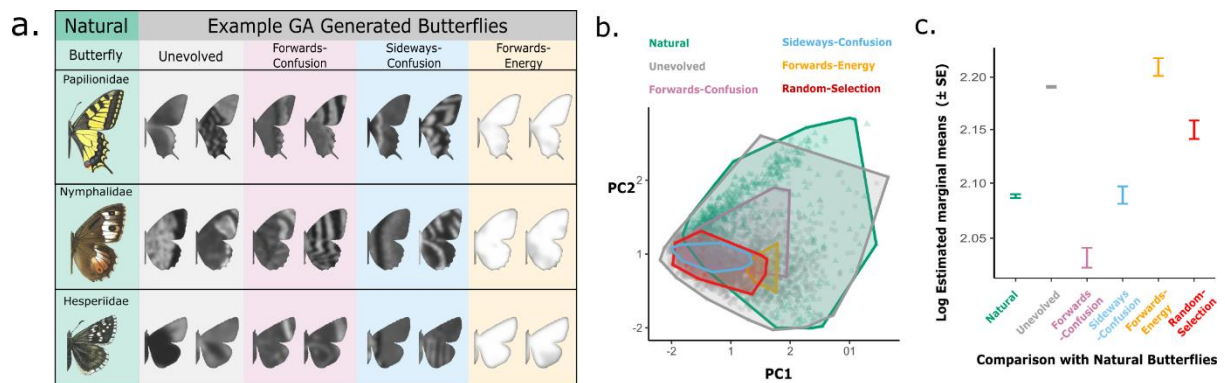


Fig.3 | Artificial evolution of motion confusing butterflies. **a.** Butterfly examples created using our genetic algorithm (GA) for three different wing shapes (for examples from each population, see the supplementary material). Unevolved butterflies were randomly generated by using random gene values, while forwards-confusion, sideways-confusion, and forwards-energy were evolved under selection for their named metric with examples being from the final generation ($G = 20$). **b.** shows PCA hulls for the four GA butterfly groups and real, naturally occurring butterflies. Here, PC components summarise variation in the butterfly wing pattern space. Random-selection butterflies evolved by randomly ranking the butterflies in each generation. **c.** shows the estimated marginal means for the pairwise distance of each group from the natural butterflies.

Summary and implications

We provide the first empirical evidence that many butterfly wing patterns are consistent with selection for motion confusion likely to deflect predator attacks in flight. Our study uses converging evidence from three biologically inspired frameworks; motion vision modelling, three-dimensional butterfly flight dynamics, and genetic algorithms. Taken together, these demonstrate how motion confusion could operate from mechanistic to evolutionary levels in a system long used as a test-bed for

evolutionary theory. We show that butterfly motion confusion can be achieved through multiple routes, with contrasting vertical forewing wing stripes, a singular vertical band, or internal contrasting wing margin patterns increasing motion confusion, while immaculate white maximises forwards-energy. Critically, the patterns that cause motion confusion are not mutually exclusive - and may be complementary to - many of the other proposed adaptive functions of butterfly wing patterns such as signalling and thermoregulation ^{14,18,27}.

Our research goes beyond previous motion illusion literature in using ‘fluid motion vision’ ^{23,28}, protecting our findings from temporal aliasing artefacts that may have limited prior findings. We show for the first time that these confusion effects are likely widespread in a taxon that is both phenotypically and evolutionarily diverse. We predict that motion confusion could offer an adaptive function for an enormous range of high-contrast patterns found in nature, such as those on the flapping wings of birds or the flicking tails of lizards and fish ^{11,29,30}. These findings also highlight the importance of studying the adaptive function of animal patterning in tandem with realistic movement, as only together do the striking effects we observe here emerge.

EMD-based motion vision has been well validated ^{9,31–33}, and is increasingly being used to investigate animal patterns during movement ^{9,23,34}. Behavioural experiments have shown that motion confusion from patterning can influence perceived direction ^{35,36} and speed, e.g. a 1.5 deg/sec decrease in perceived speed for fast moving targets ³⁷. Whilst small changes in animal patterning can meaningfully deflect predator attacks, future behavioural work should quantify how EMD-based motion confusion predictions translate to attack deflection. Further work should also incorporate more realistic simulations that take into account butterfly wing ventral patterning, as well as a wider range of flight dynamics, viewer angles and distances, and background types. However, we argue that these will likely add nuance to our findings, rather than changing any overall conclusions: for example, these factors may help to explain when a higher frequency striped pattern evolves over a singular distal stripe. Our work also suggests that motion confusion may be ancestral in butterflies ²⁶; indeed, the presence of butterfly-like striped wings in fossilised lacewings ³⁸ may suggest that early butterflies only later converged on this same defence strategy, with implications for the fundamental nature of the predator visual mechanisms that these patterns exploit.

Our findings call for a dramatic reassessment of the mechanistic function of animal patterns while in motion. We trigger exciting new avenues for research into the effects of motion confusion in other systems, together with applied uses in civil and defence sectors, such as improving biologically inspired motion detection for robotics.

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Author Contributions

Redacted for peer review.

Competing interests

The authors declare no competing interests.

Additional Information

Extended data is available for this paper at [Insert DOI].

Supplementary information is available for this paper at [Insert DOI].

Methods

Temporally fluid elementary motion detection

To quantify the influence of butterfly wings and their patterns on motion detection, we used a custom-written biologically informed elementary motion detector (EMD) ^{23,39}, using ImageJ. The model operates using spatiotemporal correlation of pixel intensity values across consecutive frames, quantified with arrays of vertically and horizontally orientated EMDs to measure motion in four cardinal directions (forwards, backwards, left, and right) ⁹. The model was first validated by Santon et al 2025 where it was used to quantify high-speed recordings of broadclub cuttlefish illusory hunting displays, *Sepia latimanus*, using the temporal and spatial resolution of green shore crabs, *Carcinus maenas*.

For our model, videos were first processed by spatially and temporally filtering contrasts not visible to the viewer. Spatial contrast limits were based on those of small passerines (~ 6 cycles/degree), while temporal limits were chosen based on a 100Hz CFF for a passerine within a forest habitat ^{40,41}. Filtering was achieved by interpolating frames and pixels using temporal ($\sigma = 5$) and spatial ($\sigma = 8$) Gaussian blur. Temporal blurring at $\sigma = 5$ reduced a 100hz flashing stimulus recorded at 1000Hz to 1% of its original amplitude ²³. In the absence of both spatial and temporal filtering, EMD outputs would have been strongly influenced by temporal aliasing resulting in “wagon-wheel” type motion artefacts that would not occur in nature ²⁸. The model then outputs motion energy values in each direction (forwards, backwards, left, and right) for every pixel and for each consecutive pair of frames.

To quantify motion confusion the strength of motion in each direction was measured as the mean energy across each frame giving a measure of forwards-, backwards-, left-, and right-energy. To measure how wing patterns ‘confuse’ motion detection relative to the dominant direction of movement (forwards), we calculated Michelson's contrast of motion for backwards compared to forwards (forwards-confusion), and for sideways compared to forwards (sideways-confusion). Sideways motion was measured using the mean of left-energy and right-energy.

$$\text{ForwardsConfusion} = (\text{BackwardsEnergy} - \text{ForwardsEnergy}) / (\text{BackwardsEnergy} + \text{ForwardsEnergy})$$

$$\text{SidewaysEnergy} = (\text{RightEnergy} + \text{LeftEnergy}) / 2$$

$$\text{SidewaysConfusion} = (\text{SidewaysEnergy} - \text{ForwardsEnergy}) / (\text{SidewaysEnergy} + \text{ForwardsEnergy})$$

Forwards-confusion gives an estimation of how patterning alters the perceived speed of a moving object, with greater values indicating a greater weighting of motion backwards compared to forwards and a slower speed. For most forward moving objects the Michelson's contrast of backwards to forwards energy should be negative, with biological motion such as flapping wings and running limbs generating cyclical periods of greater backwards compared to forwards-energy, e.g. when a limb swings backwards. Sideways-confusion on the other hand gives an estimation of how patterning alters the perceived turning rate of an object, with greater values exaggerating or dampening turns. Forwards-energy on its own can also mislead observers, with more contrasting objects, namely white, resulting in overestimation as opposed to underestimation of object speed by humans^{42,43}. Both failure to accurately evaluate the speed and turning rate of an object can result in failure to intercept a target⁴⁴.

Slow motion analysis of free flying butterfly takeoff

To pilot whether and how butterfly wing patterns influence early-stage motion detection of their flight, we recorded the take offs for five Euro-African butterfly species, two of which were recorded for dimorphic sexes, giving a total of 7 morphotypes. These were: *Anthocaris cardamines* (m), *Hypolimnas misippus* (m & f), *Papilio dardanus ochracea* (m & f), *Papilio machaon* (n/a), and *Vanessa atalanta* (n/a). For *H. misippus* and *P. d. ochracea* the females are mimics of aposematic species of the subfamily Danainae^{45,46}.

Butterfly takeoffs were recorded against a greenscreen background with a scale bar and Xrite color checker using a CHRONOS 1.4 (Kron Technologies, Burnaby, Canada). Footage was taken in RAW format at a framerate of 1057 fps and a resolution of 1280 x 1024 pixels. Each species was recorded between 2-3 times. Videos were converted from RAW to a DNG stack using the python function

pyraw2dng, these could then be imported into ImageJ and saved in a .tif format. Weka trainable segmentation followed by manual screening and adjustments was used to cluster the video, replacing the background with a dark colour and the butterfly patterning with up to a maximum of four colours⁴⁷.

Once clustered, videos were converted from sRGB to avian luminance using blue-tit double cone quantum catch^{48–50}. The background area for each video was replaced with the average luminance for a grassy background (87,87,87 RGB). Videos were reorientated and cropped in length such that the first and last position of the butterfly would follow a linear vertical line upwards (up = forwards) and the butterfly was entirely in frame for its final position. Each video was then passed through our temporally-fluid EMD using the methods described above. For each frame the forwards-confusion and sideways-confusion metrics were calculated using the measured forwards, backwards, left, and right motion energy (supplementary video 1). This process was repeated for each video with the butterfly wing patterns replaced with the averaged luminance of the butterfly, 0% reflectance (black) and 100% reflectance (white), giving a total of 4 pattern treatments: natural, averaged, black, and white.

European butterflies were caught with a butterfly net in a private garden in France (Mareil-Marly, 78750), housed temporarily in individual plastic pots with airholes, and filmed outdoors in a netted enclosure. To film the take-off, the pot was placed upside down in front of a green screen, and lifted off once the butterfly had settled on the lid; the butterfly was then allowed to take-off naturally. Butterflies were released immediately after recording. African species (*H. misippus* and *P. d. ochracea*), raised from captive-bred pupae, were filmed using a similar set-up; these butterflies were held using soft tweezers, then released for take-off. Use of butterflies for flight recordings was approved

Simulating motion confusion across European butterflies

To assess which features of butterfly wing patterns influence early-stage motion detection of butterflies in flight, we opted to use controlled 3D simulations of European butterflies in flight.

Scanning Butterfly Images

To capture the breadth of European butterfly species, we scanned pages from Collins Butterfly Guide as JPEGs using a Konica Minolta bizhub C368 office scanner [Konica House, Miles Gray Road, Basildon, Essex, SS14 3AR]⁵¹. As we were interested in patterning more than exact colour values, the accurately scaled illustrations of butterflies within the guide provided an invaluable resource with dorsal images of 397 butterfly species and a total of 757 unique morphotypes (subspecies & sexes).

For each scanned page, individual butterfly dorsal images were cropped and saved in .tif format using a custom-made ImageJ script to semi-automatically select regions of interest (ROI) selections for the right forewing and hindwing, as well as a line for the body length. ROI selections allowed for later quantification of butterfly wing pattern, shape measures, and for extraction of the forewing, hindwing, and body as .pngs for our 3D simulations³⁹. Each scan was saved with a scale of 23.583 pixels per mm.

3D Rendering in Blender

To simulate flight for the European butterfly morphotypes, we constructed a 3D animated model of a butterfly in Blender 4.0, supplementary video 2. The butterfly consisted of five 2D planes: the body, 2x forewings (left & right), and 2x hindwings (left & right). The image of each plane could be replaced with one of our avian double cone catch converted scans for the butterflies body, hindwing, and forewing. These planes were rigged with an armature for the forewings and hindwings used to generate flapping flight. The wings were animated symmetrically to match the clap and fling flight of one of our recorded *Hypolimnys misippus*, with the wings deforming and rolling and yawing distally during the upstroke and downstroke, as opposed to simply pitching upwards and downwards. When animated, the butterfly would fly forward linearly from its start frame to the end, carrying out two wing beat cycles.

A custom-written ImageJ + Python script was then used to automatically replace the images used for the butterfly's body, hindwings, and forewings with those of a selected butterfly, as well as to adjust the wing beat frequency and render the animation⁵². Across Lepidoptera a smaller wing area corresponds with a higher wing beat frequency^{22,53}. Higher wing beat frequencies are likely to interact with how patterning influences motion detectors, resulting in increased motion blur. Wing area for each butterfly was converted to the estimated wing beat frequency in Hz using an equation calculated from the near-linear relationship between butterfly mass, wing area, and wing beat frequency (see supplementary material for formula calculation)⁵⁴:

$$\text{freq} = \text{pow}(10, (-0.134346 * ((\log(\text{Wing_Area_mm}) / \log(10)) * 1.23952 - 7.843389) + 0.53418))$$

The calculated wing beat frequency was then used to rescale the length of the animation and adjust the start and end frame so that the animation consisted of one wing beat cycle with 10 additional frames lead-in and lead-out for fluid frame interpolation. When rendered, butterflies were filmed from a static bird's eye view (camera looking down on the butterfly), flying forward at a speed proportional to its body length and wing beat frequency ($\text{speed} = \text{length} * 1.93 * \text{wbf}$). Animations were rendered as a stack of .pngs at a frame rate of 2000 frames per second.

Each stack was imported into ImageJ and quantified using our temporally-fluid EMD, taking the average forwards, backwards, left, and right energy across each frame. These were used to calculate the forwards-confusion, sideways-confusion, and forwards-energy for a butterfly in flapping flight. Each butterfly was rendered with three colour treatments: its natural pattern (natural), the averaged grey value of the wing (grey), and in white to account for the effect of the wing shape alone. Additionally, each colour treatment was rendered with and without wing beat animations to determine how gliding influences motion, giving a total of six treatments. This process was carried out for all 757 morphotypes.

Butterfly wing features

To assess which features of butterfly wings influenced our EMD model, we quantified the colour, patterning, and wing shape of our butterflies using image analysis. All measures used were repeated separately for the forewing and the hindwing. Simple measures of colour were obtained by converting the butterfly scans to the CIE 1976 Lab colour space⁵⁵. This colour space is frequently used for the measurement of biological colouration and allows for the quantification of colour across three discrete image channels, L* (achromatic luminance), a* (opponent red-green), and b* (opponent yellow-blue). For each image, we measured the mean and standard deviation (contrast) of a*, b*, and of the Euclidean distance of the a* and b* channels from zero (saturation).

For patterning, we used Gabor filters set to six different orientations (0, 30, 60, 90, 120, and 150 degrees) and six octaves, the largest being 1/4x the wavelength of the wing (square root of wing area) to measure the pattern contrast, size, and orientations of our blue-tit double cone catch images^{56,57}.

The resulting stack of 24 images were then used to create spatial maps for periodicity (how big the pattern is), absolute energy (how contrasting the pattern is), direction encoded as two separate channels VH (0-90 | vertical - horizontal) and OA (135-45 | obtuse - acute), as well as the directionality (anisotropy = $\sqrt{(VH^2 + OA^2)}$ - average energy) (See Supplementary Material). These five maps (periodicity, energy, VH, OA, and directionality) allowed us to quantify pattern variation across the wing, not just the global average. For each map, we measured the pixel mean, standard deviation, horizontal gradient (x), and vertical gradient (y). For instance, a high positive mean VH would indicate a vertical rather than a horizontal (negative) pattern, a positive horizontal gradient for periodicity would indicate that periodicity increases distally from the body, and a high standard deviation of directionality would indicate that directionality varies substantially across the wing.

Lastly, butterfly size and wing shape were measured by calculating the total wing area, the estimated wing beat frequency, and the body length. Forewing and hindwing shape measurements were made by recording the length of the wing from the centre of the wing base to the most distal point on the wing⁵⁸, the breadth of the wing at the centroid of the line for the length of the wing, the rectangular length

and width of the wing, the area of the wing relative to the body length (area/bodyLength), the aspect ratio of the wing (length/breadth), the circularity of the wing ($4\pi(\text{area}/\text{perimeter}^2)$)³⁹, and the roughness of the wing (the convex area / the actual area). Altogether, this gave us 73 measures for wing features.

In Silico butterfly wing pattern evolution

The diversity of butterfly wing patterns are the product of their own unique genetic and developmental pathways, some of which have been accurately mapped^{13,59,60}. These could either limit the adaptive potential of their patterning for motion confusion or could create patterns that fit our motion confusion hypothesis by coincidence. To validate whether or not our motion confusion metrics corresponded with actual butterfly wing evolution, we opted to simulate evolution and selection for motion confusion with genetic algorithms (GAs)^{61,62}. GAs provide a powerful tool for exploring the fitness landscape of animal phenotypes, and have seen increasing use within visual ecology research, notably for animal camouflage research^{63–65}. These algorithms mimic evolution by natural selection to efficiently explore vast multi-dimensional solution spaces, such as those of animal patterns.

For our algorithm, we modified the existing animal pattern evolution framework of the CamoEvo Toolbox, which utilises decimal encoding of reaction-diffusion patterns and subsequent image modifications to produce artificial animal patterns, with mutation operators tailored for the evolution of patterning⁶⁵. This framework was altered to produce images of artificial butterflies where the parameters for pattern shape were separate for the forewing, hindwing, and body of the butterfly, allowing for them to evolve independently from one another. As with the real European butterflies the butterfly images were then transferred to blender and animated with our 3D butterfly rig.

To account for any influences wing shape might have had on evolution we selected three distinct butterfly wing shapes from three of the butterfly families: the proportionally small wings of a ‘Skipper’ Hesperiidae (*Pyrgus andromedae*), the distinct tailed wings of a ‘Swallowtail’ Papilionidae (*Papilio machaon*), and the more classically shaped wings of a Nymphalid butterfly (*Pseudochazara anthelea*)⁶⁶. For each wing shape we assigned populations of N=24 butterflies to one of three different measures of ‘fitness’ representing different selection pressures: forwards-confusion, sideways-confusion, and forwards-energy. For each generation, the top 8 individuals (i.e. those with the highest motion confusion/energy metrics) would ‘survive’, while the remaining 16 ‘died’ and were replaced by mutant recombinant offspring of the survivors in two rounds of random pairings. Additionally, we evolved butterflies under random selection, where the rank order was randomly generated each generation: this was done to ensure butterflies didn’t evolve patterns simply because of drift. Each population evolved for 20 generations, starting with a population of randomly

generated individuals, and with 10 repeats for each fitness metric per wing shape, giving a total of 120 populations (3 wing shapes, 4 selection pressures, and 10 repeats).

Butterflies were expected to become ‘fitter’ with each generation, and to select for similar features to those identified to predict motion confusion in real butterflies. As high spatial frequency patterns and speckles weren’t under selection due to spatial filtering from our fluid EMD model, both the patterns of real butterflies and the GA generated *in silico* butterflies underwent Gaussian spatial filtering ($\sigma = 8$) prior to measurement. For both sets of butterflies, we used the same wing pattern metrics as our European butterfly analysis, excluding measures of wing shape or CIE Lab colour.

Statistical analyses

All statistical analyses for our study were carried out using R version 4.3.3.⁶⁷.

To determine how wing pattern influenced our motion confusion metrics for real butterfly take-offs in free flight we used linear mixed models (LMMs), with the “lme4” package⁶⁸. For our analysis, the motion confusion metrics (forwards-confusion, sideways-confusion, and forwards-energy) were considered as dependent variables in separate models, with wing pattern type (natural, averaged, black, and white) as a factorial predictor variable. The ID number for each unique flight and the species were used as random effects. To compare differences between our factor levels, we used emmeans Tukey post hoc comparison tests⁶⁹.

Given the vast array of wing features measured, we opted for a Random Forest (RF) model to evaluate the predictive value for each of our measures for each of our motion confusion measures⁷⁰. RF provides a non-parametric ensemble learning method, utilising multiple constructed decision trees trained with random subsets of the data and the predictors. Predictions are then aggregated across the trees helping to prevent overfitting. For each of our metrics RF models were trained with 1500 trees with four predictors per split. To evaluate model performance we used the R^2 to estimate the proportion of explained variance.

Recursive feature elimination (RFE) was used to improve model interpretability by reducing redundant predictors. Predictors were systematically ranked based on their weight and model performance was evaluated for subsets from 1 to the total number of variables. R^2 values of the complete model and the reduced models were compared to ensure that the predictive accuracy was retained. To evaluate which features of our reduced model were the most important we used SHAP (SHapley Additive exPlanations) as a measure of feature importance⁷¹. Greater absolute SHAP indicates a greater importance, with positive and negative values corresponding with a positive or negative correlation, respectively.

RF models were performed using the “randomForest” and “caret” packages^{70,72}. As many of our wing features are potentially linked to phylogeny, we incorporated Wiemers et al., 2020’s complete European butterfly phylogeny into our model. Cophenetic distances were extracted from the phylogeny and converted into three phylogenetic principal components with principal coordinate analysis (PCoA) using the “phytools” package⁷³. Similar to how principal component analysis (PCA) can reduce multiple numeric variables into singular components, PCoA allows an individual’s position within the phylogeny to be redefined as a set of multidimensional coordinates. Our three phylogenetic components were included alongside our wing parameters as predictor variables within our model. Circular coordinates for our butterfly phylogeny were extracted with the “ape” package⁷⁴.

For the *in silico* butterflies LMMs were used to validate whether butterflies significantly improved in fitness for our evolution treatments. RF models were again generated for the motion confusion metrics using our reduced set of spatially filtered wing pattern variables. These models were created using the measured phenotypes from the first and last generation of the entirety of our *in silico* generated dataset, rather than for butterflies under one selection pressure, using the initial randomly generated butterflies to provide a wider range of variation. Lastly, to determine whether or not butterflies under a particular selection pressure evolved to be more or less like natural butterflies, we generated principal components for the wing pattern metrics (PC1 and PC2) and used pairwise comparison to calculate the Euclidean difference of principal components between every butterfly, both real and *in silico*, from every natural butterfly.

Instances where real butterflies of the same morphotype were compared were removed as their distance would equal 0. Butterflies were divided into six groups: natural, forwards-confusion selected (gen = 20, top 1 per population), sideways-confusion selected (gen = 20, top 1 per population), forwards-energy selected (gen = 20, top 1 per population), random-selection (gen = 20, top 1 per population), and unevolved (gen = 0, all individuals). We then used a linear model (LM) to test which group generated the lowest difference from real butterflies and whether the pairwise distance levels were significantly different from one another with Tukey post hoc comparisons. We hypothesised that the difference should be lower for those selected for motion confusion than for those that were randomly generated at the start.

Data availability

Time-calibrated butterfly phylogenetic data we used is open-access and is accessible within Wiemers et al., 2020 publication <https://doi.org/10.3897/zookeys.938.50878>. We provide a copy of their nwk tree and the R code we created for the acquisition of circular coordinates used in Figure 2 within our GitHub repository (<https://github.com/GeorgeHancock471/Butterfly-Motion-Illusions>). We also

provide our elementary motion detector data for our live butterflies and blender-rendered butterflies, as well as our pattern measures for the butterflies scanned from Collins Butterfly Guide and generated by our genetic algorithm.

Code availability

All R code used for our statistical analysis is also provided and divided by section: Take-off analyses, Collins analyses, and genetic algorithm (GA) analysis. A copy of our ImageJ plugins used is also provided, and includes within them a copy of our butterfly Blender model.

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