



Visual antipredator effects of web flexing in an orb web spider, with special reference to web decorations

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Abstract

Some visual antipredator strategies involve the rapid movement of highly contrasting body patterns to frighten or confuse the predator. Bright body colouration, however, can also be detected by potential predators and used as a cue. Among spiders, *Argiope* spp. are usually brightly coloured but they are not a common item in the diet of araneophagic wasps. When disturbed, *Argiope* executes a web-flexing behaviour in which they move rapidly and may be perceived as if they move backwards and towards an observer in front of the web. We studied the mechanisms underlying web-flexing behaviour as a defensive strategy. Using multispectral images and high-speed videos with deep-learning-based tracking techniques, we evaluated body colouration, body pattern, and spider kinematics from the perspective of a potential wasp predator. We show that the spider's abdomen is conspicuous, with a disruptive colouration pattern. We found that the body outline of spiders with web decorations was harder to detect when compared to spiders without decorations. The abdomen was also the body part that moved fastest, and its motion was composed mainly of translational (vertical) vectors in the potential predator's optical flow. In addition, with high contrast colouration, the spider's movement might be perceived as a sudden change in body size (looming effect) as perceived by the predator. These effects alongside the other visual cues may confuse potential wasp predators by breaking the spider body outline and affecting the wasp's flight manoeuvre, thereby deterring the wasp from executing the final attack.

Keywords Deimatic displays · High-contrast visual cues · Secondary defensive strategies · Visual ecology

Introduction

Animals use diverse antipredator sensory defences to prevent, interrupt, and/or stop predator attack (Ruxton et al. 2018) depending on the stage of the predator-prey attack sequence when the interaction occurs (Endler 1991). Prey often use crypsis and immobility to avoid detection, but if those defences fail, other strategies are needed to avoid being captured and killed (Heathcote et al. 2020). Most animals cannot remain still indefinitely, and any subsequent motion renders them more vulnerable to detection (Hughes et al. 2014, Umeton et al. 2017, Umeton et al. 2019, Tan and Elgar 2021). When a prey detects a predator, secondary defence strategies are triggered to prevent capture, often depriving predators of information or providing confusing cues (Caro 2014).

Secondary strategies such as motion dazzle and deimatic (startle) displays are part of the diverse repertoire of antipredator strategies in animals. Motion dazzle involves the use of high contrast patterning that hinders estimation

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of prey trajectory and speed when the target is in motion (Scott-Samuel et al. 2011, Stevens and Merilaita 2011). In contrast, deimatic displays involves the revealing of previously concealed conspicuous colouration patterns along with sudden movements directed towards the attacker (Umbers et al. 2015, Drinkwater et al. 2022). Through the use of conspicuous colouration and prey motion, both strategies are exploiting the three primary parameters of vision in animals: spectral sensitivity (colour perception), spatial resolution (visual acuity), and temporal resolution (Cronin et al. 2014). Hence, while dazzling signals deceive the predator's estimation of the prey's direction and speed (Hughes et al. 2017), deimatism involves behaviours that give rise to a sudden transition in sensory input, causing the predator to respond reflexively (Umbers et al. 2017). Both cases might produce optical illusions (i.e., errors of perception) through body colouration, movement, or manipulation of the environment (Kelley and Kelley 2014). These optical illusions may thus have evolved to hamper predation in different prey species (Kodandaramaiah et al. 2020, Valkonen et al. 2020).

Additionally, looming visual stimuli provide a visual cue of an approaching object (Spano et al. 2012), and observer animals innately respond to these cues to avoid a collision (Peron and Gabbiani 2009, Spano et al. 2012, Tyll et al. 2013, Yilmaz and Meister 2013). This behaviour has been addressed mostly from the perspective of individuals, often prey species, that respond by attempting to avoid the threat of rapidly approaching objects (Temizer et al. 2015, Vagnoni et al. 2015, Shragai et al. 2017, Donohue et al. 2022). However, such looming stimuli may also work as a defensive strategy against predators. A looming cue may be more effective when coupled with high contrast patterns, like the stripes in moving zebras that may hinder the approach and landing stages of blood-sucking flies (Caro et al. 2019). In flying insects, the processing of looming signals is crucial for navigation and object avoidance during the flight (Muijres et al. 2014, Ache et al. 2019). Furthermore, moving high contrast patterns may produce errors in motion detection mechanisms by mismatching local image contours (How and Zanker 2014).

A good model to evaluate visual signalling in a movement triggered antipredator behaviour is the interaction between web-building spiders and araneophagic wasps. These wasps use both chemical and optical information when hunting for prey (Uma and Weiss 2010). These wasps lay significant emphasis in learning and using visual information in their natural habitat (e.g. Eberhard 1970; Zeil 1993). In addition, there is evidence that spider body colouration may play a critical role at the final stages of the detection and attack sequence, making spiders with conspicuous colouration more likely to be detected by predatory wasps (Robledo-Ospina et al. 2021).

Orb-web spiders use secondary defence strategies such as dropping to the ground, changing sides on the web, and/or web vibration/flexing to avoid capture (Cloudsley-Thompson 1995, Pekár 2014, Gawryszewski 2017). Web-flexing occurs when the rapid extension-retraction of the spider legs cause motion along the web's short axis, also perceived as moving backwards and forward (Tolbert 1975). This behaviour has been recorded in numerous orb-web spiders and may be more effective on webs with decorations (stabilimenta or conspicuous silk structures attached to the web) because such decorations might help to blur the spider's outline and conceal its form (Cloudsley-Thompson 1995). However, there is no conclusive evidence of it, and spiders with decorations may also use other antipredator tactics such as crypsis and web shaking (Bateman and Fleming 2013).

Spiders are thought to use web decorations (see also Eberhard, 2020) to either attract prey (Li et al. 2004, Cheng and Tso 2007) or hide from predators (Gonzaga and Vasconcellos-Neto 2005, Nakata 2009, Soley 2019, Wang et al. 2021a), and even to protect their web from mechanical damage (Blackledge and Wenzel 1999). In spiders from the *Argiope* genus, decorations are detectable to both prey and predators (Robinson and Robinson 1970, Eisner and Nowicki 1983, Bruce et al. 2005, Rao et al. 2008). However, despite their conspicuousness and diurnal habitus, *Argiope* spp. spiders also have secondary defences (Tolbert 1975, Jackson 1992, Blackledge and Pickett 2000).

In *Argiope* spiders, web-flexing may deter predators by blurring the spider's outline (Robinson and Robinson 1970) and temporarily concealing its exact location (Tolbert 1975). However, the visually mediated functions of web decorations have not been explored from the perspective of predator visual systems (Théry and Casas 2009). Consequently, one of the outstanding questions regarding orb-weaver antipredator responses is what mechanisms deter predators based on insight from predator perception (Umbers et al. 2017). Accordingly, we studied the complex antipredator displays of *Argiope* spp. First, we hypothesised that different body parts may have different visual contrasts (chromaticity and luminance), making them useful in antipredator strategies that require high visual contrast. Second, because of the moving scene dynamism and the subsequent variation of the different scene elements presented by web-flexing behaviours under natural circumstances (i.e., the combined scene involving movements of the spider, web decorations, and background), predator perception and associated responses will depend on contrasts between these elements as viewed from different distances over the course of an attack. We hypothesised that, when such a spatio-temporal analysis was performed, we would find that web-flexing presents a looming stimulus to prospective predators, augmented by web decorations (when present). This would in turn elicit

avoidance responses rather than attraction, despite the high saliency of *Argiope* spiders when evaluated from a more static perceptual paradigm.

To investigate the mechanisms underlying the web-flexing defensive behaviour in orb-weaver spiders, we measured the body colouration, shape, and movement of an *Argiope aurantia* spider as perceived by a potential wasp predator during web-flexing behaviour. Using full-spectrum digital photography, high-speed videography, and psychophysiological models, we aimed to describe a behaviour that includes not only chromatic, but also motion perception since this type of sensory processing often underpins prey detection, avoidance of predators and communication with conspecifics (Peters et al. 2002).

Materials and methods

Adult females of *Argiope aurantia* (Araneae: Araneidae) (Lucas 1833) often perform a web-flexing behaviour as an antipredator response when disturbed (Tolbert 1975; Robledo, pers. obs.). We collected 14 adult female individuals from different locations in the city of Xalapa, Veracruz, Mexico. We housed the spiders at the Universidad Veracruzana in wooden frames (67*67*19 cm) with transparent Plexiglas covers. Spiders were fed every other day with small-to-medium (~35 mm body length) grasshoppers (Acrididae: Orthoptera) collected in the laboratory's surroundings, and water was sprayed on the web during feeding.

We established two main frameworks to evaluate the visual signals involved in web-flexing behaviour in *A. aurantia* as perceived by a hypothetical wasp predator, based on the measurement of image parameters like brightness, contrast, and spatial frequency composition, which may influence motion perception (Egelhaaf et al. 2012). Based on these measurements, (1) we estimated the detectability of the immobile spider against their web decoration and the background at different distances using a simulated wasp visual system with both chromatic/achromatic contrast perception, combining these elements with visual acuity and edge saliency. (2) We then described and measured the kinematics of the web-flexing behaviour, which allowed us to estimate the perceptual changes of body shape and size during the spider web-flexing as perceived by a wasp.

Detectability of the spider in the web

We photographed spiders using a modified Canon 7D camera without the internal ultraviolet (UV) filter (LifePixel.com), with a UV transmitting Nikkor EL 80 mm lens. We took two types of photos per spider: a visible-light photo using a Baader UV/IR Cut filter (400–700 nm), and a UV photo taken with a Baader U filter that transmits UV

wavelengths with high efficiency between 300 and 400 nm. All the images included a scale bar and two Zenith sintered PTFE 70% and 10% grey standards. We used natural sunlight as a light source (between 1000 and 1500 h) and local natural vegetation as background at constant distance from the spider (1 m). Using full-spectrum digital photography (Troschianko and Stevens 2015), we created multispectral images of the spider in its web, choosing as regions of interest (ROIs) the spider body (cephalothorax and abdomen), the web decoration, and the natural background.

All the resulting multispectral images were analysed using Quantitative Pattern Colour Analysis (QCPA), following the methods of Van den Berg et al. (2019). This methodological framework uses the receptor noise-limited (RNL) model proposed by Vorobyev and Osorio (1998) for colour vision and a visual acuity correction approach that, in our case, was based on Gaussian filters to simulate the receiver spatial acuity and viewing distance.

Regarding the visual system used for modelling, there is no information published about vision parameters like spectral sensitivity and spatial acuity for the araneophagic mud-dauber wasp, *Trypoxylon* Richards (Crabronidae), which attack and prey on *Argiope* spiders (Robledo-Ospina et al., 2021). We therefore used parameters from a related species *Philanthus triangulum* Fabricius (Sphecidae), to create a putative model of an araneophagic wasp visual system. This wasp is related to *Trypoxylon* wasps and both species are spider-hunting specialists (Robledo-Ospina et al. 2022). *Philanthus triangulum* has trichromatic vision which is typical of Hymenopterans, with sensitivity peaks at 344 nm (UV), 444 nm (SW), and 524 nm (MW, Peitsch et al. 1992). For the RNL model, we used the Weber fraction ($\omega = 0.13$) and the relative density for each receptor class (n_i) used by Defrize et al. (2010) based on *Apis mellifera* (1:0.471:4.412 ratios for the UV:SW:MW receptors, respectively). Moreover, we used the minimal resolvable angle for the visual acuity value reported for *Bembix palmata* Smith (Crabronidae) of 1.22 cycles per degree (Feller et al. 2020).

In the QCPA plugin, we simulated the wasp visual acuity to eliminate details that the receiver visual system cannot resolve (Caves and Johnsen 2017). Then, we used the RNL ranked filter to model the perception of spatial information in our wasp visual system (Van der Berg et al. 2019) at different distances of observation, simulating an approaching flying wasp (10, 5, and 2 cm). These distances were chosen based on a field study on a wasp's behavioural response to a flower dwelling predator (Rodríguez-Morales et al. 2021). We also used a colour adjacency analysis (CAA) to measure the colour pattern properties in the scene (Endler 2012), and estimated the colour diversity and pattern complexity with indices based on the Shannon diversity index. In these indices, colour patterns with uniform spacing and coverage would have a maximum value of 1 (Van der Berg et al. 2019).

Because motion-detection models based on spatio-temporal correlation depend on contrast (How and Zanker 2014), we evaluated the mean luminance (M Δ SL) and chromatic contrast (M Δ S) of the spider (cephalothorax and abdomen apart) against its web decoration and background, weighted by the mean relative abundance of each colour pattern element combination in the scene (Van der Berg et al. 2019). We also estimated the standard deviation of the RNL luminance and chromaticity contrasts following Endler et al. (2018). We used the MW photoreceptor values for the luminance channel because hymenopterans use this receptor for luminance perception (Théry et al. 2005).

Finally, after considering the wasp's visual acuity and the RNL ranked filter to the images, we used the "Local Edge Intensity Analysis" (LEIA) to quantify edge properties in the scene in terms of colour and luminance contrast in log-linear RNL colour space (Van der Berg et al. 2019). We used the measure of kurtosis for both chromatic and luminance contrast as descriptors of edge intensities of the scene from this analysis. Thus, higher kurtosis values indicate more salient patterns in the scene.

Visual signalling in motion: kinematics and shape changes

The web-flexing antipredator behaviours of *Argiope* spp. spiders have been studied from a behavioural ecology perspective (e.g. Cedhagen and Björklund 2007; Jackson et al. 1993; Li and Lee 2004; Robinson and Robinson 1970; Walter 2019). Hence, based on these findings, we induced these behaviours in live spiders by stimulating the abdomen (Hoffmaster 1982) through both high-frequency vibration stimuli (440hz) using a tuning fork (Nakata 2009) close to the spider's body (< 2 cm), or by gently touching the abdomen (Jackson 1992). Web-flexing behaviour was recorded perpendicular to the web plane using a Chronos 1.4 high-speed camera (Kron Technologies Inc., Burnaby, Canada) with a 12mm f/1.4 prime lens (Computar, NC, USA) filming at 500fps with a resolution of 1280 × 1024 pixels and saved in MP4 format. The first 5 s of the web-flexing (~2500 frames) were used as event sampling for subsequent analyses. We recorded web-flexing behaviour four times for each spider but tracked only the first cycle.

In combination with high contrast patterns, movement is a remarkable feature of this behaviour and measuring it objectively is essential to estimating how an observer may perceive it. According to most theoretical and empirical analyses of whole-scene motion, the input parameters critical to viewer perception are stimulus direction and speed (Peters et al. 2002). Consequently, we measured the kinematics of the behaviour by tracking the changes in the space of nine points in the spider's body. These focal points were selected because they represent the distal and mid portion of the medial axis of

the body: one in the cephalothorax anterior end (Head), and two in the terminal points of the abdomen's longest axis (Abd P, Abd A for the posterior and anterior ends, respectively). Six points were selected in the femur's mid-portion of the legs II to IV in both spider sides (left and right) because they are points with high contrast colouration, which favour the tracking process and may be more salient from a wasp's perspective. We used *DeepLabCut* (DLC, ver 1.9) (Mathis et al. 2018) to track the points on the spider. Using DLC, we trained a Resnet-50 network. We used 20 randomly selected frames each from 14 videos to train the network (Supplementary Material). We trimmed the videos to exclude frames where the tuning fork was visible. The network was trained for 100,000 iterations. After training, all videos were analysed for location and movement of the landmark points XY (converted to mm) positions of the points. These location sequences were then extracted and analysed using *Mathematica* Ver 12 (Wolfram Research Inc). During analysis, we measured and compared the point trajectories to assess each body part's contribution to the movement as perceived by an observer during the initial flexing cycle. The cycle in the flexing behaviour was measured from the spider resting position (Rest), going backwards in a first push (Back), going forward (Front), and then recovering the initial position.

To estimate perceived changes in body size during a cycle, we used the statistical package *concaveman* (Gombin et al. 2017) in R statistical software (R Development Core Team 2016) to calculate the area of the concave hull polygon that contains the tracked point abovementioned and fitted to the focal spider body part for every frame. Then, we estimated, and compared the area for the three cycle reference positions: rest, back, and front.

Optical flow

In flight, wasps, like other flying insects, perceive spatial information as an optic flow of moving traits (Egelhaaf 2023). Such real-time analysis of motion, both self-induced and from other (moving) objects, is critical for flight control (Srinivasan 1992, Zeil 1993, Zeil 1997, Baird et al. 2011, Cronin et al. 2014, Serres and Ruffier 2017, Chakravarthi et al. 2018, Horridge 2019). Hence, we aimed to objectively visualise the magnitude and direction of pixel displacement (Raudies 2013) involved in the optical flow vector field produced by the spider when performing web-flexing. We used an optical flow algorithm through the *ImageDisplacements* function in *Mathematica* (ver 11), which generates a dense motion field by comparing the displacement in the horizontal and vertical axis of individual pixels across the frames of the 5-s sampling video. This method allows us to have a representation of the potential perception of web-flexing motion components from the wasp's perspective, which can inform the possibility that such displays generate optical illusions

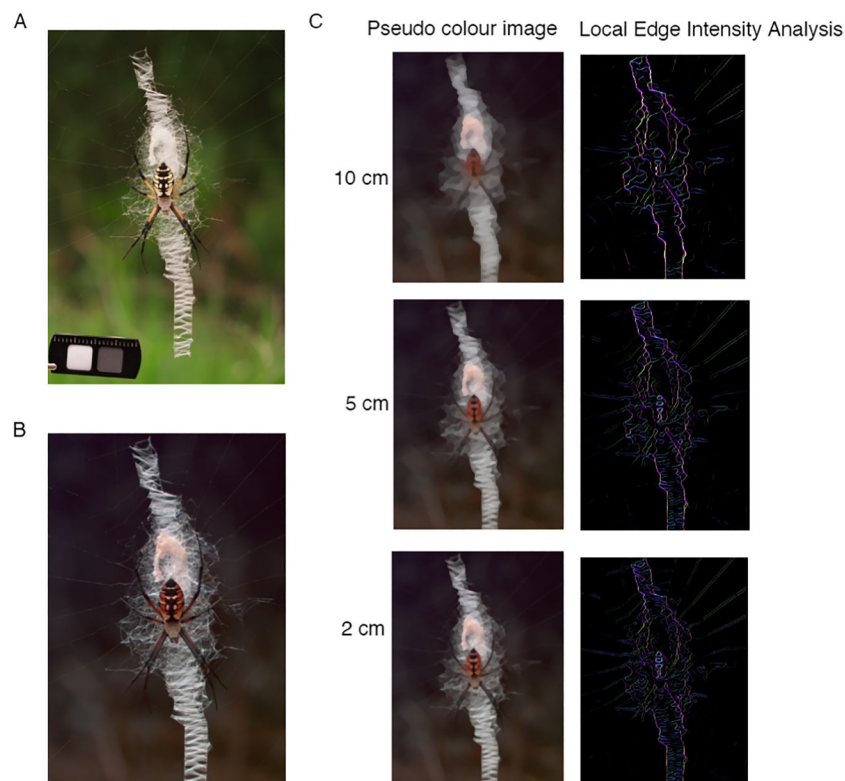


Fig. 1 Adult female of *Argiope aurantia* with a typical linear decoration in its web. **A** Note the white web decoration which is particularly large in this individual's web. **B** False colour image simulating the wasp *Philanthus triangulum* colour vision and created for visualisation purposes by assigning blue, green, and red for the UV, SW, and MW wasp photoreceptors, respectively. **C** Results of the quantitative colour pattern analysis (QCPA) of the spider as perceived by the wasp at different distances (10, 5, and 2 cm, respectively): left col-

umn shows the results of the receptor noise limited method, performing pixel noise reduction after the acuity control based on Gaussian filters while preserving chromatic and luminance edges, simulating wasp spectral sensitivity (sensitivity peaks are UV = 344, SW = 444, and MW = 524; Weber fraction = 0.13) and visual acuity (1.22 cpd) of the wasp visual system at different distances; right column presents the results of the achromatic edge intensity of the LEIA at different distances where different colours indicate different angle of contrast

for receivers (How and Zanker 2014). We therefore analysed different moving elements in the scene and their contribution to the rotational (horizontal) and translational (vertical) components of optic flow fields.

3D tracking

We reconstructed the flexing behaviour of a single spider in 3D. Web-flexing behaviour was triggered as detailed above (see kinematics section in methods). We filmed the movement of the spider at 500 fps with two synchronised and calibrated high-speed Chronos 1.4 cameras with 12mm f/1.4 prime lens. The cameras were oriented towards the spider at 45° and 60°, respectively. Only one cycle of the web-flexing behaviour (rest position, backward; front, rest position) was used for this analysis. We tracked 9 points selected according to the areas of maximum contrast representing highly visible points. Points were manually tracked using the *MTrackJ* plugin in Fiji (Meijering et al. 2012). Subsequently, we used the *X*, *Y* coordinates from

the two cameras and reconstructed the 3D position using the *pose3d* application (Sheshadri et al. 2020) in Matlab 2020b (MATLAB, 2020). The *X*, *Y*, and *Z* coordinates were then used for further analysis. To estimate the extent of displacement of each of the 9 points tracked, we used a convex hull method (Mathematica, ver 11). We computed the volume of the convex hull and used it as a proxy to determine differences in movement of the points regarding changes in depth.

Statistical analysis

From the photographic and videographic data described above, we measured the body area (as an estimation of spider size) and the web decoration area using the *ImageJ* software (Schneider et al. 2012). To evaluate if the web decoration area has some influence in the contrast perceived, we estimated the ratio between the decoration area and the spider and evaluated the relationship between the colour diversity and pattern complexity with the decoration ratio through simple linear regression.

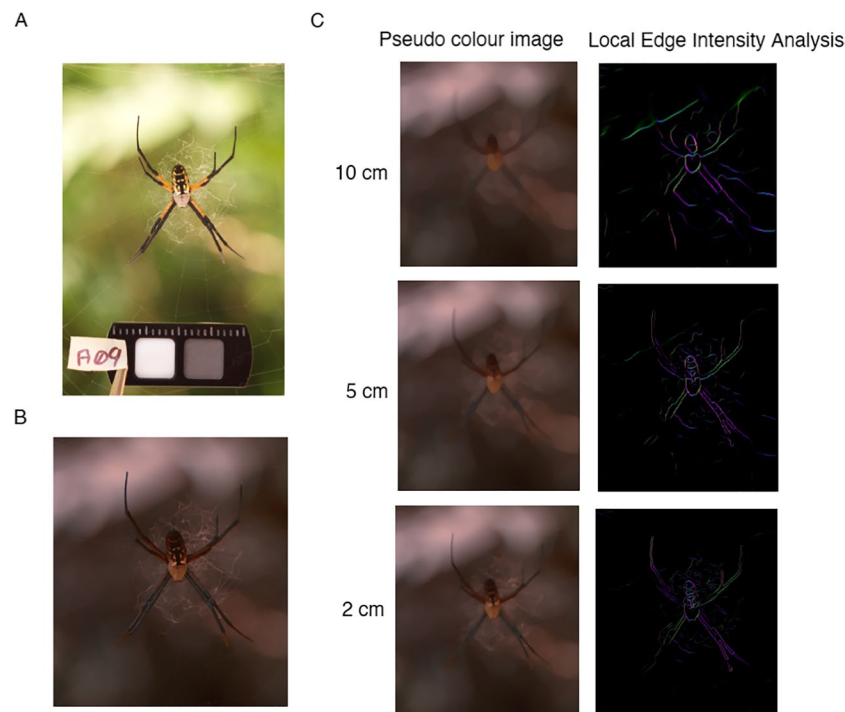


Fig. 2 Adult female of *Argiope aurantia* without a linear decoration in its web. **A** Note that in this case the area of the web decoration is smaller compared with previous figure. **B** False colour image simulating the wasp *Philanthus triangulum* colour vision and created for visualisation purposes by assigning blue, green, and red for the UV, SW, and MW wasp photoreceptors, respectively. **C** Results of the quantitative colour pattern analysis (QCPA) of the spider as perceived by the wasp at different distances (10, 5, and 2 cm, respectively): left

column shows the results of the receptor noise limited method, performing pixel noise reduction after the acuity control based on Gaussian filters while preserving chromatic and luminance edges, simulating wasp spectral sensitivity (peaks are UV = 344, SW = 444, and MW = 524; Weber fraction = 0.13) and visual acuity (1.22 cpd) of the wasp visual system at different distances; right column presents the results of the achromatic edge intensity of the LEIA at different distances where different colours indicate different angle of contrast

Applying an ANOVA test, we compared the luminance and chromatic contrast of the abdomen and cephalothorax against the web, respectively, to know which part contribute the most to the perceived contrast. The same method was applied to evaluate chromatic and luminance kurtosis variation as descriptors of edge saliency at the different observation distances (2, 5, and 10 cm), and to estimate the differences between the body size perceived at three different positions during a cycle of web-flexing behaviour. Finally, we compared the speed measured for the different tracked body parts using repeated measures ANOVA with pairwise paired *t*-tests using a Holm correction method as a post hoc test. All the statistical analyses were run in R (R Development Core Team 2016).

Results

Larger spiders had larger web decorations ($R^2 = 0.78$; $F = 43.66$; $df = 12$; $P < 0.001$). Additionally, when viewed against natural backgrounds, higher decoration area/body size ratios correspond to more complex patterns ($R^2 = 0.443$; $F = 10.57$; $df = 11$; $P < 0.001$; Figs. 1–2), and higher colour

diversity ($R^2 = 0.26$; $F = 5.26$; $df = 11$; $P < 0.05$). The abdomen was more conspicuous than the cephalothorax against web decorations in terms of luminance contrast ($F_{(1,24)} = 7.089$; $P < 0.0001$); Fig. 3A), but similar in chromaticity contrast ($F_{(1,24)} = 1.637$; $P = 0.213$). With respect to edge saliency, luminance kurtosis declines with observation distance ($F_{(1,37)} = 7.63$; $P < 0.05$; Fig. 3B), but retains similar chromatic saliency across all observation distances ($F_{(1,37)} = 2.439$; $P = 0.127$).

The body parts tracked in the spider during one cycle of web-flexing behaviour (Fig. 4A) have a mean speed of 14.6 cm/s (± 8.6 S.D.), but velocity differs between body parts ($F_{(3,96, 332,33)} = 5.062$; $P < 0.0001$). The abdomen posterior (Abd P) and anterior (Abd A) ends moved faster (15.704 cm/s) than the legs III in both sides (LegIII L and LegIII R) and the spider cephalothorax (head) (See Supplementary Table 1).

Spider body size was measured as the area of a concave hull polygon during one cycle of web-flexing as perceived by an observer in front of the spider. We found that the perceived area of the three spider reference positions during the cycle

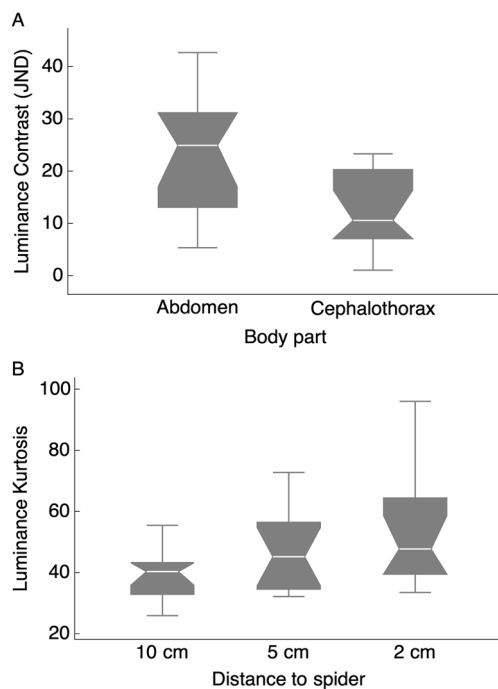


Fig. 3 **A** Luminance contrast in just noticeable units (JND) of the body parts (i.e. abdomen and cephalothorax) of *Argiope aurantia* against its web decoration as perceived by a wasp visual system using the receptor noise limited model (RNL) of Vorobyev and Osorio (1998). **B** Edge saliency through luminance contrast distribution (kurtosis) of *Argiope aurantia* in its web with decoration as perceived by a wasp visual system at different distances (2, 5, and 10 cm) using the local edge intensity analysis (LEIA) according to Van der Berg et al. (2019). We used the mid wavelength (MW) photoreceptor for luminance perception in both cases. The whiskers represent the maximum and minimum values; the box, the interquartile range, and the notch represent the confidence interval of the median

were significantly different (Fig. 4B). The perceived spider size varies during the web-flexing behaviour (Fig. 4C), and the spider was perceived as bigger in the front position ($X^2 = 13.471$, $df = 2$; $P < 0.001$; Fig. 4D). On the other hand, the perceived movement of the flexing behaviour by an observer in front of the spider is mainly composed of vertical vectors in the optical flow (Fig. 5). Finally, when we included a third dimension depicting the web-flexing behaviour, we found evidence that the spider position varies in depth (Fig. 6).

Discussion

We evaluated the visual signals involved in the web-flexing behaviour of *Argiope aurantia* as perceived by an approaching, visually oriented predatory wasp. We modelled the perception of the wasp, focused on chromatic and achromatic vision, visual acuity, and a *proxy* of movement perception (temporal resolution). Overall, we find that the general contrast and detectability of the spider varies depending not only

on the observer distance but also on web decoration ratio. Additionally, while the spider's abdomen exhibits the highest visual contrast when the spider is immobile, it is also the body part that moves the most during web-flexing displays. This heightened movement may startle predatory wasps and/or make the spider look larger at key moments during their deimatic display.

The interaction between *Argiope* spp. and araneophagic wasps is not rare. Even though *A. aurantia* adults were thought to be too big to be captured by most temperate North American wasps (Blackledge and Wenzel 1999), juveniles of *A. aurantia* and juveniles and adults of *A. trifasciata* were preyed on by mud dauber wasps from the *Trypoxylon* spp. genus (Muma and Jeffers 1945), and juveniles and adults of *A. argentata* were found in nests of *T. tridentatum* (Robledo-Ospina et al. 2021). Additionally, it has been reported that the wasp *Sceliphron caementarium* hunts *Argiope* spiders by bumping into the web, forcing the spider to drop. These wasps then chase the spider by searching around in the underlying vegetation in gradually enlarging circular patterns (Blackledge and Pickett 2000). Because these spiders exhibit high visual contrast against the background (Robledo-Ospina et al. 2021), this suggests that visual cues, in conjunction with the chemical cues (Uma and Weiss 2010), may be available for wasp predators seeking to prey on these spiders.

The abdomen of *Argiope aurantia* is the body part with the highest contrast, and its conspicuousness is further enhanced when viewed against web decorations. Similar to our results, *A. radon* abdomen have high achromatic contrast against web decorations as seen by hymenopterans (Rao et al. 2009). However, the saliency of the high-contrast pattern edges reported here may function to disrupt body shape recognition and detection (Cuthill et al. 2005, Schaefer and Stobbe 2006, Stevens and Merilaita 2009). We suggest that this may be the case for *A. aurantia*, at least for a hymenopteran visual system, because disruptive colouration like this is thought to be effective in preventing improvements in camouflage breaking during search image formation by predators (Troschianko et al. 2018).

In the case of *A. aurantia*, in addition to a highly conspicuous abdomen, web decoration increases detectability and contributes to a more visually complex signal even when the spider remains still. This relation between the decoration and the body colouration suggests that web decorations may be critical to consider when investigating the antipredator visual signals of this species. The absence of web decorations in nocturnal spiders supports a visually mediated function of these structures (Théry et al. 2011). Lubin (1974) suggested that the infrequent occurrence of web decorations in Galapagos Island populations may be due to a lack of visually oriented predators. However, this should be interpreted cautiously because species do not rely only on one

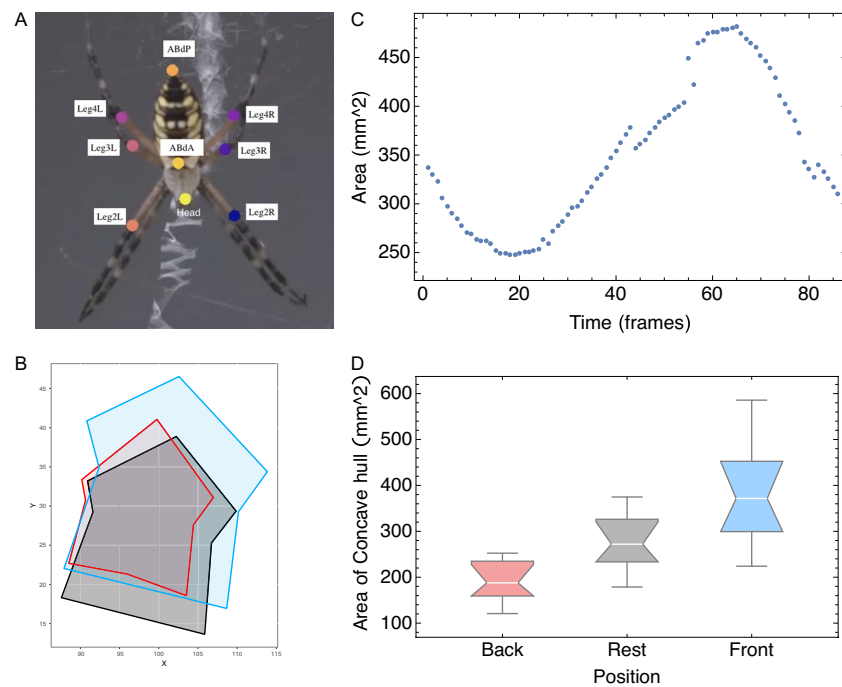


Fig. 4 Body size changes during one cycle of web-flexing behaviour as might be perceived by an observer in front of the spider. **A** Locations tracked on the spider's body during the web-flexing behaviour. **B** Spider body size represented by the concave hull polygons containing the body marks tracked in the spider body in the three positions of reference in one cycle of web-flexing behaviour: rest position (grey polygon), back when the spider pushes backwards (red polygon), and front when the spider moves towards the observer (blue polygon). **C**

Changes in body size (area mm^2) in every frame recorded as might be perceived by an observer in front the spider during one cycle of web-flexing. **D** Perceived body size of the spider (polygon area mm^2) at the three positions of reference during one cycle of web-flexing. The whiskers represent the maximum and minimum values; the box, the interquartile range, and the notch represent the confidence interval of the median

secondary strategy. Some diurnal species possess a repertoire of strategies, such as dropping to the ground, changing sides on the web, or fleeing from the web to a refuge. Bruce (2006), when writing about the controversy of the ecological significance of web decoration, suggested that decorations could potentially protect spiders by improving spider camouflage, by making the spider look bigger to deter certain gape-limited predators, or by acting as a physical barrier during predator attack. Nevertheless, we cannot ignore the body of evidence that suggests that web decoration functions as a prey attraction device. Even though those hypotheses are not mutually exclusive, solving this controversy will require future research from a visual ecology perspective (Eberhard 2020).

With respect to the visual protection provided by decorations in *Argiope* spp., available data suggests that the decoration of *A. mascalzoni*, even though conspicuous, could provide some camouflage for spiders seen by hymenopterans, either prey or predator (Bruce et al. 2005). Here, we suggest that in *A. aurantia*, disruptive high-contrast patterns like those in the abdomen, which are difficult to visually process and could therefore hamper body shape recognition,

might provide visual protection by breaking the body outline against web decoration (Wang et al. 2021b).

Many antipredator secondary strategies involve high contrast fast-moving signals (e.g. deimatic displays) to deter the predator attack. Movement does not necessarily compromise camouflage; there are several ways in which prey may specifically incorporate motion into their defence strategy repertoire to compromise the cues used by their natural enemies (Tan and Elgar 2021). In addition to conspicuous high contrast colouration, the fast movements of the *A. aurantia* during web-flexing may present a challenge for predators in terms of image processing. In this regard, our results agree with several biological systems in which a deimatic display involving high contrast colouration might be more effective if the colouration is coupled to the defensive behaviour (Umbers et al. 2015, Umbers et al. 2017, Cox et al. 2021, Martin et al. 2023). Here, we present evidence of a complex scene in terms of pattern and colour diversity. When the spider flexes in the web, it might generate a sudden increase in the visual stimuli input, particularly from the abdomen.

In flying animals like wasps, visual motion detectors are highly contrast-sensitive (Haag et al. 2004) and respond to

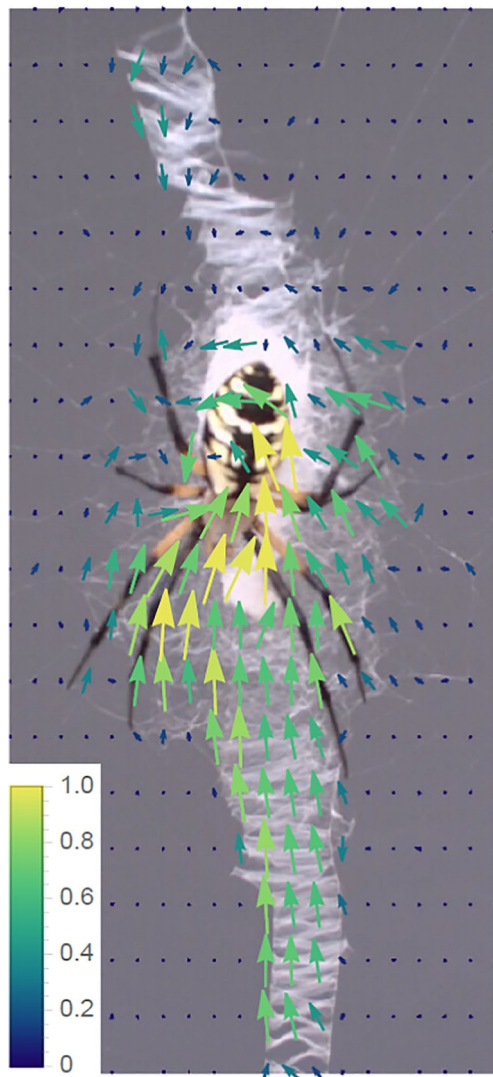


Fig. 5 Optical flow of *Argiope aurantia* while doing one cycle of web-flexing as might be perceived by an observer in front of the spider. The arrows represent the vectors indicating the normalised magnitude (size and colour) and direction of the movement perceived

spatiotemporally correlated changes in luminance (Derrington et al. 2004) that might occur from the moving edges of the target across the background and the internal contrast of the target patterns (Umeton et al. 2019). In hymenopterans, the edge detection is mainly mediated by the long-wavelength receptors (MW) (Vasas et al. 2017). We used MW receptors for luminance perception, showing that the abdomen was the most conspicuous body part, suggesting that this body region may have evolved to interact with and/or confuse motion perception by the MW receptors of its predators. The contrast of the background and body markings may affect the perception of movement in several ways (Kelley & Kelley 2014). Umeton et al. (2019) showed that prey with high-contrast stripes become less visible when moving with sufficient speed when

compared to prey with background-matching patterns because the stripes can reduce detection of moving prey by exploiting the spatiotemporal limitations of predator perception.

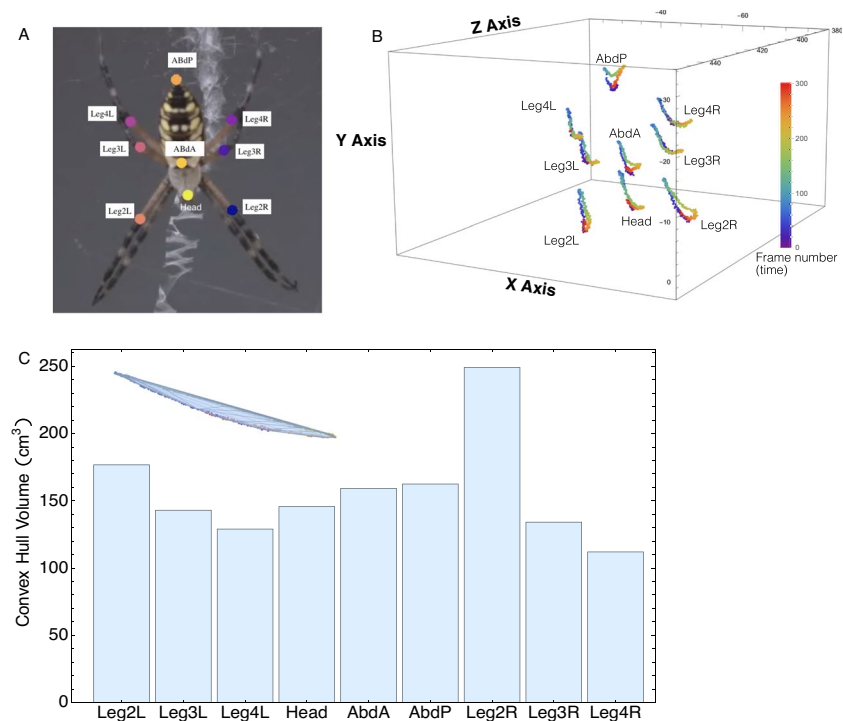
The visual stimuli, here consisting of the spider, the decoration, and the web-flexing behaviour, are the input to the wasp visual system and are not static images. To compensate for this dynamism in the visual scene, incessant eye and head movements continuously reformat input signals, transforming spatial patterns into temporal modulations on the retina (Rucci et al. 2018). Understanding how movement perception may drive animals' behaviour is essential to determining the function of spider web-flexing in the predatory responses by wasps. For example, hymenopterans are known to use relative motion cues from the edges of objects to estimate their height and guiding landing. Additional, compensatory head roll movements while flying are driven by visual inputs based on motion detection in some wasps (Viollet and Zeil 2013).

Because nearby objects are often more behaviourally relevant than objects further away, object detection via optic flow often weights objects according to their distance and, thus, their functional relevance (Egelhaaf et al. 2012). Our optical flow results suggest that when the spider engages in web-flexing behaviour, the scene is mainly composed of translational (vertical) vectors, which are highly relevant for spatial information because they are distance-dependent (Egelhaaf et al., 2012), and would exaggerate the perception of how close the spider is. This represents a dynamic scene in which the spider's general appearance and position in the space changes as the predator approaches. More specifically, web-flexing may make the spider appear to be rapidly approaching the wasp, thereby inducing a looming response and/or baffling the depth cues that a predator relies on during attack.

There is evidence that sudden changes in body size and colouration might deter predators from attacking via deimatic displays (Martin et al. 2023). We propose that the perceptual changes in the spider's body size, speed, and position, alongside the effect of approaching object, may accentuate looming visual stimuli from the spider to the wasp and exploit innate behaviours based on basic neural processing to avoid collision of an "approaching" object. This could be explained by changes in the edges of the scene (spider + web decoration) when the looming stimulus occurs (i.e. when the spider moves towards the viewer looking bigger) that produces the ON (bright stimulation) and OFF (dark stimulation) antagonistic effect in the wasp's motion perception because increasingly brighter-than-background shape increase neural response to approaching stimulus (Santer 2013), exploiting an innate aversion to approaching objects.

In conclusion, from a visual ecology perspective, a high-contrast abdomen in conjunction with rapid and sudden movements towards (and away from) an approaching

Fig. 6 3D tracking of the different body parts in *Argiope aurantia* while doing one cycle of the web-flexing behaviour. **A** Marks tracked in the spider's body during the web-flexing behaviour. **B** Trajectories described by each mark tracked in three dimensions. The colours in the inset represent the time sequence in frames during one cycle of the web-flexing behaviour. **C** Volume (cm³) of the convex hull (see inset showing a single leg, not to scale) containing all the trajectories for each body part during one cycle of web-flexing. The convex hull is very flat due to limited movement in the one of the three dimensions



flying predator can result in a highly visible yet dynamic signal that threatens (Tolbert, 1975) and confuses wasp predators (Caro and Ruxton 2019). Web-flexing behaviour might therefore have evolved to present a looming effect that produces a recoil effect in wasp predators similar to responses documented in other predators (Shragai et al. 2017, Vagnoni et al. 2015). Furthermore, the web-flexing display may also interfere with the wasp's optic flow perception and flight manoeuvre control (Ache et al. 2019), deterring the wasp from executing the final attack. Future studies should evaluate this antipredator behaviour against different flying insects in order to assess the potential costs for the spider when performing the web-flexing behaviour.

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Author contributions Luis E. Robledo-Ospina: conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (equal); writing—original draft (lead); writing—review and editing (equal). Nathan Morehouse: conceptualization (supporting); methodology (supporting); writing—review and editing (equal). Federico Escobar: conceptualization (supporting); methodology (supporting); writing—review and editing (supporting). Horacio Tapia-McClung: formal analysis (supporting); methodology (equal); writing—review and editing (equal). Ajay Narendra: data curation (supporting); formal analysis (supporting); methodology (supporting); writing—review and editing (equal). Dinesh Rao: conceptualization (supporting); data curation (supporting); formal analysis (supporting); methodology (equal); project administration (equal); resources (lead); writing—review and editing (equal).

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Data availability statement The data will be archived and made available on GitHub (<https://github.com/dinrao/Argiope>).

S1 High-speed video (500 fps) showing the web-flexing behaviour of *Argiope aurantia*. S2 high-speed video (500 fps) showing the marks tracked in the spider body to evaluate the kinematic behaviour. These are also available as supplementary materials online.

Declarations

Conflict of interest The authors declare no competing interests.

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