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IDEAS & PERSPECTIVES

# Dangerous visions: a review of visual antipredator strategies in spiders

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## Abstract

Many animals use visual traits as a predator defence. Understanding these visual traits from the perspective of predators is critical in generating new insights about predator–prey interactions. In this paper, we propose a novel framework to support the study of strategies that exploit the visual system of predators. With spiders as our model taxon, we contextualise these strategies using two orthogonal axes. The first axis represents strategies using different degrees of conspicuousness to avoid detection or recognition of the spider and deter predator attacks. The second axis represents the degree of honesty of the visual signal. We explore these issues with reference to the three main vision parameters: spectral sensitivity, visual acuity, and temporal resolution, as well as recent tools to study it, including multispectral digital imaging.

**Keywords** Synthesis · Visual defences · Visual ecology · Cognition · Attention

## Introduction

Many animals use visual traits as a defence against predators. Historically, these visual traits have been evaluated subjectively, and constrained by the biases of human vision. The colour and patterns of animals were represented with scientific and artistic illustrations (Poulton 1890; Thayer 1909; Cott 1940; see discussion in Rouyan 2019). However, these colours and patterns are a consequence of natural and sexual selection operating on them, and in order to understand their functional significance, it is necessary to view them through the perspective of conspecifics, prey and predators. Two methods have been widely used to represent animal colours and patterns. The first, spectrophotometry, is a method to objectively quantify the spectral properties of a sample (e.g., Norris and Lowe 1964). The

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second, digital imaging, is the use of specially modified digital cameras and lenses to capture parts of the light spectrum (such as ultraviolet) that are invisible to human eyes. Both these methods provide the raw data which must then be transformed into an animal-subjective representation using psychophysical visual modelling (Vorobyev and Osorio 1998).

Using these representations, we can study animal perception of antipredator strategies based on the three vision parameters (Cronin et al. 2014): Colour perception (Renoult et al. 2015), visual acuity (Land 1997; Caves et al. 2018), and motion vision (Zanker and Zeil 2001). Using spectral and reflectance data (Cardoso and Gomes 2015; Gawryszewski 2018), calibrated full spectrum digital photographs (Troscianko and Stevens 2015; Rodríguez-Gironés and Ruiz 2016; Caves and Johnsen 2017), or both (Maia et al. 2019), we can analyse natural scenes and complex animal signalling, including spectral sensitivity and visual acuity in animal visual systems (van den Berg et al. 2020).

Both spectrophotometry and digital imaging so far suffer from the drawback that they largely ignore moving displays of colour and pattern. Integrating motion perception in this model is more complicated logistically and conceptually. The animal visual system is more like a computer than a camera in its continuous processing of moving targets (Johansson 1975). Mathematical models were used early in the study of motion perception (Kinchla and Allan 1969). In recent decades, a multidisciplinary approach has produced different methods to provide the current conceptual and methodological basis to study this visual parameter (see review by Derrington et al. 2004). As a case study, optical flow methods, generally used in the characterisation of the flow of particles, was used to quantify the movement of the tail flick of a Jacky Dragon lizard against a moving vegetation background (Peters et al. 2002). A related approach, where motion data was represented and analysed in manner similar to spectrograms, was used to quantify courtship display patterns in jumping spiders (Elias et al. 2006).

The use of these modern techniques to represent colour and pattern puts the emphasis back on the observer. As a result of selection pressure, many animals have developed strategies to avoid the attention of a foraging predator. The typical predation sequence consists of the following stages: prey encounter, detection, recognition, approach, subjugation and finally consumption (Cloudsley-Thompson 1995; Nelson and Jackson 2011; Ruxton et al. 2018). At each step in the process, prey have appropriate defences such as seeking refuge, cryptic body colouration, toxicity etc. Visual antipredator strategies generally operate in the first part of the predation sequence, to avoid being detected or identified as a prey item. One approach to the study of visual anti-predator strategies is to apply signalling theory (Smith and Harper 2003; Connelly et al. 2011) to distinguish the signaller (the prey), the receiver (the predator) and the signal in the biological system we are interested.

In this paper, we propose a conceptual framework to classify strategies that exploit the visual system of predators. Reviews of anti-predator strategies generally approach them as discrete entities operating independently. However, all strategies use two basic components: the level of conspicuousness of the signal and the degree of honesty. Conspicuousness operates at a visual level and the degree of honesty operates at a cognitive level in the predators. The interaction between these two levels allows us to create a framework to locate the different anti-predator strategies. To contextualise these strategies (Fig. 1), we propose one axis ranging from inconspicuous to conspicuous visual signals to represent those strategies intended to avoid detection/recognition and deter predator attacks. A second orthogonal axis represents the honesty of the signal; from those that could be considered honest to strategies that seek to deceive the predators' eyes or manipulate their behaviour. We also highlight the defences involving movement perception, considering that while the methods to study visual signalling recently are technically more sophisticated,

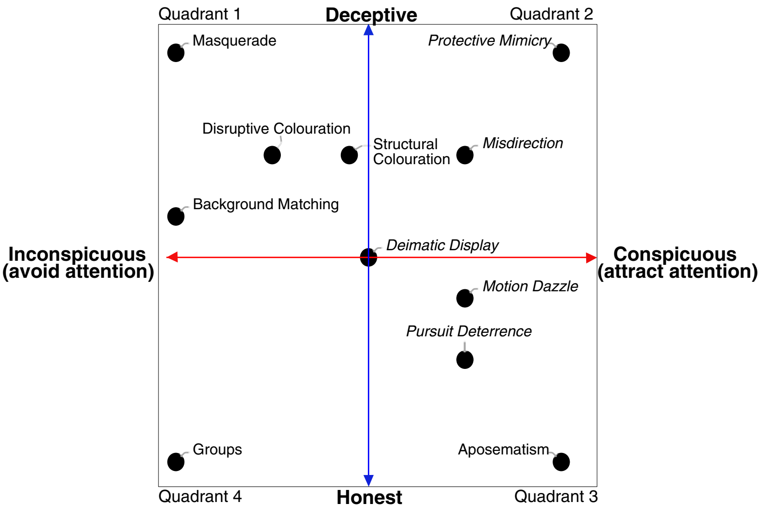

**Fig. 1** Schematic representation of visual antipredator strategies in spiders clustered in quadrants following two axes: The X-axis represents the visual signal's conspicuousness while the Y-axis represents its honesty. We highlighted the strategies that involve movement in italics. Quadrant numbers go clockwise, starting from the top left. Spatial position of the strategies is according to the rationale provided in Table 1

these investigations remain primarily shaped by a focus on stationary animals in a static heterogeneous background (see Tan and Elgar 2021 and references therein).

We have chosen spiders as our model taxon, but the principles are broadly applicable to other terrestrial systems. Though mainly considered as predators, spiders themselves are prey to many organisms (Nyffeler and Birkhofer 2017). The overall appearance of spiders represents a trade-off between foraging and being predated upon (Oxford and Gillespie 1998; Théry and Casas 2002), which makes them a good model to study the evolution and underlying mechanisms of visual anti-predator strategies. Most spider predators, such as birds, lizards, other spiders, and wasps, are visually oriented and diurnal (Foelix 2011). One way to avoid these predators is by adopting a nocturnal habit (Gawryszewski 2017).

Predation on spiders drives the evolution of diverse strategies oriented towards deception of predator perception (Fig. 2), based on morphological (body colouration or shape) and behavioural adaptations, some of which are static. In the first type of strategies (primary or passive defence), spider detection or recognition is hindered and includes strategies such as crypsis, masquerade, aposematism, and Batesian mimicry (Ruxton et al. 2004). The secondary defence prevents the spider's capture once it has been detected and involves strategies such as dropping to the ground, web vibration, and bouncing, among others (Cloudsley-Thompson 1995). Thus, the first type of defences operates independent of the predator presence, and some stimulus from the predator triggers the latter types.

**Table 1** Theoretical scores and rationale for the spatial position of different visual anti-predator strategies

| Quadrant | Strategy | Score (x,y)- > (Conspicuous,Honesty) Possible scores: (±1, ±0.5, ±0.2, 0) | Rationale for score |
|---|---|---|---|
| 1 | Masquerade | −1, 1 | Inconspicuous by mimicking inanimate objects, aids in predator mis-categorisation |
| | Disruptive Colouration | −0.5, 0.5 | Certain body patterns are conspicuous, while entire form is inconspicuous; hinders predator from recognising body form |
| | Background Matching | −1, 0.2 | Inconspicuous, but by mimicking environmental background; purely visual effect leading to predator evasion; little or no cognitive manipulation |
| | Structural Colouration | −0.2, 0.5 | Conflicting evidence for conspicuousness; more likely to be deceptive since they may hinder recognition |
| 2 | Protective Mimicry | 1, 1 | Conspicuous but deceptive (i.e., they depend on predator mis-categorisation) |
| | Misdirection | 0.5, 0.5 | Conspicuous but of only certain body parts, directs attacks to non-vital body part |
| 3 | Motion Dazzle | 0.5, −0.2 | Conspicuous, with motion leads to confusing signals. Hinders predator attack at a visual level |
| | Pursuit Deterrence | 0.5, −0.5 | Conspicuous signal sent to predators to deter pursuit, may be honest, but lack of conclusive empirical evidence |
| | Aposematism | 1, −1 | Aposematic animals are conspicuous to advertise their toxicity/ defences/ unprofitability |
| 4 | Groups | −1, −1 | Individuals within a group are inconspicuous, though the group as a whole is conspicuous and there is no attempt to deceive predators |
| Centre | Deimatic Display | 0, 0 | Behaviour cycles between conspicuous and inconspicuous, as well as between deceptive and honest |

**Fig. 2** Some examples of the visual antipredator defences discussed in the Text. Quadrant 1: **a** Cryptic spider *Talthybia* sp. (Araneidae) matches the background colouration. **b** Masquerading *Pasilobus* sp. spider (Araneidae) that resembles bird droppings. **c** *Chrysilla* sp. spider (Salticidae) with structural colouration. Quadrant 2: **d** *Synemosyna* sp. (Salticidae) that mimic morphological and behavioural traits of an ant. **e** *Phiale* sp. (Salticidae) probably resemble some traits of the general aspect of a mutillid wasp. **f** *Cyclosa* sp. (Araneidae) has in its web decorations made of debris that misdirect the predator's attack away from the actual spider location. Quadrant 3: **g** *Argiope aurantia* (Araneidae), which builds a web decoration, and performs a fast web flexing behaviour when a predator attempts to attack the spider. **h** *Latrodectus* sp. (Theridiidae) with aposematic colouration thought to warn the predator about its potential defences. Quadrant 4: **i** *Anelosimus eximius* (Theridiidae) spiders that might gather protection against visually oriented predators with its social habits. Photos **a**–**c**, **h**–**i** by Nicky Bay; **d**–**e** by Thomas Shahan; and **f**–**g** by Dinesh Rao

## Quadrant 1: inconspicuous and deceptive

### Visual camouflage: avoiding attention

The first barrier a predator has to overcome is detection or recognition of the spider as prey. Different forms of crypsis and masquerade are the most common visual defensive strategies in spiders (Pekár 2014). Crypsis or visual camouflage is achieved through body pattern colouration (Defrize et al. 2010), attaching debris from the microhabitat to special setae in the cuticle as seen in *Stephanopis* spp. (Gawryszewski 2014), or even changing the body colouration according to the background, as seen in many crab spider species (Insausti et al. 2012).

Several studies have evaluated spider crypsis through body colouration from the perspective of a predator in a visual ecology context using spectrophotometry (Théry and Casas 2002; Théry et al. 2005; Clark et al. 2011) or digital imaging (Robledo-Ospina et al. 2021). Thus, combining digital imaging and visual modelling to evaluate entire body patterns showed that spiders might present different types of crypsis with different ecological implications depending on the microhabitat they use (Bonte and Maelfait 2004). This new approach provided evidence for background matching to avoid detection and disruptive colouration to avoid recognition from a predator in jumping spiders that forage on either leaf litter or foliage vegetation (Robledo-Ospina et al. 2017).

There is no need for a perfect colour match between the spider and the background to be effective against predator vision, as shown by Rodríguez-Gironés and Maldonado (2020) using both spectrophotometry and visual modelling. Visually complex scenes can be measured by combining spectral sensitivity and spatial acuity (e.g., spiders located at different positions in the same flower with the viewer located at different distances) which showed that the detectability of the spider from a given visual system also depends on the context where the spider is seen (Rodríguez-Morales et al. 2018). Hence, it is essential to recognize the type of trait and the visual context (i.e., visual context and illumination conditions) to measure the spider body colouration and detectability objectively.

On the other hand, colour change in spiders for crypsis can be reached slowly through the synthesis and degradation of pigments (Insausti and Casas 2008, 2009; Riou and Christidès 2010), or rapid ($<5$ s) via pigment movement at sub dermal level (Wunderlin and Kropf 2013; Hawes 2017). These mechanisms allow the spider to conceal its body, by changing body pattern colouration to respond to environmental signals or physiological stress (Stevens 2016; Figon and Casas 2018).

For visually oriented predators, phenotypic plasticity of arthropod prey can have profound effects on the sensory mechanisms of the predator and its perceptual mechanisms (e.g., learning processes) (Troscianko et al. 2013). Prey variability and different crypsis strategies affect the predator's search image formation process and therefore maintain the prey population's variability via apostatic selection (Hemmi et al. 2006; Troscianko et al. 2018, 2021).

However, the search image formation process with spiders as prey has been traditionally neglected though visual camouflage and colour polymorphism are evident in many spiders at a population level (e.g., Oxford and Gillespie 2001; Croucher et al. 2011; Messas et al. 2014; Rao and Mendoza-Cuenca 2016). Colour polymorphism might result from the selective pressure exerted by visually oriented predators such as birds and hymenopteran parasitoids that exhibit search image formation (Vasconcellos-Neto et al. 2017). This situation highlights the search image formation process in spider predators as a future avenue worth exploring (Ximenes and Gawryszewski 2019).

## Masquerade and web decoration

Unlike cryptic spiders, masquerading species appear to closely resemble inedible and generally inanimate objects such as twigs, leaves, stones, and bird droppings (Skelhorn et al. 2010a, b). This resemblance can be achieved through morphological or behavioural modifications. One way to differentiate between crypsis and masquerade from the predator's perspective is to evaluate if they exploit a predator's sensory or cognitive process, respectively (Skelhorn 2015). Traditionally, this strategy has been evaluated using natural history studies (Kuntner et al. 2016) or behavioural assays (Zhang et al. 2015). However, with modelling of potential predator vision, spiders that look like bird droppings (Liu et al. 2014; Yu et al. 2021) or *Eucalyptus* twigs (Xavier et al. 2018) can be evaluated more realistically.

We can also include in this quadrant orb web spiders that use decorations in their webs (i.e., debris, prey carcasses, egg sacs and silk). Some spiders use this decoration to either attract prey (Li et al. 2004) or hide from predators (Gonzaga and Vasconcellos-Neto 2005; Nakata 2009). Tan et al. (2010) studied the role of web decoration in *Cyclosa ginnaga* using spectrophotometry and visual modelling of hymenopteran vision. They found that signalling created by web decorations may be considered a deceptive visual signal because, when viewed together, spider and decoration look remarkably like bird droppings. Field studies have demonstrated that these structures reduce the likelihood of predation. In *Argiope* spiders, silk decorations are detectable to prey and predators (Robinson and Robinson 1970; Eisner and Nowicki 1983; Bruce et al. 2005). Silk decorations may also serve as misdirection; a recent study showed that birds were more likely to attack the conspicuous decorated area of the web than the spider body part in a controlled experiment (Wang et al. 2021).

In a recent and remarkable work, Eberhard (2020) proposed that the hypotheses of prey attraction and visual defence are not mutually exclusive when discussing web decorations, because a visible defensive structure could also attract prey. We agree with the author in highlight the importance of using comparative studies instead of generalising from direct and simple measures to avoid an oversimplification of the biological model.

## Structural colouration

So far, we have focused on the colouration produced by pigments. However, spiders possess another type of colouration that has not adequately tested for an anti-predator function yet, structural colouration (Oxford and Gillespie 1998; Hsiung et al. 2017, 2019). The better-known structural colours in spiders are perceived by the human eye as metallic hues, that varies depending on the angle of the incident light and angle of view (Meadows et al. 2009). In spiders such as theraphosids and jumping spiders, this colouration arise from modified hairs (scales) or the solid cuticle (Foelix et al. 2013).

Jumping spiders have been shown to use the UV spectra as an intraspecific communication signal (Ingram et al. 2011), in male-male confrontations (Lim and Li 2007, 2013), and in sexual selection by females (Painting et al. 2016). However, as shown recently for the first time in arthropods, structural colouration also can serve a counterintuitive function: concealment. Glossy backgrounds like the surface of many leaves further enhance the effect of this protective function (Kjernsmo et al. 2020). Given that jumping spiders like *Paraphidippus aurantius* have an iridescent abdomen, and these spiders tend to forage over the foliage in the understory, the assessment of this type of colouration as an anti-predator resource is an idea to explore in future research.

Similarly, another colour produced by cuticular surfaces reported in spiders is the silver colour (Hsiung et al. 2015). This colouration does not change in hue with the angle of light and may have a thermoregulatory function in diurnal spiders (Robinson and Robinson

1978; Nakata 2021). Silver coloured spiders, which are highly conspicuous even in the UV spectra, are thought to attract prey (Rao et al. 2009). However, behavioural evidence has shown that silver colouration species reduced predation effectiveness compared to black coloured morphs of *Cyclosa argenteoalba* (Nakata and Shigemiya 2015). Though silver camouflage is generally considered useful in underwater habitats (Stevens and Merilaita 2011), it is common in spiders and provides an opportunity to evaluate it as an anti-predator defence (but see Franklin et al. 2022).

## Quadrant 2: conspicuous and deceptive

### Protective mimicry

Batesian mimicry deceives the predator by making the spider looks similar to unpalatable, noxious or dangerous organisms (Ruxton et al. 2004). Batesian mimicry in spiders is protective in nature (Sherratt 2017), while aggressive mimicry is less common (e.g., Pekár and Křál 2002; Jackson and Cross 2013). The best-known cases involve myrmecomorphic (ant-like) spiders (Nelson et al. 2006; Durkee et al. 2011; Cushing 2012). Most of the studies with this model evaluated the degree of accuracy of Batesian mimicry of these spiders using traits such as the general body shape and colour (Pekár and Jarab 2011; Corcobado et al. 2016), locomotion pattern (see Cross and Jackson 2018), chemical mimicry (Uma et al. 2013), and recognition of conspecifics and prey (Nelson and Jackson 2007). Another example of Batesian mimicry is seen in some spiders (generally in the Clubionidae, Salticidae, and Gnaphosidae families) that resemble mutillid wasps (Nentwig 1985). It has been demonstrated that lizards that feed on invertebrates do not prey on mutillid wasps and ignore the salticid *Phidippus apacheanus*, which, the authors claimed, mimics them (Edwards 1984).

A few studies have focussed on the imperfect mimicry in spiders (Pekár and Jarab 2011; Pekár et al. 2011), a phenomenon in which the mimic does not appear to resemble their models particularly closely (Sherratt 2002; Wilson et al. 2013). However, predator perception of this imperfect mimicry is an omission in these analyses, even when there are cases in which mimics seem imperfect to humans but are good mimics to predators (Cuthill and Bennett 1993; Dittrigh et al. 1993). It is important to avoid the "eye of the beholder" problem, i.e., when this type of mimicry may be due to an anthropocentric projection instead of a real predator perception (see Kikuchi and Pfennig 2013). Furthermore, this visual mimicry is directed toward vertebrates rather than invertebrate predators (Gall et al. 2018). Striking new evidence suggests that imperfect myrmecomorph spiders are effectively protected against birds, and those predators might drive the evolution of this form of Batesian mimicry in spiders (Veselý et al. 2021).

### Locomotory mimicry

When classifying prey visually, a predator can rely on static features like colour, shape, and size. However, another intriguing possibility is whether a predator can also categorize prey based explicitly on the movement patterns (Cross and Jackson 2018). Locomotory mimicry is a strategy for palatable prey to avoid capture by imitating the model's gait. This type of mimicry arises when two species appear alike in behaviour: the mimic has a corresponding suite of morphological, physiological, and biomechanical traits in common with its model (Srygley 1999).

There have been a few attempts to measure the resemblance of spider mimic and its models regarding gait and locomotory patterns. Those studies evaluated the gait of *Myrmarachne formicaria* and its models using high-speed cameras and behavioural experiments, finding that the mimic closely resembles its model to observers with slow visual systems (Shamble et al. 2017). Additionally, 3D animations were used to measure the response of visual predators to *Myrmarachne* spp. spiders, showing a similar response of ant-eating predators to locomotory patterns of ant mimic and their models (Nelson and Card 2016). Jumping spiders have also been reported to mimic the appearance and movement of parasitoid wasps (Hurni-Cranston and Hill 2018). Nevertheless, the cognitive process inherent to the predator experience when looking for prey and forming a search image is not usually included in most studies that search on the interaction between spiders and its predators. Motion perception and, most importantly, the subjectivity of how the predator perceive a moving target has not been adequately assessed.

### Misdirection

When a prey defends itself against predators with the use of deceptive markings that disguise the position of vital body parts or to draw an attack towards non-vital body parts, it has usually been termed as *deflection* (Ruxton et al. 2004). We propose the term '*misdirection'* as a more suitable alternative to refer to this phenomenon since misdirection involves some manipulation of predator cognition (Kjernsmo and Merilaita 2013; Ruxton et al. 2018). Furthermore, *deflection* implies a physical barrier such as armoured body parts that hinder prey capture, as seen in beetles. In *Cyclosa* spp. and *Allocyclosa bifurca*, the use of web decoration (pellets) made of debris, egg-sacs, and prey carcasses misdirect predator's attacks (Eberhard 2003; Théry et al. 2011). Even cruciform silk decoration in orb webs may serve the same function (Wang et al. 2021). Pellets may function as decoys to distract predator attack and conceal the spider position in the web, as seen in studies using spectral measurements, visual modelling, and behavioural experiments (Tan and Li 2009; Tseng and Tso 2009; Ma et al. 2020).

## Quadrant 3: conspicuous and honest

We have discussed strategies that operate when prey remains motionless or imitate the appearance or movement of unpalatable species. These strategies help the spider to avoid detection, recognition, or confrontation. Nevertheless, when spider is detected and the attack commences, secondary defence strategies are triggered to prevent capture, deceiving predators by (1) depriving it of information, (2) providing confusing cues, and (3) through easily perceived signals (Caro 2014). Secondary strategies usually include both motion and conspicuous colouration, which allows for the exploitation of all the vision parameters mentioned above.

As a secondary defence, some jumping spiders freeze when they perceive acoustic cues from potential predators (Shamble et al. 2016). Other spiders, like *Tylorida striata* (Tetragnathidae), escape through fast movements and visual camouflage by changing their colouration. When disturbed, the spider drops from its web and changes from a conspicuous yellow to a dark colouration that matches the ground substrate (Hawes 2017). Orb weavers' secondary defences include not only dropping to the ground but also changing sides on the web and web vibration/flexing to avoid capture (Pekár 2014; Gawryszewski 2017).

Web flexing is a fast motion of the orb web along the short axis caused by the rapid extension and retraction of a spider's legs. The observer could perceive it as a rapid movement backwards and forward (Tolbert 1975). This behaviour, recorded in orb-web spiders like *Argiope* genus, may blur the spider's outline, making it appear less spider-like and maybe particularly effective on webs with web decorations (Cloudsley-Thompson 1995). However, this has not been appropriately tested despite the evidence that moving high-contrast patterns may produce errors in motion detection mechanisms by mismatching local image contours (How and Zanker 2014).

## Motion dazzle

In Motion dazzle displays, high contrast patterns deceive predator's estimation of the prey's direction and speed when the target is in motion (Scott-Samuel et al. 2011; Hughes et al. 2017) or when the predator, in this case a biting insect, is in motion (How et al. 2020). While highly contrasting stripes are commonly found in spiders, there is no formal investigation of the relevance of these patterns as anti-predator strategies. Motion dazzle patterns may also be seen in the decorated webs of some spiders, especially in association with the web flexing behaviour of orb web spiders.

## Deimatic display

Deimatic displays or startle displays are behaviours where the prey suddenly shows a hitherto hidden brightly coloured or highly contrasting body part that induce an approaching predator to stop its attack or retreat (Umbers et al. 2017). These displays can either be honest or dishonest signals (Umbers et al. 2015; Cox et al. 2021). The objective is to cause the predator to respond reflexively to that sudden transition in its sensory input (Umbers et al. 2017). Deimatic displays function best as a loop, cycling from inconspicuous to conspicuous and back again, hindering the ability of the predator to localise the prey during pursuit. Deimatic displays might create optical illusions (i.e., errors of perception) through body colouration and movement (see Kelley and Kelley 2014). These illusions were shown to hamper predation in different animals (Kodandaramaiah et al. 2020; Valkonen et al. 2020). The deterrent effect on the predators is enhanced by the evolution of conspicuous visual display components and rapid movements (Holmes et al. 2018). In spiders, Deimatic displays have been recorded in genera such as *Phoneutria*, which when threatened, raises the first pair of legs, which have high contrasting white markings, as well as reveal their brightly coloured fangs while swaying side to side (Schenberg and Pereira Lima 1978; Nentwig and Kuhn-Nentwig 2013).

## Pursuit deterrence

This is described as a signal from the prey that advertises to the predator that it was detected (Ruxton et al. 2004). The prey may advertise 1. the presence of mechanical or chemical defences, 2. that it is hard to capture or 3. that the prey is unprofitable, causing the predator to give up its approach (Caro 1995). Unlike deimatic or startle displays, the predator's behavioural response to the pursuit-deterrence signalling depends on the signal honesty (Cooper 2011). Empirical data is scarce regarding pursuit deterrence in general and has not been explicitly studied in spiders.

### Aposematism

Contrary to cryptic and masquerading strategists, aposematic species often incorporate a visually conspicuous display with high-contrast components (Summers et al. 2015). Even when aposematism has been linked to honest signalling of prey's unprofitability, animals advertise many other types of defences (Caro and Ruxton 2019). Spiders with aposematic colouration have contrasting colours (black/white, black/red, black/yellow) and obvious defences (Pekár 2014). Those defences might include large fangs, spines, urticating hairs, or potent venom (Gawryszewski 2017). Hence, aposematic spiders do not try to conceal themselves but rather communicate to the predator through conspicuous signals that the spider's defences are dangerous (Nelson and Jackson 2011).

Aposematism in spiders has been widely linked to the *Latrodectus* genus because of its venom. However, the evidence supporting this hypothesis is not conclusive. In contrast, widow spiders are known to use silk as a secondary defence against predators rather than venom (Nelson and Jackson 2011). Nevertheless, Brandley et al. (2016), using behavioural trials, spectral measures, and visual modelling, showed that predators are less likely to attack black widows with high-contrast marks than without it. Moreover, the marks were more conspicuous to (vertebrate) predators than prey. It is necessary to evaluate honest signalling within a population and the mechanisms producing the relationship between conspicuousness and toxicity from both theoretical and empirical approaches (Summers et al. 2015).

Ximenes and Gawryszewski (2020) evaluated aposematic colouration in *Gasteracantha cancriformis* through behavioural experiments. They found that black spiders were attacked more often than yellow and red models. *G. cancriformis* possess mechanical defences provided by stiff spines in the abdomen. However, with the exception of toxicity, empirical evidence for aposematism as a visual signal for anti-predator defences is still scarce (Caro and Ruxton 2019).

## Quadrant 4: inconspicuous and honest

### Groups

Though spiders are primarily solitary, they could aggregate, forming big colonies and communal webs, gaining survival benefits (Viera and Agnarsson 2017). These strategies were linked to protection against predators via the dilution effect, reducing the individual risk of predation in colonial spiders (Uetz and Hieber 1994). Solitary individuals are more likely to face predation risk in comparison to spiders that aggregate (Henschel 1998). Furthermore, spiders that live in groups have other defences such as the 'early warning effect' (Uetz et al. 2002). A new aspect of those groups in spiders is the confusion effect from the predator perspective. In aquatic systems, shoaling or schooling of fish achieve the same effect through a coordinated movement. Whether immobile or not, this effect occurs when a predator is trying to prey on a group of prey and is attributed to the information processing constraints of predators. The confusion effect relies on a high degree of similarity among individuals (see review by Tan and Elgar 2021). The group as a whole may be conspicuous, but each individual is relatively inconspicuous.

An additional aspect considering groups as visual defensive mechanism, is related to differences in individual movement, which increases the scene complexity for the predator perspective. Some group-living spiders like *Anelosimus eximius* (Theridiidae) have high-contrast disruptive colouration (black body with red marks), which also could aid the confusion effect via dazzling camouflage, leading to predator misperception of speed or trajectory estimation (Ruxton et al. 2018).

## Conclusions

To study visual signalling in antipredator strategies in spiders, use of the latest techniques for the representation and simulation of natural phenomena is essential to evaluate signals involved in predator–prey interactions as viewed by ecological relevant observers in an integrative manner. Apart from the visual aspects of body colouration and pattern (van den Berg et al. 2020), studying the temporal resolution of movement may be the next frontier in visual ecology (Donner 2021).

From the spatial positioning of different defensive strategies on the two axes of conspicuousness and honesty, our framework implicitly incorporates the cognitive aspect of predation avoidance. With few exceptions, spider colour and patterns are largely selected for by predation pressure. Some strategies such as Background matching operate at a visual level, whereas others such as misdirection manipulate predator attention. This framework can be extended to other terrestrial and perhaps aquatic animals.

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**Consent for publication** All authors approved the manuscript.

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