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Context-dependent crypsis: a prey's perspective of a color polymorphic predator

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Abstract

Many animals use body coloration as a strategy to communicate with conspecifics, prey, and predators. Color is a trade-off for some species, since they should be visible to conspecifics but cryptic to predators and prey. Some flower-dwelling predators, such as crab spiders, are capable of choosing the color of flowers where they ambush flower visitors and pollinators. In order to avoid being captured, visitors evaluate flowers visually before landing. The crab spider *Mecaphesa dubia* is a polymorphic species (white/purple color morphs), which inhabits the flower heads of a dune plant, *Palafoxia lindenii*. Using full-spectrum photography of spiders and flowers, we evaluated how honeybees perceived the spiders at different distances. Using visual modeling, we obtained the chromatic and achromatic contrasts of the spiders on flower heads as perceived by honeybees. Purple morphs were found mainly on the receptacle area and white morphs were equally likely to be found in the flowers and receptacle. According to theoretical modeling, white morphs were visible to honeybees from a distance of 10 cm in receptacle area but appeared to be cryptic in the flower area. Purple morphs were cryptic on the receptacle and less so when they were on the flowers. Spiders on flower heads are predicted to be more easily detected by honeybees using chromatic contrast. Our study shows that the conspicuousness of flower dwelling spiders to honeybees depends on the color morph, the distance of observation, and the position of spider on the flower head.

Keywords Predator-prey interactions · Achromatic and chromatic contrast · Visual model · Honey bees · *Mecaphesa dubia*

Introduction

Camouflage is an evolutionary adaptation observed in some animals that decreases the probability of being detected by potential predators and prey (Merilaita 2003). This optical effect can help an individual to avoid predators and to deceive prey (Osorio and Srinivasan 1991; Théry et al. 2004; Stevens et al. 2009); either by using colors and patterns similar to the individual's surroundings, i.e., background matching (Stevens et al. 2009), or by adopting high-contrasting patterns that obscure the body shape, i.e., disruptive coloration (Defrize et al. 2010; Robledo-Ospina et al. 2017). For many insects, vision is an important mechanism for recognizing and discriminating objects, particularly through contrasts between the object and its background (Olsson et al. 2017). Color can have a direct effect on the behavior of the organisms that are capable of perceiving it (Vorobyev and Osorio 1998; Théry et al. 2004; Kelber and Osorio 2010). These organisms can respond to color with basic behaviors such as foraging, socialization,

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searching for and selecting mates, and avoiding predators (Renoult et al. 2015).

Some predators, such as crab spiders (Araneae: Thomisidae), are capable of changing the color of their bodies to match the color of the substrate where they are found, which are usually flowers where they wait to ambush their prey (Oxford and Gillespie 1998; Théry et al. 2004; Brechbühl et al. 2010; Anderson and Dodson 2014). Some crab spiders have been observed to exhibit color polymorphism (Oxford and Gillespie 1998; Morse 2007; Ajuria Ibarra and Reader 2013; White and Kemp 2016; Gawryszewski et al. 2017). This color polymorphism can be continuous, as a response to environmental conditions (e.g., color change) (Oxford and Gillespie 1998), or it can be discrete, having a genetic origin (Oxford 1983; Ajuria Ibarra and Reader 2013). Other species of crab spiders are able to choose flowers that match the color of their bodies in order to avoid detection or exhibit a contrasting color (usually in the ultraviolet) to attract prey to flowers through deceptive signaling (Heiling et al. 2003; Heiling et al. 2005; Brechbühl et al. 2010; Vieira et al. 2017). Using visual models, we can approximate how flower visitors, particularly honeybees, perceive the variation in coloration in crab spiders. This information is fundamental to understand the evolutionary processes that involve cryptic or polymorphic organisms (Heiling et al. 2005; Ajuria Ibarra and Reader 2014).

The identification or recognition of crab spiders with respect to the background on which they are found depends on the prey's ability to perceive color and their visual acuity (Caves et al. 2018). For example, honeybees (*Apis mellifera*) are trichromats and possess receptors that can have peaks in the green, blue, and UV part of the light spectrum (Vorobyev and Osorio 1998). Honeybees use achromatic contrast (brightness) for the detection of objects at long distance, using only the green photoreceptor (MW), while chromatic contrast is used for the detection of small objects and patterns at short distance, with all three photoreceptors (Vorobyev and Osorio 1998; Théry et al. 2004). The use of these three photoreceptors allows honeybees to see color (Avarguès-Weber and Giurfa 2014) and perceive separate dimensions of hue, saturation, and brightness and to detect most of the variation in natural spectra (Kelber and Osorio 2010).

It is critical for honeybees to be able to detect the color of a potential enemy on the flowers, and this has to occur at an appropriate distance to be able to avoid landing on a dangerous place. Various studies have found that honeybees can identify crab spiders on flowers through chromatic and achromatic contrasts (Théry and Casas 2002; Théry et al. 2004; Llandres and Rodríguez-Gironés 2011; Gawryszewski et al. 2017). Nevertheless, in most of these studies, it is assumed that spiders are static, i.e., they maintain a fixed position on the flowers and are usually on top of the petals. However, spiders tend to move to different places on the flower or inflorescence depending on their color characteristics (Théry and Casas 2002; Morse 2007). Therefore, it is important to determine if color contrasts and/or the spiders' position on flowers are factors that influence the crypsis of spiders in the visual system of honeybees.

We studied the chromatic and achromatic contrasts as perceived by honeybees, of color polymorphic *Mecaphesa dubia* crab spiders on *Palafoxia lindenii* flowers. This plant has composite flowers, also known as flower heads, with 18–30 flowers held by a common receptacle (Álvarez-Molina et al. 2013). We simulated how the spiders could be potentially viewed by honeybees when observed at different distances, using false-color images (sensu Troscianko and Stevens 2015) and different spider color morphs located at distinct places on the flowers. We used full-spectrum digital photography (Stevens et al. 2006) instead of measuring selected points on the abdomen of the spiders and flowers using a spectrometer (sensu Chittka 2001; Heiling et al. 2003; Théry and Casas 2002, also see Teodore and Johnsen 2012), since this allows us to measure the entire body coloration of spiders and whole flower. We asked the following questions: (1) is there variation in spider position on the flower head according to morph's color and (2) what is the likely effect of distance, spider's color morph, and its position on flowers, on the likelihood of detection by a model of potential prey?

Materials and methods

Study site

The study was carried out at La Mancha (19°36′N; 96°22′W; < 50 m a.s.l.) in 2014 and at El Farallón (19°37′N; 96°23′W; < 50 m a.s.l.) in 2016. Both sites are located in the municipality of Actopan in Veracruz, México. The climate in this area is humid with rainfall in the summer, ranging from 1200 to 1500 mm on average, and the mean annual temperature ranges between 22 and 26 °C (García-Franco and Rico-Gray 1997; López-Rosas et al. 2005).

Study species

The crab spider *Mecaphesa dubia* (Thomisidae) is distributed from USA to South America (Morse 2007). It is commonly found on flowers where they prey on insects (honeybees, bumblebees, flies, etc.) (Welti et al. 2016) that feed on nectar and pollen (Morse 2007).

Spiders were collected from the flower heads of *Palafoxia lindenii* A. Gray (Asteraceae), a drought-tolerant species endemic to the Gulf of Mexico which can be found mainly in sunny areas near to the coast and dunes, where it is one of the first species on colonize (Álvarez-Molina et al. 2013). Flower heads of *P. lindenii* last for approximately 5 days, and the anthesis occurs from the exterior to the center of the flower head) (Álvarez-Molina et al. 2013) (Fig. 1a, b).

In the study sites, the most frequent color morphs of *M. dubia* found on *P. lindenii* were white, purple, and white with purple, which resemble the colors of the flower heads (Fig. 1c, e).

Position of spiders on flower heads

During 2014, we recorded spider position on the flower heads of *P. lindenii* in a population located at the beach of La Mancha. We observed 38 spiders of the three different color morphs (white, purple, and white with purple) and recorded their frequency at the flowers or on the receptacle, since these are the most common sites used to capture floral visitors (Fig. 1g). Each spider was observed in their position on the flower head, and we found 38 spiders and observed them for 1–4 times during the day (08:00–11: 00 h, period of the major insect activity). We also observed some spiders on the leaves of *P. lindenii* rarely, but without any prey, and later, they were seen on the flower heads.

Statistical analyses

A generalized linear model (GLM) with a binomial link function was used to compare the frequency of spider color morphs on the flowers and between their position on the flower head specifically in the receptacle and flowers. We considered frequency of the spiders as the dependent variable, and position on the flower head and color morph, and the interaction between color morph and position, as independent variables. Post hoc tests were carried out using contrasts. All statistical analyses were carried out in the program JMP ver. 9.0.1.

Acquisition of digital images

To evaluate the chance of detection of *M. dubia* spiders on the flower heads of *P. lindenii* from the perspective of the visual system of honeybees, we obtained digital photographs of the dorsal part of 11 spiders ($n = 6$ white morph, $n = 5$ purple morph), as well as digital photographs of the lateral part of the flower heads where the spiders were found. The white with purple morph was not included in the analysis of the visual model

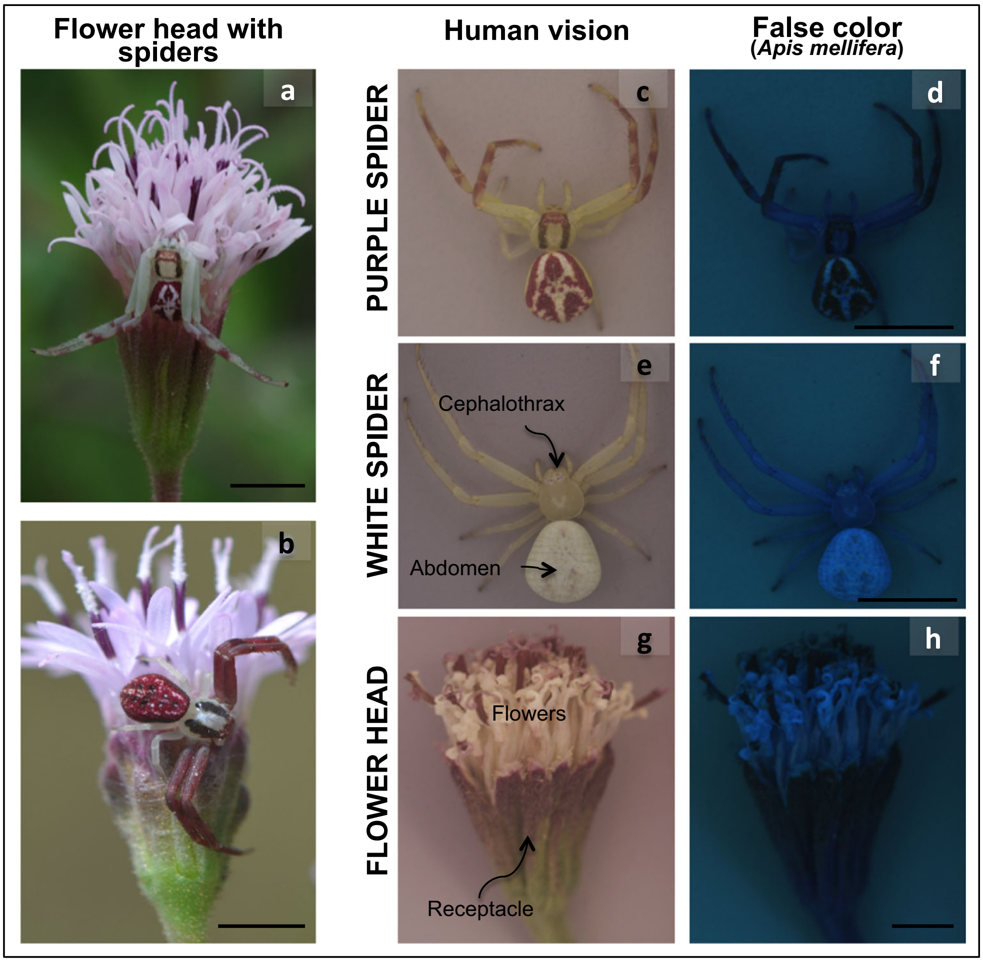


Fig. 1 Images of *Palafoxia lindenii* (Asteraceae) flowers and *Mecaphesa dubia* (Thomisidae) spiders. **a**, **b** Flower head with a *M. dubia* spider between the receptacle and the flowers. **c** Purple spider. **e** White spider (arrows indicate the cephalothorax and the abdomen of the spiders, which were the regions considered in the analysis comparing the chromatic and achromatic contrasts between the different areas of the flower heads). **g** *P. lindenii* flower head (the area of the receptacle and the flowers are pointed out). **d**, **f**, **h** False-color images of purple and white spiders and the flower head. The black bar represents 1 cm

because we did not find enough spiders of this morph during the survey of the specimens for photography. Spiders were kept in the laboratory at the Universidad Veracruzana and fed with *Anastrepha ludens* (Diptera: Tephritidae) flies. The flowers were placed individually in a rack with dampened OASIS® floral foam inside a cooler to keep the flowers hydrated.

Photographs were taken in a dark room with a full spectrum (300–700 nm) Iwasaki EYE Color lamp (70 W 1.0 A, Venture Lighting Europe Ltd. Hertfordshire, UK) as a light source. We used an Olympus Pen E-PM2 camera converted to full spectrum (by removing the UV filter, LifePixel.com), fitted with an EL-Nikkor 50 mm 4.5–22 f lens. We used a minimum aperture size (f 4.5), and shutter speed and integration time were adjusted for each sample in order to obtain an optimum exposure for each image and avoid saturation of the sensor (Stevens et al. 2007). Two series of images were taken, using Baader Venus UV pass and UV/IR cut filters, to obtain images in ultraviolet (UV) (~ 300–400 nm) and in the human visible part of the spectrum (~ 400–700 nm). A white reflectance standard of 93% and a gray reflectance standard of 7% were included in each photograph, as well as a size scale. Images were saved in RAW format. A PTFE sheet was used to diffuse the light to avoid unwanted shadows and reflections in the images. To immobilize the spiders when taking the photographs, they were sedated with CO_2 for 7 min.

Images were processed using the Multispectral Image Calibration and Analysis (MICA) Toolbox (Troscianko and Stevens 2015) for ImageJ v.1.49 (Schneider et al. 2012). The MICA Toolbox performs a linearization of the response of the camera to light changes and the equalization of the different color channels. This process is necessary to obtain camera-independent spectral reflectance values and carry out the modeling of the visual systems (Garcia et al. 2013; White and Kemp 2016).

A multispectral image was created with the MICA toolbox by combining the UV (300–400 nm) and the human visible (~ 400–700 nm) channels for each spider and flower head (Troscianko and Stevens 2015). This resulted in an image with four channels corresponding to different parts of the spectrum: UV, short wavelength (SW), medium wavelength (MW), and long wavelength (LW) (Robledo-Ospina et al. 2017; Ajuria-Ibarra et al. 2017). The multispectral image was then used to create a false-color image, simulated according to the visual system of honeybees (Troscianko and Stevens 2015). In order to create those false-color-UV images, we used the UV channel as input for the UV photoreceptor, the blue for the SW photoreceptor, and the green for the MW photoreceptor.

Spatial resolution of spiders on flower heads as perceived by honeybees

Apart from spectral sensitivity, which allows animals to discriminate colors, visual acuity determines the spatial resolution with which they perceive objects (Caves et al. 2018). Visual acuity is used during foraging and the active search for places to land on, as well as assessing the quality and quantity of resources, and potential predators (Olsson et al. 2017; Caves and Johnsen 2017). Therefore, we simulated the visual acuity of honeybees when observing the spiders (white and purple morphs) located on different positions on flower heads (over the flowers and on the side of the receptacle) at different distances (1, 5, and 10 cm). This was performed using the R package AcuityView (Caves and Johnsen 2017), which allowed us to use images with cone catch quanta values (mapped from multispectral images) in order to simulate the visual acuity of honeybees. In addition to visual acuity, a false-color-UV image was used to include the spectral sensitivity of honeybees to obtain a more realistic perspective from this visual system in the analysis (Fig. 1d, f, h).

To generate the images representing the visual acuity of honeybees viewing the spiders on flower heads at different distances using the false-color-UV images (Troscianko and Stevens 2015), we calculated the angular width of each image (α) using Eq. 3 described by Caves and Johnsen (2017). For the minimum resolved angle, we used the inverse of the visual acuity (in cycles/degree), which is reported in the literature as 0.5 for *A. mellifera* (Wehner 1981; Land 1997).

Detection of *M. dubia* spiders on *P. lindenii* flowers by honeybees

The following regions of interest (ROIs) were selected in the multispectral images: (1) the whole body of the spider, including the first two pairs of legs, for both the white and the purple morphs; (2) the whole flower head (includes the area of flowers and receptacle); (3) the flowers; and (4) the receptacle (Fig. 1e, g). The selection of the ROIs of the spiders and the flower heads was performed separately to compare the chromatic and achromatic contrasts of the spiders in each area of the flower head as perceived by the visual system of honeybees.

Contrasts were calculated with the ImageJ plug-in MICA (Troscianko and Stevens 2015) using the receptor noise limited (RNL) model (Vorobyev and Osorio 1998), which indicates the minimum perceptible difference in units of just-noticeable-differences (JNDs) from values of cone catch quanta obtained from the images. In order to use this model, it was necessary to know the spectral sensitivities for each camera's channel (peaks for each channel were UV 369 nm, SW 477 nm, MW 556 nm, and LW 596 nm; see Robledo-Ospina et al. 2017 for further details of the setup), and for each photoreceptor of the bee's visual system (peaks in UV 344 nm, SW 436 nm, MW 556 nm; Land 2012). We used cone class proportions (ni) of 1:0.41:4.412 for the UV/SW/MW channels in the bee visual system and a Weber fraction (wi) estimated from the standard deviation of the noise in each photoreceptor (σ) equal to 0.12. We used the following equation $w_i = \sigma/\sqrt{n_i}$ (Vorobyev and Osorio 1998).

We evaluated the ability of the honeybees to discriminate the spiders on the flower heads, and on which area of the flower head the spiders of each color morph are more easily discriminated. A discrimination threshold of 1 JND is commonly used in studies of color discrimination, according to the RNL model, where stimuli with values greater than 1 JND are more likely to be discriminated or detected by honeybees (Vorobyev and Osorio 1998). We compared the JND values of the different spider color morphs on the flower heads, the flowers alone, and the receptacle. We included the whole flower head, since the spiders place their anterior legs on the area of the flowers and the rest of the body on the receptacle. However, instead of a hard threshold or the binomial approach (detected or not) which requires a model calibration, we considered a conservative interpretation of the RNL model in terms of the probability that the spiders were being detected (Renoult et al. 2015), where the higher the JND values, the more likely it is for the spider to be detected. Although this model has been generally used to detect small differences, it has also been applied to estimate larger differences in some visual systems (Renoult et al. 2014; Fleishman et al. 2016).

The Supplementary Material includes images that show the different parts of the spiders (cephalothorax and abdomen) on the flower heads, which were used for comparisons.

Statistical analyses

An analysis of variance (ANOVA) was carried out to compare JND values from chromatic and achromatic contrasts of the spiders of different color morphs (white and purple) on the different areas of the flower heads (flowers and receptacle). A separate ANOVA was performed for each color morph. All statistical analyses were carried out in JMP 9.0.1®.

Results

Position of spiders on flower heads

Thirty-eight predominantly white, white with purple, and predominantly purple spiders were observed on the flower heads (14, 14, and 10 individuals per color morph, respectively). Spiders were found to occupy different positions on the flower heads depending on their body color (GLM: $X^2 = 10.91$, df = 2, $P < 0.004$). White spiders show no significant differences between the positions they occupy in the flower head, flowers 50.4% and receptacle 49.6% ($P = 0.171$), while white with purple (58.6%) and purple (78%) spiders were found mainly on the receptacle of flower heads ($P < 0.017$ and $P = 0.001$, respectively) (Fig. 2). Full details of the statistical tests are presented in a supplementary material (Table 1).

Spatial resolution of spiders on flower heads as perceived by honeybees

At 10 cm distance, white spiders are predicted to be more conspicuous as seen by honeybees when they are on the receptacle, but if they are over the flowers, the possibly of detected is lesser (Fig. 3). On the other hand, at the same distance, purple spiders appear to be more visible over the flowers, but they do not appear detectable on the receptacle. In this case, the color of the abdomen matched the color of the receptacle, and the legs are cryptic due to their resemblance to the flowers. The conspicuousness of spiders increased as the distance between bees and flowers decreased. This can be observed when contrast between spider and flower head is reduced, that is, when white spiders are over the flowers and purple spiders are on the receptacle (Fig. 3 shows images at 1 and 5 cm distance for both color morphs in the different sites of the flower head). It is also evident that at a 1 cm distance, white spiders are visible on the receptacle, while purple spiders appear to be less detectable in this area, but they are possibly more visible on the flowers.

Detection of *M. dubia* spiders on *P. lindenii* flowers by honeybees

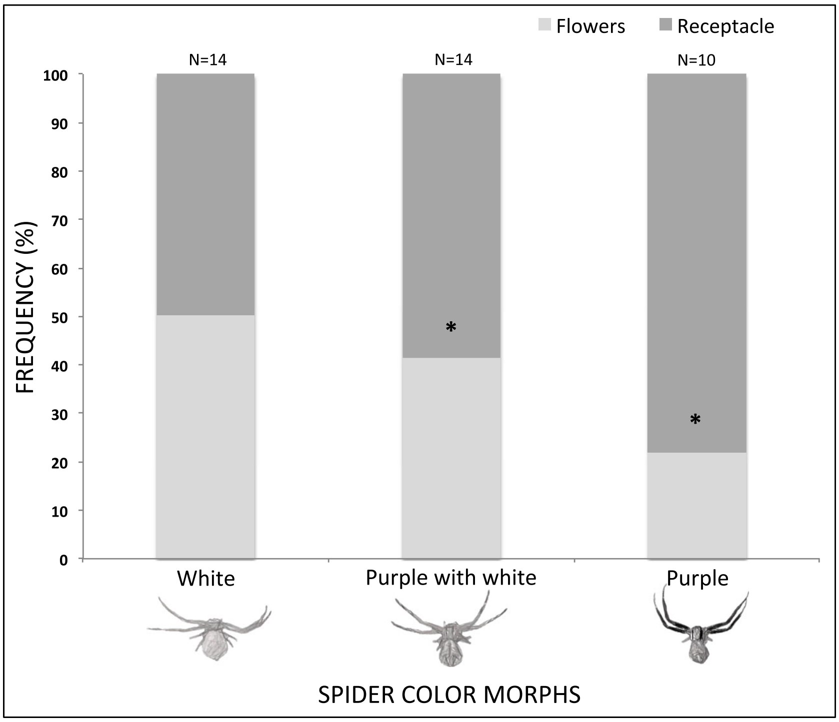
Our results indicate that when using achromatic contrast, white spiders are more likely to be conspicuous to honeybees when they are on the receptacle of the flower head (ANOVA: F = 20.03, df = 2, $P < 0.001$; Tukey test $P < 0.05$; Fig. 4a), with values of 7.31 ± 0.62 JNDs (mean ± standard error), when compared to the area of the flowers and the whole flower head. In the flower head, JND values are lower and honeybees potentially do not detect white spiders.

In the case of chromatic contrast (detection at a shorter distance), white spiders are more likely to be conspicuous to honeybees when they are on the receptacle of the flower head (5.40 ± 0.41 JND) than when on the flowers (1.75 ± 0.41) or the whole flower head (2.16 ± 0.41) (ANOVA: F = 22.94, df = 2, $P < 0.001$; Tukey test $P < 0.05$; Fig. 4b).

We obtained similar results for purple spiders with achromatic contrast. Purple spiders are more likely to be conspicuous when they remain on the receptacle (5.38 ± 0.80) (ANOVA: F = 5.86, df = 2, $P = 0.016$; Tukey test $P < 0.05$), compared to the area of the flowers (2.30 ± 0.80) and the total area of the flower head (1.75 ± 0.80), where the spiders are likely to remain undetected (Fig. 4c).

The results for chromatic contrast for purple spiders show that they are equally conspicuous in all the areas of the flower head, since no significant differences among areas were found (ANOVA: F = 1.33, df = 2, $P = 0.299$; Tukey test $P < 0.05$; Fig. 4d).

Fig. 2 Frequency of the different color morphs of *M. dubia* on the different areas of the flower heads of *P. lindenii* (on the flowers and on the receptacle). Asterisks inside bars represent significant differences between flower head areas for each color morph



Discussion

Our results show that *M. dubia* spiders may be selectively positioning themselves on different areas on the flower heads of *P. lindenii* according to their body coloration, and this choice has implications on the probability of detection by potential prey such as honeybees. At the studied site, white with purple and purple spiders are mainly on the receptacle area, whereas white spiders are equally likely to be found on any area of the flower head. However, due to a relatively low sample size, we cannot consider these results as definitive but rather as indicative of selective positioning. Both purple and white morphs are more likely to be conspicuous to honeybees at a different distance using achromatic contrast, and this effect is pronounced when spiders are on the receptacle. On the other hand, honeybees are predicted to more easily detect white spiders on the receptacle using chromatic contrast, whereas the position of purple spiders on the flowers does not affect detectability. Furthermore, our results suggest that the detection of the morphs could be influenced not only by the spectral sensitivity (chromatic and achromatic contrast) but also by the spatial resolution (acuity) the bee has at different distances (Caves et al. 2018).

When honeybees visit flowers, they have to make decisions based on the quality and quantity of the resources of the flowers (Chittka and Spaethe 2007). Nevertheless, they also have to evaluate potential risks on flowers, where crab spiders are common predators (Morse 2007). Crab spiders can use two possible strategies in order to maximize their chance of prey capture. First, they can occupy flowers that have the same coloration as their bodies and thus avoid detection (using a background matching strategy (Stevens and Merilaita 2009)). For example, Théry et al. (2004) found that *Thomisus onustus* spiders efficiently match the color of the center of marguerite daisies where they are imperceptible to Hymenopteran prey, while they are likely to be easily detected in the periphery of the flowers. In the field, *T. onustus* spiders were always found positioned at the center of the flowers. Some crab spiders can change colors, and they usually occupy a flower and change their body color to match the substrate, usually over several days (Brechbühl et al. 2010; Riou and Christidès 2010).

Second, crab spiders can occupy flowers that contrast in coloration with their bodies, especially in the UV, and thus act as floral guides (i.e., a visual lure strategy; Tso 2013). For example, *Thomisus spectabilis* spiders have been found to position themselves in the area of daisy flowers that is most favorable for prey capture (Heiling et al. 2006). Honeybees were found to prefer flowers with *T. spectabilis* spiders on the peripheral lingulate florets, instead of vacant flowers or flowers with spiders on the center. On the lingulate florets of the flowers, the UV reflection of *T. spectabilis* generates a strong color contrast that attracts honeybees (Heiling et al. 2003, 2005). Even some males of Thomisidae family choose the substrate on which they are found according to their body color (Bonte and Jean-Pierre 2004).

Nevertheless, crab spiders frequently move around the flower head (flowers and receptacle). As they change positions, the perception of the spider by the potential prey should also change according to the different contrasts made by the spider with the floral background. We found that white with

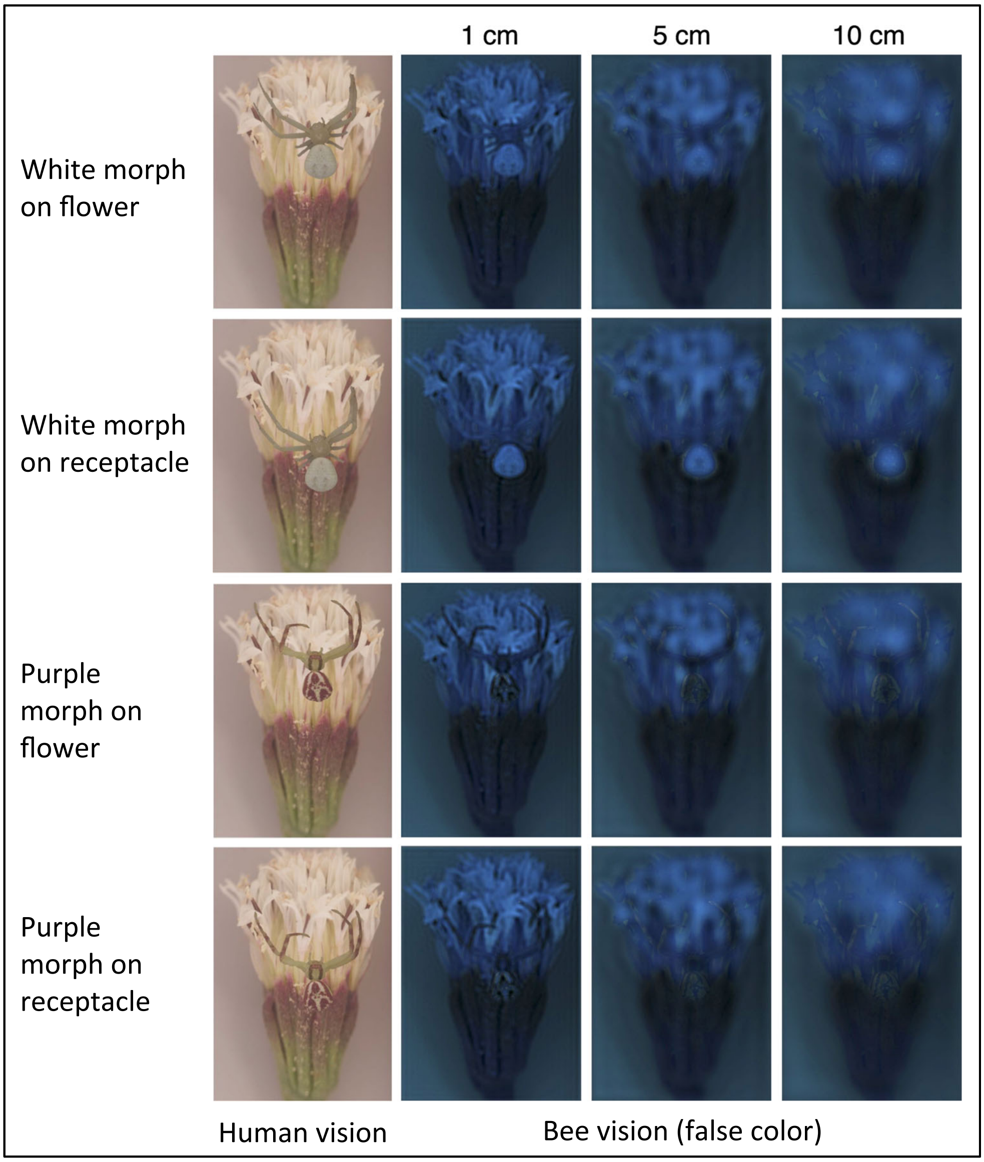


Fig. 3 Model of the perception by honeybees (*A. mellifera*) of the white and purple color morphs of *M. dubia* on the different areas of the flower heads of *P. lindenii* at different distances. The first column shows images as perceived by the human visual system. The second, third, and fourth columns show false-color images simulating the perception of the visual system of honeybees at different distances (1, 5, and 10 cm, respectively). Rows show the two color morphs positioned on the different areas of the flower heads (on the flowers and on the receptacle)

purple and purple *M. dubia* spiders are more frequently on the receptacle of the *P. lindenii* flower heads, possibly because in this area, the colors of the spider body with the receptacle matches. However, purple spiders are more likely to be detected on this area of the flower head when honeybees using achromatic contrast, and they have an equal probability of detection on any area of the flower head by the chromatic contrast. On the other hand, white spiders, which were equally likely to be found in either area of the flower head, showed significantly higher achromatic and chromatic contrasts on the receptacle. Since *M. dubia* spiders reflect UV light, and white spiders reflecting more than purple spiders (DRM, in prep), it is possible that when white spiders appear conspicuous on the area of the receptacle, they could be functioning as a visual lure, as has been observed in other species of crab spiders (Heiling et al. 2005, 2006; Bhaskara et al. 2009) as well as in orb web spiders (Tso 2013).

The false-color images (Fig. 3) provide an approximation of how honeybees perceive the spiders on flower heads. In these images, honeybees can potentially detect white spiders when they are on the receptacle of the flower head from a distance of 10 cm, and this morph is more visible as the distance becomes shorter. The observation distances evaluated in this study are biologically relevant since, at these distances, honeybees are able to make important decisions about whether to visit a flower with a potential predation risk or a risk-free flower (Dukas 2001; Gonçalves-Souza et al. 2008).

At close distances, honeybees can decide to not visit the flower head especially if spiders move during this process (Llandres and Rodríguez-Gironés 2011). Purple spiders appear less likely to be detected when they are on the flowers of the flower head at a 10-cm distance, but they become more likely to be detected at 5 and 1 cm. The opposite occurs when the spider is on the receptacle where the crypsis appears to be

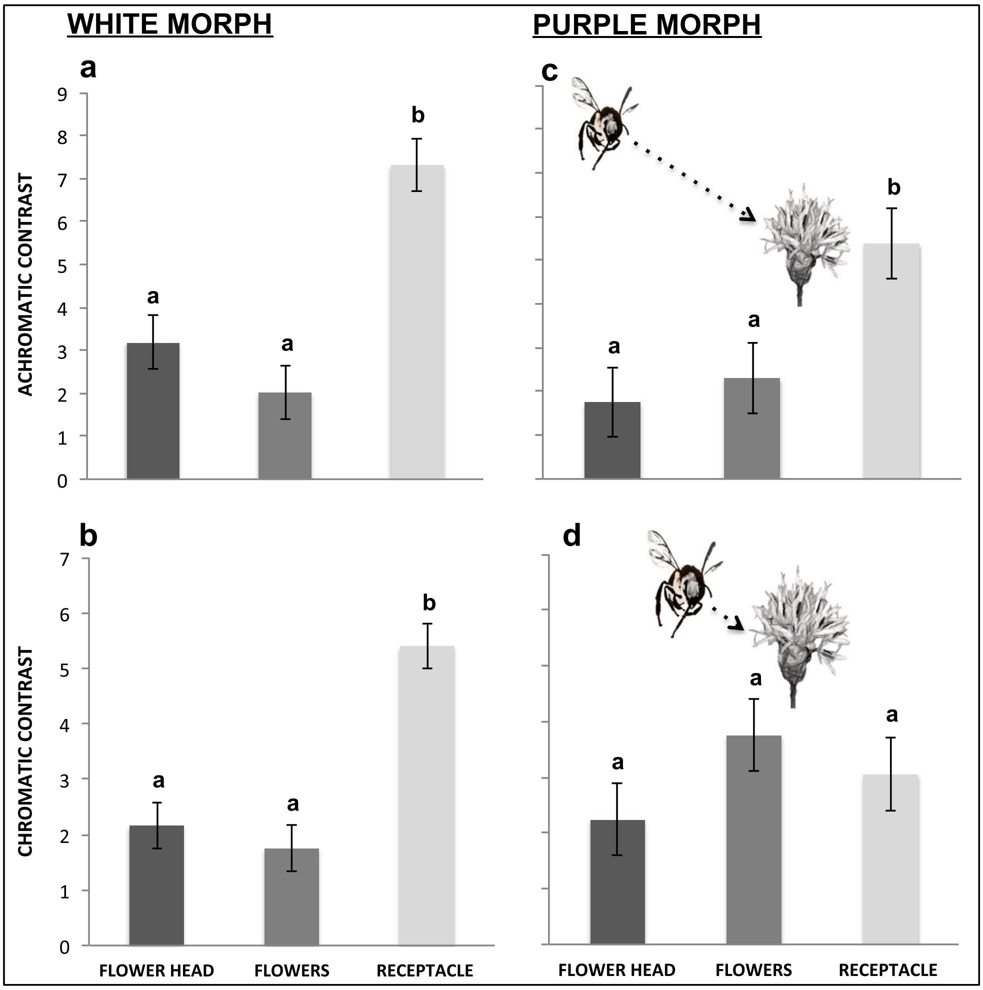


Fig. 4 Chromatic and achromatic contrasts of JND values for the white and purple morphs perceived by the visual system of honeybees (*A. mellifera*). Here, we considered the coloration of the whole spider body on the whole flower head of *P. lindenii* and its different areas flowers and receptacle. **a**, **b** Achromatic and chromatic contrast, respectively, of white spiders ($N = 6$ spiders). **c**, **d** Achromatic and chromatic contrast, respectively, of purple spiders ($N = 5$ spiders). Lines above bars represent standard errors, and different letters above bars indicate significant differences

more effective, and it is possible that the purple morph has an advantage over the white morph when they are in the area of the receptacle, particularly at short distances. This is a possible explanation for the greater frequency of purple and white with purple spiders in the study site (Rodríguez-Morales 2015). Although these results are consistent with the results obtained from the chromatic and achromatic contrasts of the spiders on the flower heads by the visual system of honeybees, these ideas need to be tested further with controlled behavioral experiments.

Since the visual acuity of honeybees is limited, especially in comparison to that of vertebrates (Land and Nilsson 2002; Caves et al. 2018), it is unlikely that honeybees can recognize the shape of the spiders at a distance. Plants enhance their floral display by color patterns and morphological features to facilitate detection and pollination by insects (Hempel de Ibarra et al. 2015). Therefore, spiders might be able to exploit particular features of flowers that are easier to detect at larger distances and that target visually guided behaviors of pollinators (Hempel de Ibarra et al. 2015). Such features could be strong contrasts created by UV reflection or the presence of "dark spots" in some particular parts of the flowers, both of which have been observed to attract honeybees (Dafni and Giurfa 1999, Vieira et al. 2017).

Our results suggest that *M. dubia* spiders are conspicuous or cryptic depending on the area where they are on the flower head of *P. lindenii*. In general terms, spiders of different morphs have the capability to switch between conspicuousness and camouflage based on their location over the flower head. This suggests that *M. dubia* spiders are using two strategies resulting in dynamic crypsis based on position, similar to what has been reported for cinnabar moth caterpillars (Barnett et al. 2018). Therefore, the conjunction of color polymorphism, position, and differential theoretical detectability at different distances results in a highly dynamic strategy that may not only optimize the probability of prey capture but also diminish the probability of prey learning.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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