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Background colour matching by a crab spider in the field: a community sensory ecology perspective

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SUMMARY

The question of whether a species matches the colour of its natural background in the perspective of the correct receiver is complex to address for several reasons; however, the answer to this question may provide invaluable support for functional interpretations of colour. In most cases, little is known about the identity and visual sensory abilities of the correct receiver and the precise location at which interactions take place in the field, in particular for mimetic systems. In this study, we focused on *Misumena vatia*, a crab spider meeting the criteria for assessing crypsis better than many other models, and claimed to use colour changes for both aggressive and protective crypsis. We carried out a systematic field survey to quantitatively assess the exactness of background colour matching in *M. vatia* with respect to the visual system of many of its receivers within the community. We applied physiological models of bird, bee and blowfly colour vision, using flower and spider spectral reflectances measured with a spectroradiometer. We observed that crypsis at long distance is systematically achieved, exclusively through achromatic contrast, in both bee and bird visions. At short distance, *M. vatia* is mostly chromatically detectable, whatever the substrate, for bees and birds. However, spiders can be either poorly discriminable or quite visible depending on the substrate for bees. Spiders are always chromatically undetectable for blowflies. We discuss the biological relevance of these results in both defensive and aggressive contexts of crypsis within a community sensory perspective.

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Key words: background colour matching, bee vision, mimetism, crab spider, *Misumena vatia*, crypsis, sensory ecology.

INTRODUCTION

Crypsis through background matching has been reported for a wide range of animals, including both vertebrates and invertebrates (Marshall, 2000; Ruxton et al., 2004; Mäthger et al., 2008; Stuart-Fox et al., 2008). Background matching is defined as a strategy preventing detection by changing the colour and patterning of the body to match those of the background (Stevens and Merilaita, 2009). Many species have been described as cryptic on the basis of human vision but colour contrast, which involves both chromatic and/or achromatic contrasts, has rarely been tested from the perspective of the usual receiver and in natural conditions (Stevens and Merilaita, 2009). There are several reasons for this lack of data: (i) the correct prey and/or predators of the 'cryptic' organism may not yet be clearly identified, (ii) the assessment of chromatic and/or achromatic contrast(s) in the prey/predator visual system requires knowledge of the physiological basis of both types of contrasts in the species concerned, particularly in terms of the number and nature of the different photoreceptor types. These physiological works must be supplemented by (iii) behavioural studies, which are also required to determine not only whether true colour vision and colour blind mechanisms are used by an observer but also the colour discrimination thresholds. True colour vision is the ability to discriminate between two lights of different spectral compositions, regardless of their relative intensity (Kelber et al., 2003), and colour discrimination threshold is defined as the lowest contrast between two stimuli that can be detected by an observer. Spectral sensitivities are known for a wide range of species but both true colour vision and colour discrimination thresholds have been studied in detail in only a few species, including bird and bee species (Menzel and Backhaus, 1989; Vorobyev and Osorio, 1998; Hart et al., 2000). Moreover, cryptic animals are rarely caught in the act of either catching prey (for cryptic predators) or escaping detection (for cryptic prey). As a corollary, the location at which the interaction occurs is known only imprecisely and is described in broad, generic terms (e.g. 'rocks', 'grasses'). This may be problematic in cases in which the substrate colour and patterns vary over short distances within the range of habitat use of the cryptic species. A survey of the literature shows that, unlike most background-matching species, crab spiders, including the species we will focus on, *Misumena vatia* (Araneae, Thomisidae), meet the criteria for addressing questions of this kind better than many other models (Théry et al., 2010). They are mainly sedentary and are found in large numbers on flowers. Moreover, one of the main prey of the crab spiders such as *M. vatia*, besides flower-visiting flies, is foraging bees (see Table S1 and Table S2 in supplementary material), the colour vision of which has been studied in detail.

Misumena vatia has been studied for more than a century, due to their amazing ability to be the same colour as the colour of some of the flowers on which they hunt (Heckel, 1891; Weigel, 1941; Insausti and Casas, 2008; Insausti and Casas, 2009) (reviewed in Théry and Casas, 2009). This apparent colour matching is particularly spectacular because it involves a change in the colour of the entire body from white to yellow (and back) over the space of a few days, depending on the colour of the flower (Weigel, 1941;

Théry, 2007). It is widely assumed that this apparent flower matching is not only a form of aggressive mimicry against nectar- and pollen-feeding prey but also a form of defensive mimicry, especially against birds. This is an assumption, as exceedingly few bird attacks have been reported so far, despite intense sampling of gut contents (Bristowe, 1971) and decades of long field work (Morse, 2007). Studies with bee physiological vision models recently revealed that *M. vatia* can produce both chromatic and achromatic contrasts well below the discrimination thresholds of their Hymenopteran prey (Chittka, 2001). At first sight, these results are thus consistent with the above hypothesis of crypsis against prey. However, chromatic and achromatic matching have been quantitatively assessed in *M. vatia* on two flower species only (*Chaerophyllum temulum* and *Senecio vernalis*) (Chittka, 2001) and for two individual spiders only. *Misumena vatia*, however, has been detected on a much wider range of flower species in the field (Heckel, 1891; Rabaud, 1923; Weigel, 1941). Moreover, crab spiders ambush numerous prey species (Fig. 1), with different visual abilities.

We therefore carried out a systematic field survey in a given geographical region, using a statistical test, to produce a quantitative assessment of the exactness of the colour matching of *M. vatia* on all flower species on which spiders were observed, with respect to the visual system of not only their main putative predator, insectivorous birds, but also their main prey, bees and flies.

MATERIALS AND METHODS

Spider and flower collection

Juvenile and adult female *Misumena vatia* Clerck 1757 crab spiders were collected from all of the flower species on which *M. vatia* was observed at various sites in the surroundings of Tours (47°20′18″N, 00°42′52″E), France, from April to October, in 2007 and 2008. All of the flowers of each patch were carefully inspected to prevent sampling bias. Once caught, the spiders and the flowers on which they were sitting were placed in a plastic box with a piece of damp cotton wool and transferred to the laboratory. We measured the reflectance of the spiders and the flowers on the same day. We also measured the length of the prosoma to test whether a relationship between the stage of development and the contrasts on the substrate occurred in the field.

Misumena vatia goes through seven juvenile instars, the first of which is spent in the egg sac (Gertsch, 1939). We captured spiders with a prosoma size ranging from 1 mm (fourth juvenile instar) to 3 mm (adults). Total size (prosoma + opisthosoma) varied between 2.5 mm and 12 mm. Second and third instar spiders were not captured, as their abdomen dimensions were smaller than the diameter of the optic sensor. We collected 75% (110/146) of the spiders studied on ‘white’ flowers whereas only 18% were caught on ‘yellow’ flowers and 7% on ‘red’ and ‘blue’ flowers. This heterogeneity did not result from a sampling bias. Indeed, large numbers of ‘yellow’-flowered species were carefully inspected without the detection of *M. vatia*. Among these 146 spiders, 20 were found only once or twice on a specific flower species. We decided that only flower species on which at least five spiders were found would be included in the analysis. Thus, crypsis in the perspective of the receivers was analysed on 126 spiders found on six flower species. Spiders hunting on *Filipendula ulmaria* Maximowicz 1879 (‘Meadow sweet’) and *Senecio* sp. L. (‘Ragwort’) were collected from homogeneous patches, consisting of single flower species whereas spiders found on *Achillea millefolium* L. (‘Common yarrow’), *Heracleum sphondylium* L. (‘Common hogweed’) and *Cleome spinosa* L. (‘Spiny spiderflower’) were collected from heterogeneous patches, consisting of at least two flower species. *Leucanthemum vulgare* Lamarck 1779 (‘Oxeye daisy’) was the only plant species from which spiders were collected in both homogeneous and heterogeneous patches. Spiders were caught in eight different patches. The smallest patch had an area of 20 m × 20 m. All of the spiders collected were found on the flower petals.

Spectroradiometric measurements

We measured the reflectance of both spiders and flowers with a spectroradiometer (Avantes Avaspec 256, Eerbeek, The Netherlands) and a deuterium–halogen lamp (Avantes Avalight D/H-S) emitting light of wavelengths between 215 nm and 1100 nm. Reflectance was expressed relative to a 99% (300–700 nm) reflectance standard. A reference reading was taken, and dark current calibration was carried out before taking the measurements for each spider and each flower. An optic fiber sensor 1.5 mm in diameter and equipped with a quartz window cut at a 45 deg. angle was used. Spiders were anesthetised with CO_2 before recordings of the reflectance spectrum of the

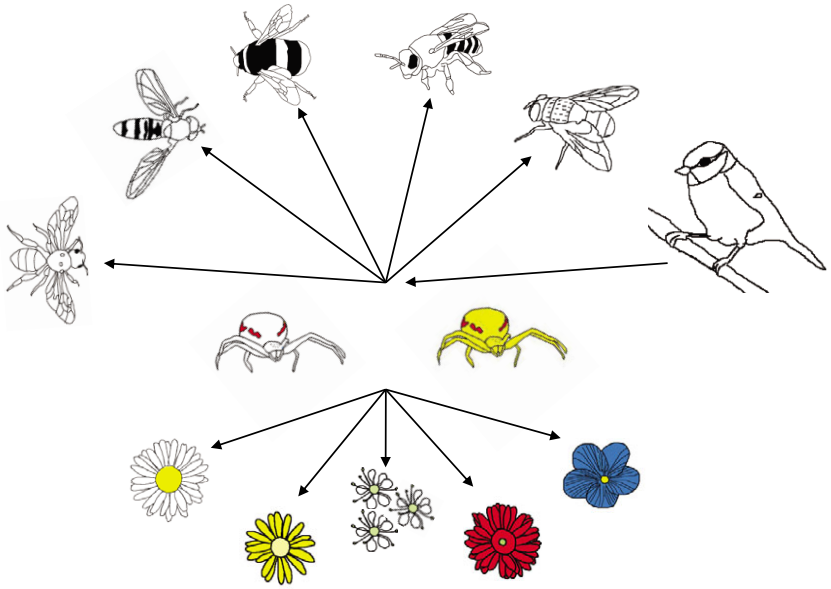

Fig. 1. Schematic representation of both multi-substrate and multi-receiver communities considered in this study. From left to right: *Halictus sp.* (solitary bees), *Episyrphus sp.* (Syrphid flies), *Bombus terrestris* (bees), *Apis mellifera* (bees), *Lucilia sp.* (blowfly) and blue tit (Passeriformes). The represented abstract flower colour types on which *Misumena vatia* can be found are at the bottom.

abdomen were taken (Fig. 2A). Spiders and flowers were placed on a flat mounting stand for measurements. We assessed both chromatic and achromatic contrasts of each spider, by measuring the reflectance of the exact part of the flower on which *M. vatia* was found (Fig. 2B–D). We obtained three reflectance spectra for each abdomen and for each flower. A mean reflectance spectrum was then calculated for each spider and each flower.

Modelling chromatic and achromatic contrasts in both bee and bird visual systems

We measured the chromatic and achromatic contrasts created by *M. vatia* against its substrate using the physiological model developed by Vorobyev and Osorio (Vorobyev and Osorio, 1998; Vorobyev et al., 2001). The model developed by Chittka (Chittka, 1992) has also been widely used for assessments of the chromatic and achromatic contrasts of crab spiders against their substrates. However, the model of Vorobyev and Osorio (Vorobyev and Osorio, 1998) has the advantage of including a powerful colour discrimination threshold, as it includes the total receptor noise. Total receptor noise is the sum of photon ('quantum') noise and internal receptor ('neural') noise. Indeed, this physiological model, based on the observation that the ability to discriminate between colours is limited by total receptor noise, has been shown to predict well the ability to discriminate between colours in animals, including primates, birds and the honeybee *Apis mellifera*. The chromatic and achromatic contrasts between two spectra are measured in units of just noticeable difference (JND). A value of 1 JND between two spectra corresponds to the discrimination threshold under ideal conditions and under which two spectra are considered to be indistinguishable (Wyszecki and Stiles, 1982). The relationship between noise level and light intensity is however not linear (Anderson and Laughlin, 2000; Vorobyev et al., 2001), and this model does not incorporate physiological mechanisms that may affect colour discrimination such as spatial and temporal summation (Dyer and Neumeyer, 2005). Despite these shortcomings, Vorobyev and Osorio's model remains the most efficient colour vision model to date. In the following, we present the colour computation in the bee visual system first, followed by the bird vision system. The fly colour vision model, which is very different, is presented last.

The quantum catch Q for a given spectrum in the respective photoreceptor i is calculated as:

$$Q_i = \int_{300}^{700} R_i(\lambda)S(\lambda)I(\lambda)\mathrm{d}\lambda \,, \quad (1)$$

where R_i is the spectral sensitivity function of the ultraviolet (UV), Blue (B) and Green (G) receptors for trichromatic bees with sensitivity peaks at 340 nm, 435 nm and 540 nm, respectively (Peitsch et al., 1992). We used bee templates to obtain absorption curves (Stavenga et al., 1993). $S(\lambda)$ is the spectral reflection function of spiders or substrates, and $I(\lambda)$ is the illuminating daylight spectrum (CIE D65). Here we assume that almost all visual interactions occur in sunny daylight.

The colour distance ΔS, in JND units, between each spider and its flower, for the trichromatic eyes of bees, is given by:

$$(\Delta S)^2 = \frac{e_{\mathrm{UV}}^2(\Delta f_{\mathrm{G}} - \Delta f_{\mathrm{B}})^2 + e_{\mathrm{B}}^2(\Delta f_{\mathrm{G}} - \Delta f_{\mathrm{UV}})^2 + e_{\mathrm{G}}^2(\Delta f_{\mathrm{UV}} - \Delta f_{\mathrm{B}})^2}{(e_{\mathrm{UV}}e_{\mathrm{B}})^2 + (e_{\mathrm{UV}}e_{\mathrm{G}})^2 + (e_{\mathrm{B}}e_{\mathrm{G}})^2} \,, \quad (2)$$

where e_i is the internal receptor noise for each receptor class i of bees (UV, B, G) and Δf_i is the natural log of the quantum catches for receptor i (UV, B and G for bees) between spiders (Sp) and flowers (F):

$$\Delta f_i = \ln(Q_{i\mathrm{Sp}} / Q_{i\mathrm{F}}) \,. \quad (3)$$

Crab spider–prey interactions occur in conditions of high light intensity, and a large proportion of spiders were found on bright 'white' and 'yellow' flowers. Internal receptor noise is thought to predominate at high light intensity (Vorobyev et al., 2001). The internal receptor noise ei, is calculated as:

$$e_i = \omega / \sqrt{\eta_i} \,, \quad (4)$$

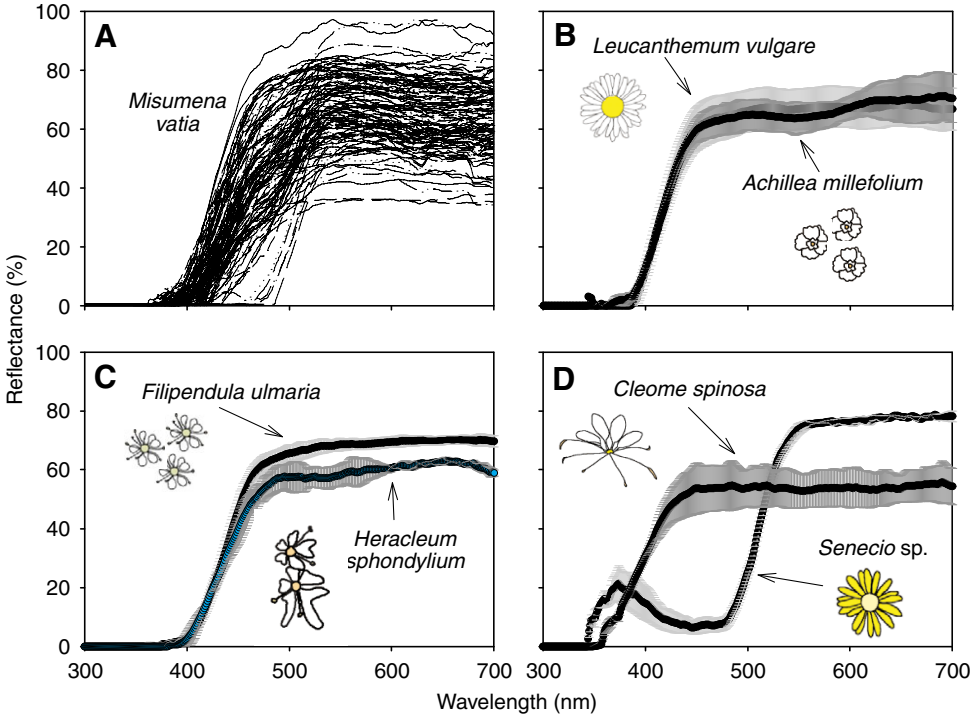

Fig. 2. Mean (±s.d.) reflectance spectra of *Misumena vatia* analysed in this study (A), and of the flower species used as substrate by *M. vatia* (B–D).

where ω is the Weber fraction assigned to each receptor class [0.13 (Vorobyev and Osorio, 1998)] and η_i is the relative density of the receptor class *i* of bees. Within a honeybee eye, ommatidia do not contain similar sets of photoreceptors. Wakakuwa et al. indeed found three types of ommatidia containing either one UV, one B and six G receptors (Type I), or two UV, one B and six G receptors (Type II), or one UV, two B and six G receptors (Type III) (Wakakuwa et al., 2005). They also revealed that the ratio of the Types I, II, III was 44:43:10 (Wakakuwa et al., 2005). Moreover, Spaethe and Briscoe showed that this heterogeneity also occurs in bumblebees (Spaethe and Briscoe, 2005). We thus used the ratio of 1:0.471:4.412 for all bees (for UV, B and G receptors, respectively). This ratio takes into account both the ommatidia heterogeneity and the ratio of Types I, II, III.

Chromatic contrast is the dominant cue used by foraging bees for the identification of flowers at short distance, when a flower subtends a visual angle of at least 15 deg. (Giurfa et al., 1996). However, at long distance, when a flower subtends a visual angle between 5 deg. and 15 deg., honeybees and bumblebees use green contrast for flower detection, looking for a difference between background and target green receptor signals (Giurfa et al., 1996; Spaethe et al., 2001).

The green contrast between a spider and its flower can be calculated as:

$$\Delta S_G = \Delta f_G / e_G = \ln (Q_{GSp} / Q_{GF}) / e_G , \quad (5)$$

in which S_G is the spectral sensitivity of the L-wavelength photoreceptor of bees. Δf_G is the natural log of the quantum catch (Q) for the Green ($_G$) receptor class between spider ($_{Sp}$) and flower ($_F$). Q_{GSp} and Q_{GF} are the quantum catch (Q) for a spider ($_{Sp}$) and a flower ($_F$) spectrum, respectively, in the Green ($_G$) receptor class of the bees. e_G is the internal receptor noise of the Green ($_G$) receptor class of bees.

For bird colour vision, we used the spectral sensitivities of the tetrachromatic insectivorous blue tit *Cyanistes caeruleus*, taking into account visual pigment, oil droplet and ocular media transmittances (Hart et al., 2000; Hart, 2001). Spectral sensitivity functions were taken directly from avian templates generously provided by Doris Gomez. The presence of blue tits has been reported in the meadows around Tours (Théry et al., 2005).

We measured the quantum catch (see Eqn 1) for a given spectrum in the ultraviolet sensitive (UVS), short-wavelength sensitive (SWS), medium-wavelength sensitive (MWS) and long-wavelength sensitive (LWS) photoreceptors of blue tits, as we did for bees.

The colour distance ΔS between each spider and flower for the tetrachromatic eyes of birds is given by:

$$(\Delta S)^2 = ((e_{UVS}e_{SWS})^2(\Delta f_{LWS} - \Delta f_{MWS})^2 + (e_{UVS}e_{MWS})^2 (\Delta f_{LWS} - \Delta f_{SWS})^2 + (e_{UVS}e_{LWS})^2 (\Delta f_{SWS} - \Delta f_{MWS})^2 + (e_{SWS}e_{MWS})^2 (\Delta f_{LWS} - \Delta f_{UVS})^2 + (e_{SWS}e_{LWS})^2 (\Delta f_{MWS} - \Delta f_{UVS})^2 + (e_{MWS}e_{LWS})^2 (\Delta f_{SWS} - \Delta f_{UVS})^2) / ((e_{UVS}e_{SWS}e_{MWS})^2 + (e_{UVS}e_{SWS}e_{LWS})^2 + (e_{UVS}e_{MWS}e_{LWS})^2 + (e_{SWS}e_{MWS}e_{LWS})^2) , \quad (6)$$

where e_i is the internal receptor noise for each receptor class *i* of birds (UVS, SWS, MWS and LWS) and Δf_i is the natural log of the quantum catches for receptor *i* (UVS, SWS, MWS and LWS) between Sp and F (see Eqn 3). The relative density of the receptor

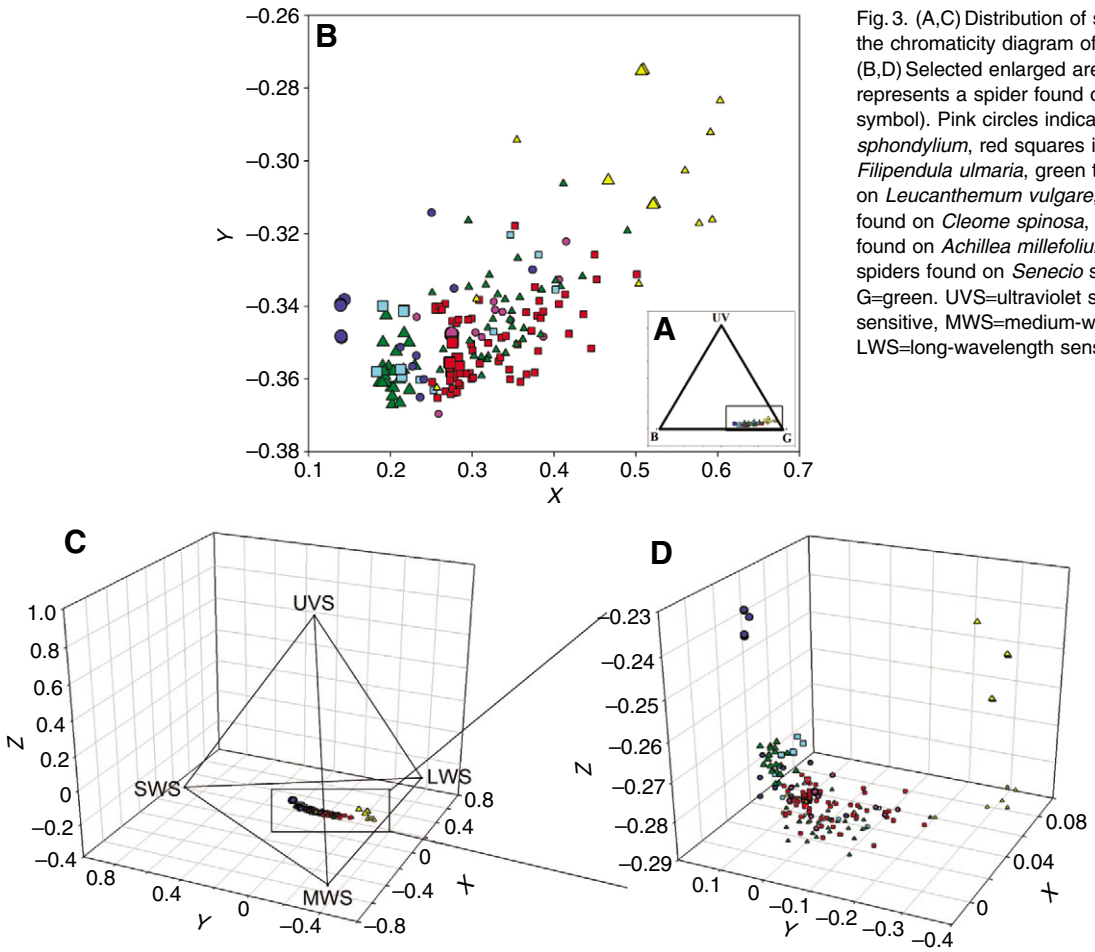

Fig. 3. (A,C) Distribution of spider and flower colour loci on the chromaticity diagram of bees (A) and birds (C). (B,D) Selected enlarged area. Each small coloured symbol represents a spider found on a flower species (larger symbol). Pink circles indicate spiders found on *Heracleum sphondylium*, red squares indicate spiders found on *Filipendula ulmaria*, green triangles indicate spiders found on *Leucanthemum vulgare*, blue circles indicate spiders found on *Cleome spinosa*, blue squares indicate spiders found on *Achillea millefolium*, yellow triangles indicate spiders found on *Senecio* sp. UV=ultraviolet, B=blue, G=green. UVS=ultraviolet sensitive, SWS=short-wavelength sensitive, MWS=medium-wavelength sensitive, and LWS=long-wavelength sensitive.

class *i* taken from *Pareus caeruleus* was 1, 1.92, 2.68 and 2.7 for UVS, SWS, MWS, LWS photoreceptors, respectively (Maier and Bowmaker, 1993). We also achieved the calculations with different photoreceptor ratios [1, 2, 2, 4 (Schaefer et al., 2007); 1, 1, 1, 2 (Lind and Kelber, 2009)] to assess how sensitive the results are to this choice.

For the receptor noise value in birds, we proceeded as Schaefer et al. (Schaefer et al., 2007). Our reasoning was that not only (i) are the noise levels in avian photoreceptors still unclear (Lind and Kelber, 2009), but also that (ii) the absolute value of noise varies quite a lot, depending on the viewing conditions (Ghim and Hodos, 2006; Schaefer et al., 2007; Harmening et al., 2009). We thus performed calculations with several values of Weber fraction. Increase of the Weber fraction results in a corresponding increase of the threshold value in JND. The lowest Weber fraction was estimated as 0.1 from behavioural data (Maier and Bowmaker, 1993) and corresponds to a threshold of 1 JND. Because noise above 0.5 is physiologically implausible, we assumed that Weber fraction can increase up to 0.5, which corresponds to a threshold of 5 JNDs. We assumed that spiders with a contrast against their substrates higher than 5 JNDs can always be detected.

Birds use also achromatic contrast at long range (Osorio et al., 1999a; Osorio et al., 1999b), through double-cones. Thus, the achromatic contrast between a spider and its substrate is then measured as:

$$\Delta S_{DC} = \Delta f_{DC} / e_{DC} = \ln (Q_{DC-Sp} / Q_{DC-F}) / e_{DC} , \quad (7)$$

in which S_{DC} is the spectral sensitivity of the double-cone photoreceptors of birds. Δf_{DC} is the natural log of the quantum catch for the double cone ($_{DC}$) receptor class between spider ($_{Sp}$) and flower ($_{F}$). $Q_{DC\text{-}Sp}$ and $Q_{DC\text{-}F}$ are the quantum catch (Q) for a spider ($_{Sp}$) and a flower ($_{F}$) spectrum, respectively, in the double cone ($_{DC}$) receptor class of the birds. e_{DC} is the internal receptor noise of the double cone ($_{DC}$) receptor class of birds. Chromatic and achromatic contrasts were calculated with Avicol© software (Paris, France; available upon request from D. Gomez at dodogomez@yahoo.fr) (Gomez and Théry, 2007).

We plotted the position of each flower and spider in the chromaticity diagram of both bees and birds, following the calculation given in Kelber et al. (Kelber et al., 2003). Trichromatic bees have a two-dimensional chromaticity diagram (Fig. 3A,B) whereas it is three-dimensional for tetrachromatic birds (Fig. 3C,D).

We also performed a more complex analysis using an assumption about bird vision, which is natural but will need further testing. Studies have shown that the contrast threshold of birds is strongly affected by viewing conditions, especially the spatial frequency of the stimuli (Ghim and Hodos, 2006; Harmening et al., 2009). Indeed, contrast sensitivity functions display an inverted-U shape (Ghim and Hodos, 2006; Harmening et al., 2009). In the case of the motionless *M. vatia*, each spatial frequency corresponds to a specific distance at which birds observe spiders. These studies thus provide contrast threshold according to a wide range of distances. However, contrast thresholds are given in 'Michelson contrast' values that cannot be used in the model developed by Vorobyev et al. (Vorobyev et al., 2001). Using the method described below, we thus transformed contrast threshold values into Weber fractions that can be integrated into the model developed by Vorobyev et al. (Vorobyev et al., 2001).

We first determined the contrast discrimination threshold (the inverse of contrast sensitivity) for each distance from a bird to a spider. Generally, the contrast discrimination threshold for a given spatial frequency corresponds to the lowest Michelson contrast (luminance max. – luminance min.) / (luminance max. + luminance min.) at which maximum contrast sensitivity occurs. In the starling, the maximum contrast sensitivity has a Michelson contrast value of 16% for 1.1 cycles deg.$^{-1}$ (Ghim and Hodos, 2006). We created two spectral reflectance curves that display not only a Michelson contrast of 16% but also a LWS receptor contrast equal to 16%, because Weber fraction are often calculated from LWS class cone (Vorobyev et al., 1998).

We assumed that these two spectra computed with the 'limiting Weber fraction' in Vorobyev and Osorio's model (Vorobyev and Osorio, 1998) should have an achromatic contrast equal to 1 JND. Thus, by identifying the 'Weber fraction' that allows us to get an achromatic contrast between these two spectra equal to 1 JND, we also identify the 'limiting Weber fraction' at which the maximum contrast sensitivity occurs (16%). In this study, we used the maximum contrast sensitivity of the starling (16% at 1.1 cycles deg.$^{-1}$), as no such data exist for *C. caeruleus*.

We estimated the most relevant range of 'Weber fraction' to use by referring to contrast threshold values computed in the starling *Sturnus vulgaris* (Passeriformes) (Ghim and Hodos, 2006). Following the same steps as above, we also calculated the Weber fractions at the lowest (0.3 cycles deg.$^{-1}$) and highest (7 cycles deg.$^{-1}$) spatial frequencies at which the lowest contrast sensitivities occur. We thus found a set of 'Weber fractions', ranging from 0.2 to 0.5, which is close to the range used by Schaefer et al. (Schaefer et al.,

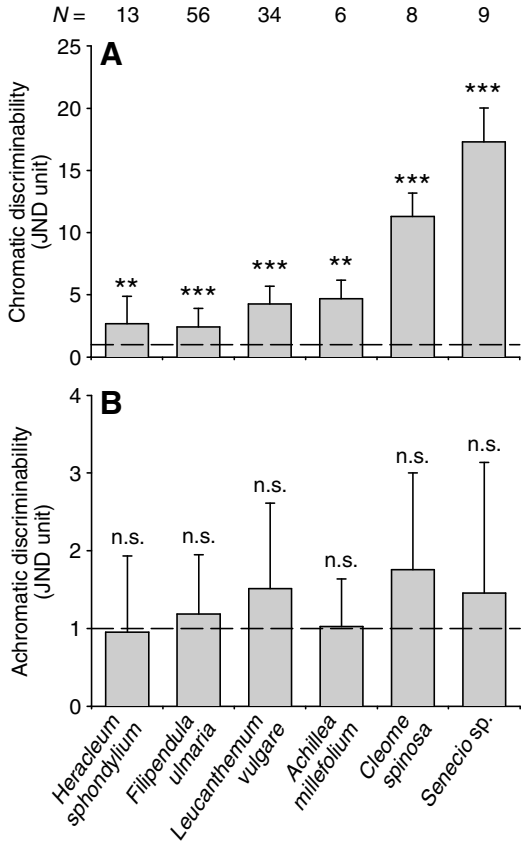

Fig. 4. Mean (±s.d.) chromatic (A) and achromatic (B) discriminability, measured in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for the trichromatic prey, bees. Horizontal broken lines indicate the threshold for crypticity in the bee's visual system. Note the difference in scale on the *Y*-axis of the two graphs. n.s.=non significant. ***P*<0.01, ****P*<0.001.

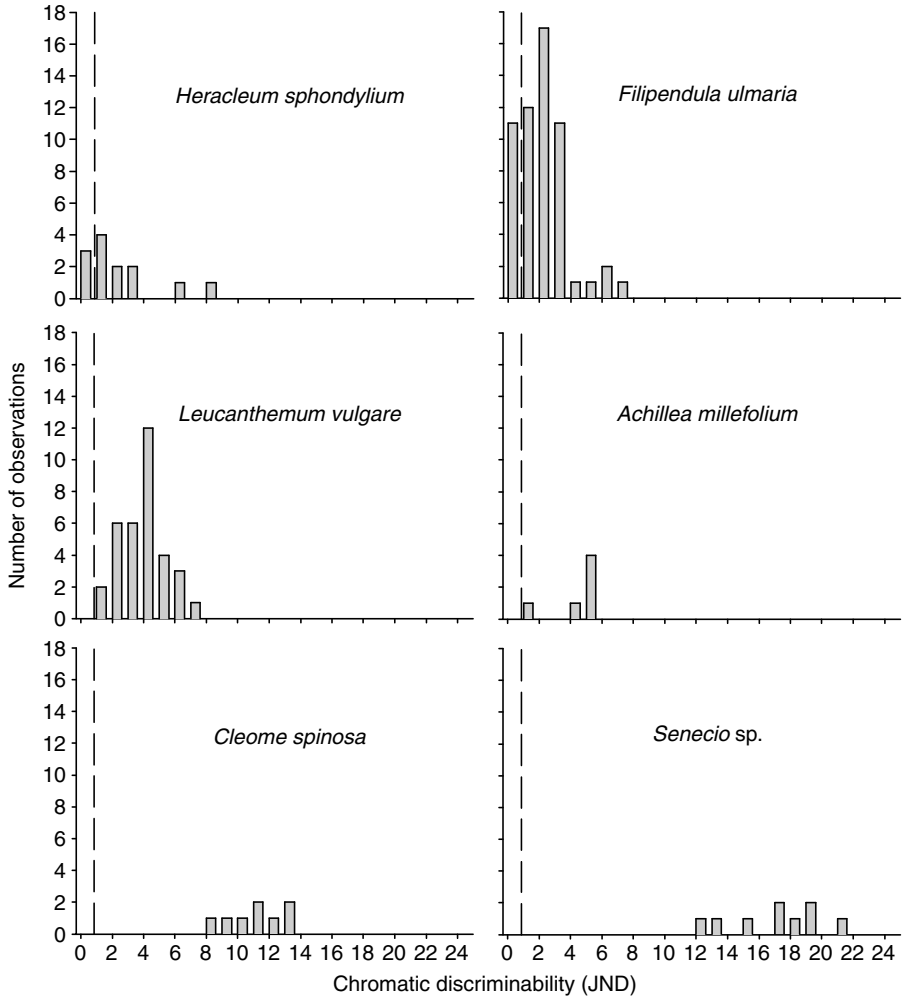

Fig. 5. Individual chromatic discriminability distribution, in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for bee vision. Vertical broken lines indicate the threshold for crypticity in the bee visual system.

2007). On the basis of an 8 mm size for spiders, we finally assessed the distance of birds to spiders corresponding to each spatial frequency.

Assessing chromatic contrast in the fly visual system

Classical colour vision models used for bees or birds do not fit the vision of flies, despite good knowledge of spectral sensitivities of several fly species (Horridge et al., 1975; Bernard and Stavenga, 1979; Hardie, 1979; Hardie and Kirschfeld, 1983), and receptor noise values of fly photoreceptors involved in the colour vision process (Anderson and Laughlin, 2000). Indeed, whereas bees and birds display a continuous colour vision, Troje showed that the flower-visiting blowfly *Lucilia* sp. possesses a categorical colour vision (Troje, 1993). For this species, the wavelength spectrum consists of four categories (UV, Blue, Yellow and Purple). *Lucilia* sp. discriminated monochromatic lights belonging to different categories. However, no discrimination occurs within a category. Troje (Troje, 1993) proposed a colour opponent mechanism that matches its result well. Despite the fact that this model needs to be further tested and improved, we use it because (i) it is, to our knowledge, the single one available for any fly, (ii) it is based on behavioural experiments, and (iii) *Lucilia* sp. is a flower-visiting species that may suffer predation by crab spiders.

This model involves four types of central photoreceptors, named R7p, R7y, R8p and R8y, with a peak at 341 nm, 362 nm, 465 nm and 537 nm, respectively (Hardie and Kirschfeld, 1983). The model consists of two subsystems made of the pairs R7p/R8p and R7y/R8y, R7 and R8 being antagonistically connected in each one. The differences R7–R8 gives input to a threshold mechanism such that each subsystem can have one of the two values (+, –). Each combination of values (+/+, +/–, –/+, –/–) corresponds to a specific category. For each stimulus, we thus calculated the differences 'R7p–R8p' and 'R7y–R8y'. Two stimuli eliciting the same combination of values are considered as similar for *Lucilia* sp.

The quantum catch for a given spectrum in the respective fly photoreceptors is calculated as in Eqn 1 (see above), and spectral sensitivities of *Lucilia* sp. are taken from Hardie and Kirschfeld (Hardie and Kirschfeld, 1983). We used templates fitted to *Lucilia*'s spectral sensitivities (Stavenga et al., 1993). We did not compute the achromatic contrast for blowflies, as nothing is known about this aspect in flies.

Is perfect chromatic matching due to chance only?

We investigated whether perfect chromatic matching (JND<1) on the whitish *F. ulmaria* (harbouring the largest number of spiders) was due to chance alone, by first calculating the chromatic discriminability, against *F. ulmaria*, of the spiders found on other flower species. We then compared the proportion of undetectable spiders in the simulated spider–*F. ulmaria* pairs with the proportion of undetectable spiders actually found on *F. ulmaria*. We assumed that if the observed matching was due to chance alone, the proportions

of undetectable spiders would be similar in both sets of spiders. Thus, in this case, spiders hunting on flower species other than *F. ulmaria* would have matched *F. ulmaria* petals equally well as spiders hunting on *F. ulmaria*. A mean colour spectrum of *F. ulmaria* was used to measure chromatic contrast in the two sets of spiders. The same protocol was tested with the whitish *H. sphondylium*, the flower species harbouring the second largest number of spiders.

Statistical analysis

We used various statistical tests to compare mean contrast values with chromatic and achromatic discrimination thresholds for bee and bird colour visions. We first tested the normality of distributions, using the Shapiro test, and then performed one-sample *t*-test for normally distributed variables and the non-parametric rank sign test for variables with non-normal distributions. We also assessed whether the proportions of perfect chromatic matching between two distributions were similar using a normal approximation of the chi-squared test. All statistical analyses were performed with *R* and Statistica (Statsoft France, France).

RESULTS

Chromatic and achromatic contrast values for bees

We observed no correlation between the stage of spider development and both the chromatic and achromatic contrast values (R^2=0.0221, P=0.14 and R^2=0.034, P=0.10, respectively; N=126). We analysed the chromatic and achromatic discriminabilities using first the mean contrast values. The mean chromatic contrast values are above the discrimination threshold (1 JND) (*t*-test, P<0.01 for *H. sphondylium*; sign test, P<0.001 for *F. ulmaria*; sign test, P<0.001 for *L. vulgare*; *t*-test, P<0.01 for *A. millefolium*; *t*-test, P<0.001 for *C. spinosa*; sign test, P<0.001 for *Senecio* sp.) (Fig. 4A). Mean achromatic discriminability values for the spiders did not significantly exceed the discriminability threshold value (1 JND) in honeybees (sign tests: P=0.86, P=0.17, P=0.11, P=0.74 for *H. sphondylium*, *F. ulmaria*, *L. vulgare* and *Senecio* sp., respectively; *t*-tests: P=0.84, P=0.13 for *A. millefolium*, *C. spinosa*, respectively). Thus, *M. vatia* would not be detected by the green receptor of bees at long range (Fig. 4B). To sum up the results for mean contrast values, we show that spiders always appear detectable at short range but undetectable at long distance for bees.

If we consider individual chromatic contrast between pairs (Fig. 5), the situation is more complex than that described above on the basis of mean values. Spiders may be either perfectly cryptic (undetectable spiders have values that are <1 JND) or poorly discriminable (pairs with values between 1 and 4 JNDs) on *H. sphondylium* (23% and 61%, respectively) or *F. ulmaria* (19% and 71%, respectively). On *L. vulgare*, *A. millefolium*, *C. spinosa* and *Senecio* sp., respectively, 47%, 33%, 0%, 0% of pairs produce values between 1 and 4 JNDs but no perfect chromatic matching was observed. All spiders hunting on *C. spinosa* and *Senecio* sp. appear quite visible (JND>4) for bees.

A similar analysis with achromatic contrast distributions revealed low levels of variability in individual pairs (data not shown) and a larger proportion of spiders near the discrimination threshold of bees (0<JND<4) (100%, 100%, 97%, 100%, 87%, 88% for *H. sphondylium*, *F. ulmaria*, *L. vulgare*, *A. millefolium*, *C. spinosa* and *Senecio* sp., respectively), in contrary to what was found for chromatic contrast.

Finally we observed no difference in the degree of contrast between spiders hunting on a given species in either homogeneous or heterogeneous floral patches.

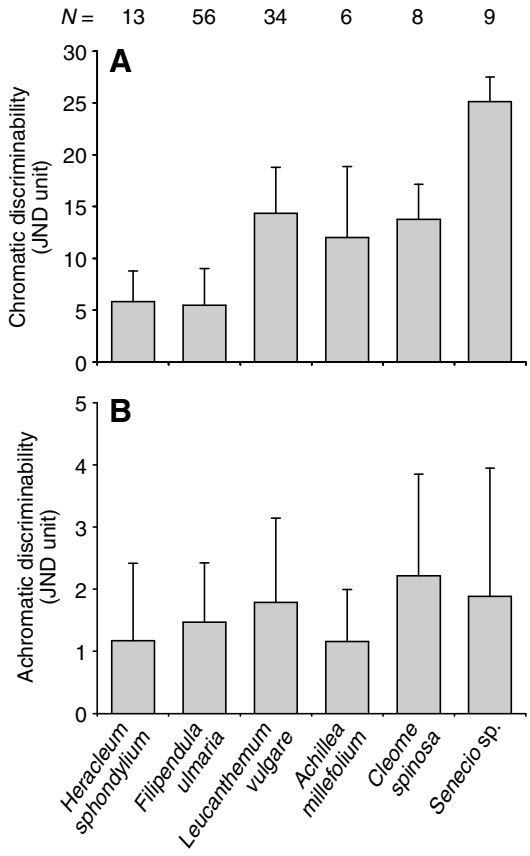

Fig. 6. Mean (±s.d.) chromatic (A) and achromatic (B) discriminability, measured in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for a tetrachromatic passerine bird. JNDs of 1 to 5 represent the range of most likely threshold values obtained in the literature.

Chromatic and achromatic contrast values for birds

Our results revealed that, at short distance, *M. vatia* can be always chromatically detected on *L. vulgare*, *A. millefolium*, *C. spinosa* and *Senecio* sp. by birds, as their mean chromatic contrasts are significantly higher than 5 JNDs (P<0.01, *t*-test for *A. millefolium*; P<0.001 *t*-tests for *L. vulgare*, *C. spinosa*, and for *Senecio* sp., sign test). Spiders hunting on *H. sphondylium* and *F. ulmaria* will be also detectable, except if receptor noise reaches values of 0.45 (P=0.051 for *H. sphondylium*, *t*-test and P=0.13 for *F. ulmaria*, sign test) (Fig. 6A). At long distance, we observed that *M. vatia* is achromatically undetectable whatever the flower species and the value of noise. Indeed, mean achromatic contrasts did not differ significantly from 1 JND (Fig. 6B).

Individual chromatic contrast values allowed us to confirm that on each flower, a high proportion of spiders are always chromatically detectable (higher than 5 JNDs) (53%, 48%, 94%, 83%, 100% and 100% for *H. sphondylium*, *F. ulmaria*, *L. vulgare*, *A. millefolium*, *C. spinosa* and *Senecio* sp., respectively) (Fig. 7). All of these conclusions remained valid when calculations are performed with different photoreceptor ratios (1, 2, 2, 4 and 1, 1, 1, 2 for UVS, SWS, MWS, LWS, respectively).

We obtained similar results when taking into account the distance at which birds forage (Fig. 8). Indeed, *M. vatia* is detectable at short distance through chromatic signal. However, we noticed that this chromatic contrast is quite dependent of the foraging distance. On all of the flower species, *M. vatia* is most conspicuous when birds are 50 cm away from spiders. At very short distance (16 cm), at which

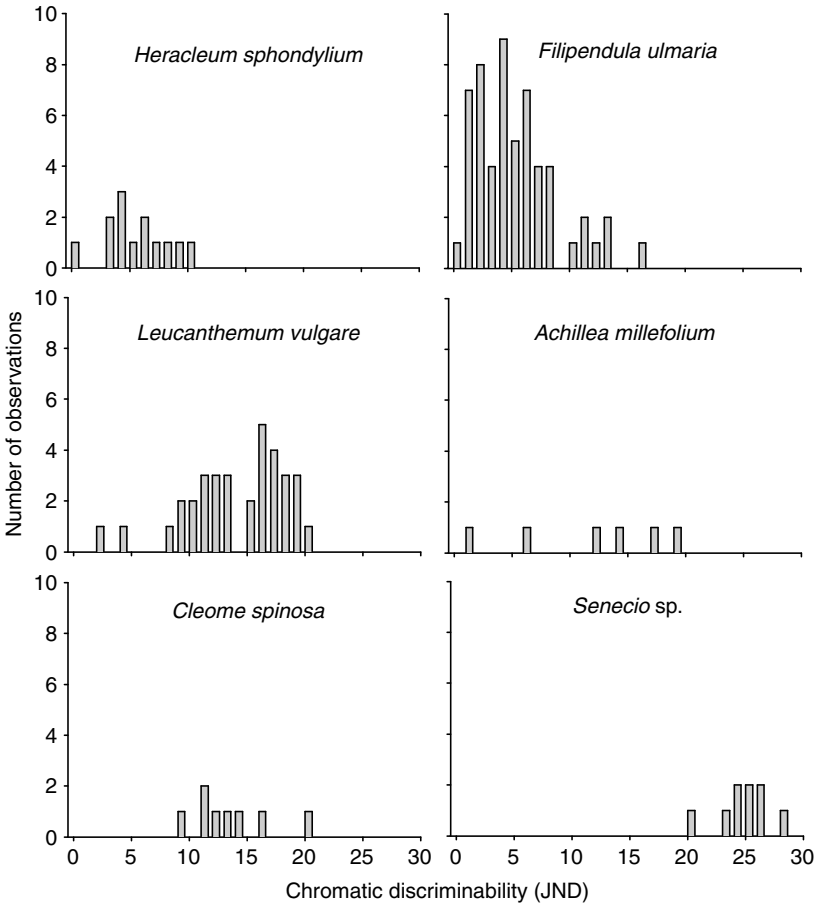

Fig. 7. Individual chromatic discriminability distribution, in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for bird vision.

chromatic signal should be used, we observed that *M. vatia* is always detectable. At the opposite, *M. vatia* is always achromatically undetectable whatever the distance at which it is observed by birds, especially at long distances when achromatic signals are most relevant.

Chromatic contrast in the fly visual system

Using the colour opponent model developed by Troje (Troje, 1993), we found that all spiders would appear cryptic for *Lucilia* sp., both spiders and substrates being ranked as (+/+) in the fly vision (N=126).

Proportions of perfect chromatic matching for simulated spider–flower pairs in bee visual system

We showed that perfect chromatic matching occurred in assessments of the chromatic contrast of spiders found on different flower species against petals of *F. ulmaria*. The proportion of matching did not differ significantly between spiders actually hunting on *F. ulmaria* and spiders initially found on the flowers of other species and then randomly assorted to *F. ulmaria* (11/56 and 12/70, respectively, d.f.=124, P=0.77). Similar proportions of undetectable spiders were also obtained between spiders initially hunting on *H. sphondylium* in assessments of the chromatic discriminability of spiders found on other flower species with respect to those on *H. sphondylium* (3/13 and 20/113, respectively, d.f.=124, P=0.59).

DISCUSSION

We observed that crypsis at long distance is systematically achieved, exclusively through achromatic contrast, in both bee and bird visions. At short distance, *M. vatia* is mostly chromatically detectable whatever the substrate for bees and birds. However, spiders can be either poorly discriminable or quite visible depending on the substrate for bees (Table 1). Indeed, *M. vatia* hunts sometimes on flowers on which it yields a high chromatic contrast for bee vision whereas other flowers provide substrate on which perfect chromatic crypsis can be achieved. The same trend was already suggested using Chittka's model but with two spider individuals only (Chittka, 2001). We show that these perfect matchings (JND<1) result from a purely random process, implying no particular local adaptation of the spiders to their flowers. This explains the small number of perfectly cryptic spiders observed in this study. A model proposed that colouration in a visually heterogeneous habitat can be optimised by either finding a compromise in the degree of crypsis between microhabitats or by increasing the degree of crypsis in one of the microhabitats at the expense of another (Merilaita et al., 2001). Here, we noticed that it is unlikely that the resulting colouration of *M. vatia* is a form of crypsis optimised for visually heterogeneous environments. Unlike for bees and passerine birds, chromatic crypsis seems to be always achieved for the blowfly *Lucilia* sp. In the following, we focus on both the chromatic and achromatic contrasts elicited by *M. vatia* and discuss their biological relevance in defensive and aggressive mimicry contexts.

Is crypsis at long distance sufficient to avoid bird attacks?

Our results suggest that the detectability of *M. vatia* through chromatic signal varies according to the distance at which passerine birds forage. *Misumena vatia* appears chromatically visible at short distance for insectivorous passerines on the substrate on which it

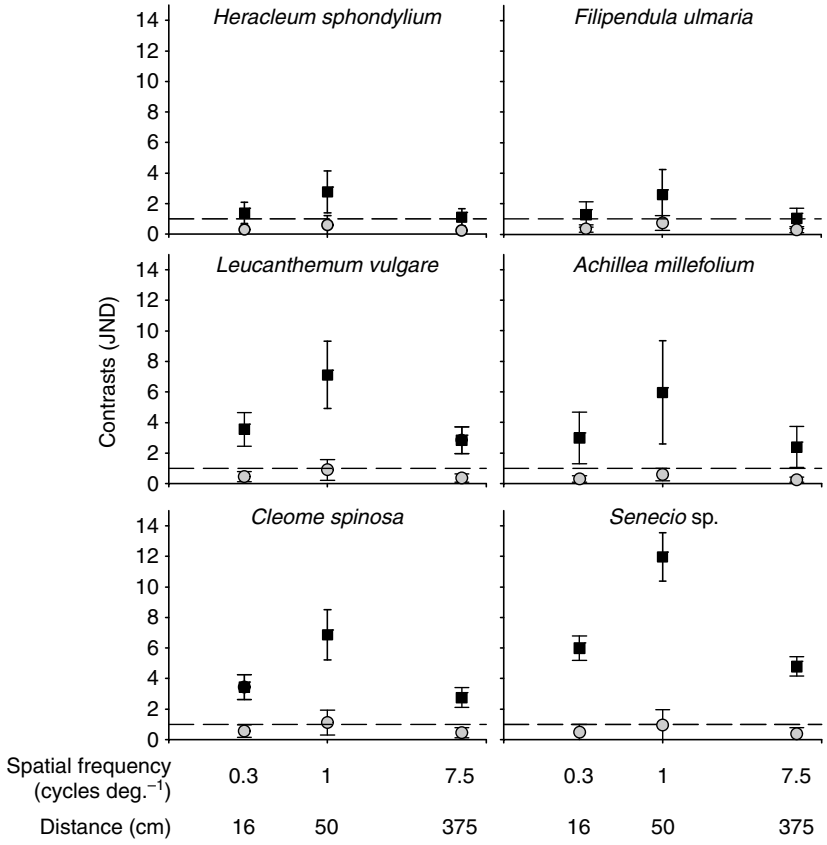

Fig. 8. Mean (±s.d.) chromatic (black squares) and achromatic (grey circles) contrasts of spiders against different substrates in the perspective of birds, according to different spatial frequencies. On the basis of 8 mm-long spiders, we also assessed the distance of birds to spiders corresponding to each spatial frequency. A logarithmic scale is used for the *x*-axis.

sits. Despite this chromatic conspicuousness, the predation pressure from birds on *M. vatia* is very low. Indeed, Morse (Morse, 2007) has not recorded any case of bird predation in 30 years of intensive field research on crab spiders. Moreover, Bristowe's (Bristowe, 1971) records of over 10,000 spiders eaten by birds from sampling their stomach contents contain only four *M. vatia*, a very low number. Thus, these observations indicate that the lack of predation cannot be explained by vision at short distance. This raises the question whether bird attacks are low because birds are actually avoiding visible *M. vatia* or because protection is efficiently achieved through achromatic crypsis at long distance? Answering this question will require us not only to quantify the range of visual angles at which chromatic signals are used but also to relate the foraging paths taken by birds in the vegetation to the positions of their prey.

Are *M. vatia* under selection by prey for crypsis?

Bees, when reaching a new patch, detect flowers first through the achromatic signal (Spaethe et al., 2001), according to the visual angle at which chromatic vision may occur [>15 deg. honeybees (Giurfa et al., 1996)] and their spatial resolution (2.8 deg. × 5.4 deg. in honeybees; 5 deg. in bumblebees) (Autrum and Wiedemann, 1962; Eheim and Wehner, 1972; Meyer-Rochow, 1981). However, within a patch, bumblebees forage with a flight height ranging from 23 mm to 50 mm, depending on the flower diameter (Spaethe et al., 2001). From these data, it is likely that both chromatic and achromatic contrasts elicited by spiders are noticed by prey.

Other crab spider species have been reported to be either chromatically cryptic on a substrate in the perspective of bees, as for *Thomisus onustus* (Théry and Casas, 2002; Théry et al., 2005), or achromatically cryptic, as for the Australian crab spider *Thomisus spectabilis* (Heiling et al., 2005). However, there is a lack of knowledge about the role of the chromatic and achromatic crypsis in the prey capture rate and survival rate against birds. Indeed, despite the growing number of studies using crab spider–prey interactions, there is not yet any evidence, for any prey, that decreasing chromatic and/or achromatic contrasts provides the spider with a benefit in terms of predation efficiency (Gonçalves-Souza et al., 2008; Yokoi and Fujisaki, 2009; Brechbühl et al., 2010a;

Table 1. Detectability of *Misumena vatia* according to the distance at which it is perceived for different visual observers

	Short distance		Long distance	
	Chromatic contrast	Achromatic contrast	Chromatic contrast	Achromatic contrast
Bees	Mostly detectable	⊘	⊘	Undetectable
Blowfly	Undetectable	?	?	?
Blue tits	Mostly detectable	⊘	⊘	Undetectable

Cross circles indicate no neurophysiological relevant situations. Question marks indicate that there is a lack of study allowing us to fill in the boxes. Distances are relative distances. However, for honeybees, calculations allow us to determine that an 8 cm-diameter flower would be identified with chromatic signal until a distance of around 30 cm. For foraging distances higher than 30 cm, honeybees will identify flowers with achromatic (green) signal.

Brechbühl et al., 2010b). These studies, however, revealed that the way prey behave in response to a crab spider is not only species specific but also individual specific. We discuss these aspects in turn.

Some species of solitary bees and syrphid flies have been reported to be deterred by the presence of *M. vatia* (Brechbühl et al., 2010b), *Thomisus labefactus* (Yokoi and Fujisaki, 2009), *Xysticus* species (Brechbühl et al., 2010a) and an artificial *Misumenops argenteus* (Gonçalves-Souza et al., 2008). Syrphid flies *Sphaerophoria* spp., for instance, show a 100% flower rejection rate when flowers on which a spider sits are presented to them (Yokoi and Fujisaki, 2009). However, the lack of information about levels of contrasts and the relative importance of chromatic cues in these anti-predatory behaviours precludes us to conclude about any gain in being chromatically and achromatically cryptic.

The evidence for selection for crypsis is also lacking when discussed from the honeybee and bumblebee point of view, for which it is relatively easy to assess the degree of contrasts, and for which it has been shown that flower chromatic cues affect visitation rates (Lunau et al., 1996). In these species, predator-avoidance learning has been shown to modulate the level of predator detection. While naive bumblebees *Bombus terrestris* visit white flowers harbouring a 'white' or 'yellow' artificial *M. vatia* at the same rate, those having suffered several unsuccessful spider attacks can increase inspection times and display false alarms (erroneous rejection of flowers without predators), both decreasing their foraging efficiency (Ings and Chittka, 2008). Increased level of detection in bees suggests that crypsis could be beneficial. However, not only false alarms but also the fact that some bumblebees and honeybees decide to leave the patch of flowers after several spider attacks (Dukas and Morse, 2003; Dukas and Morse, 2005), induce a loss of available prey, even for poorly discriminable spiders. Moreover, recent field experiments, which do not take into account the 'learning state' of visiting bees, suggested that the selective pressure of learning on crypsis may be less important than expected. Indeed, the number of honeybees and bumblebees visiting flowers with a highly chromatically contrasting *M. vatia* is similar to flowers without spiders (Dukas and Morse, 2003) (Brechbühl et al., 2010b). Thus, the proportion of experienced bees efficiently avoiding crab spiders may be too low to significantly impact the encounter rate and to drive the spider colouration towards crypsis.

Why then do spiders choose flowers on which they yield a high chromatic contrast? *Misumena vatia* will systematically produce high chromatic contrast on several floral reflectance types due to its inability to cover the entire flower colour spectrum, particularly the UV range (Herberstein et al., 2009). However, *M. vatia* can be found hunting on UV-reflecting flowers, such as *C. spinosa* and *Senecio* sp. Nothing is known about *M. vatia*'s spectral sensitivities and whether a UV contrast may also act as an attractive stimulus for honeybees, in a similar fashion as the UV-reflecting Australian crab spider *T. spectabilis* hunting on UV-absorbing flowers (Heiling et al., 2005; Bhaskara et al., 2009). Lunau et al. showed that bees innately prefer flowers with strongly contrasting markings (Lunau et al., 1996). So, whether conspicuous colouration may be an alternative to crypsis on some substrates for an efficient predation is still unknown.

Conclusions

This spider has been assumed to be chromatically cryptic for more than a century. We show here, through a quantitative study carried out in the field, that the degree of chromatic contrast is quite dependent of the receiver and the substrate on which *M. vatia* sits. These results raise concerns about drawing conclusions based on human visual assessments. They also highlight the importance of studying background matching, in the field, from the sensory ecology of all main receivers. For generalist predators, a visual ecology community perspective seems mandatory before statements on adaptation of crypsis can be issued. This endeavour also leads to the identification of major gaps in our knowledge, such as the neuroethology of colour vision in flower-visiting flies, in particular the abundant syrphid flies (Brechbühl et al., 2010b) and of the crab spiders themselves.

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