

Camouflage of Predatory Crab Spiders on Flowers and the Colour Perception of Bees (Aranida: Thomisidae / Hymenoptera: Apidae)

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The crab spider species *Misumena vatia* (Clerck 1757) can match its colour to the flowers it preys on. It can reversibly change between the colours white and yellow. For the first time, the spectral reflectance functions (including the ultraviolet) of such spiders are measured, and compared with the flowers on which they wait for prey. The bee-subjective similarity of the predators with their flowers is assessed using a model of colour vision for bees. While spiders are well matched to white flowers, the colour similarity between spiders and yellow flowers is not perfect. The UV-absorbing spiders often present themselves on UV-reflecting yellow flowers. From longer distances or for smaller flowers, however, bees may use only their green receptors, and spiders may therefore be well camouflaged. Also, spiders do not necessarily catch insects on the very flowers on which they sit; they sometimes move rapidly within respective inflorescences.

Key words: *Apis mellifera* Linnaeus 1758 - *Bombus terrestris* Linnaeus 1758 - *Misumena vatia* (Clerck 1757) - *Chaerophyllum temulum* (Linnaeus 1753) [Apiaceae] - *Senecio vernalis* (Linnaeus 1753) [Asteraceae] - camouflage - crypsis - mimicry - predation - ultraviolet

CHITTKA L [Zool II, Biozentr, Univ, D-97074 Würzburg]: **Tarnung bei räuberischen Krabbenspinnen auf Blüten und die Farbwahrnehmung von Bienen (Aranida: Thomisidae / Hymenoptera: Apidae).**- Entomol Gener 25(3): 181-187; Stuttgart 2001-06. - [Abhandlung]

Krabbenspinnen der Art *Misumena vatia* (Clerck 1757) können ihre Körperfärbung den Blüten anpassen, auf denen sie nach Insekten jagen. Ein reversibler Farbwechsel zwischen weiß und gelb ist möglich. Hier werden zum ersten Mal die spektralen Reflektionskurven (inklusive des Ultravioletts) solcher Spinnen vermessen, und mit denen der Blüten verglichen, auf denen die Tiere auf Beute warten. Die bienen-subjektive Ähnlichkeit der Räuber mit ihrem Hintergrund wird mit Hilfe eines Farbsehmodells für Bienen abgeschätzt. Während die Tarnung auf weißen Blüten sehr effizient ist, ist die Anpassung an gelbe Blüten nur partiell. Die UV-absorbierenden Spinnen präsentieren sich häufig vor UV-reflektierenden Blütenteilen. Aus größeren Entfernungen (oder zum Auffinden kleiner Blüten) benutzen Bienen jedoch lediglich ihren Grünrezeptor. Unter diesen Bedingungen sind auf Beute wartende Krabbenspinnen gut getarnt. Außerdem jagen diese Spinnen nicht notwendigerweise nur auf den Blüten, auf denen sie Beute erwarten, sondern können sich innerhalb von ganzen Infloreszenzen oft sehr schnell bewegen.

Schlüsselbegriffe: *Apis mellifera* Linnaeus 175 - *Bombus terrestris* Linnaeus 1758 - *Misumena vatia* (Clerck 1757) - *Chaerophyllum temulum* (Linnaeus 1753) [Apiaceae] - *Senecio vernalis* (Linnaeus 1753) [Asteraceae] - Beutegreifer - Mimikry - Tarnung - Ultraviolet

1 Introduction

Some species of crab spiders [Thomisidae] stalk insects on flowers. The species *Misumena vatia* has received much attention because the adult females can reversibly adapt their skin colour to the flowers on which they forage [WEIGEL 1941; HINTON 1976; SCHMALHOFER 2000]. They can adopt the colours yellow and white [SCHMALHOFER 2000]. A very substantial portion of the prey taken by these spiders are bees [MORSE & FRITZ 1982; MORSE 2000; DUKAS 2001]. Thus, it makes sense to evaluate the colour mimicry of crab spiders in terms of the colours in which they appear to flower-visiting bees [BRISCOE & CHITTKA 2001; SPAETHE et al 2001].

2 Materials and Methods

Spectral reflectance functions of spiders and their flowers was measured using a spectrometer (Ocean Optics S2000 with a Deuterium/Halogen light source). The relative amount of light absorbed by each spectral receptor type is:

$$P = R \int_{300}^{700} I_S(\lambda) S(\lambda) D(\lambda) d\lambda \quad (1)$$

$I_S(\lambda)$ is the spectral reflectance function of the stimulus; $S(\lambda)$ is the spectral sensitivity function of the receptor. (The functions of [PEITSCH et al 1992] for the UV, blue, and green receptors of *Bombus terrestris* Linnaeus 1758 were employed). These receptors are very similar to those of other bees and therefore representative. $D(\lambda)$ is the illuminant (normfunction D65). The sensitivity factor R in eqtn. 1 is determined by:

$$R = 1 / \int_{300}^{700} I_B(\lambda) S(\lambda) D(\lambda) d\lambda \quad (2)$$

$I_B(\lambda)$ is the spectral reflection function of the green foliage background to which the receptors are assumed to be adapted. With this model, the photoreceptors yield half their maximal response when stimulated by the light reflected from the adaptation background. When the maximum excitation E_{\max} of the photoreceptors is normalised to unity, the photoreceptor excitation is given by

$$E = P / (P + 1) \quad (3)$$

where P is the stimulus strength (eqtn. 1), in units such that for $P = 1$, $E = 0.5$ (i.e. half the maximum potential; for details see [CHITTKA 1996]) where P is the stimulus strength (eqtn. 1), in units such that for $P = 1$, $E = 0.5$ (i.e. half the maximum potential). Thus, for the adaptation background, E equals 0.5 in each photoreceptor. Green contrast is the difference in green receptor signal produced by two adjacent objects. Because excitation can range from 0-1. the maximum green contrast is 1.0.

For calculation of hexagon colour loci from receptor excitation values, see [CHITTKA 1996]. Colour distance in the colour hexagon is correlated with the degree to which two stimuli are perceived as differently coloured. It can range from 0-2, where 0.1 is equivalent to about 70% discriminability [CHITTKA 1996]. Measurements were taken of the white form of *Misumena vatia*, found on white *Chaerophyllum temulum* (Linnaeus 1753) [Apiaceae], and of the yellow form, found on *Senecio vernalis* (Linnaeus 1753) [Asteraceae] (Fig 1), which has yellow flowers with a strongly UV-reflecting periphery). All samples were collected near Fulda, Germany.

3 Results

The measurements are depicted in Fig 2a,b, together with the reflectance functions of the flowers on which the spiders were found. The match between the curves is not perfect in either case. The white form, just like the flowers of *C temulum*, is UV-absorbing, so that both appear blue-green in the colour perception of bees. However, the curves are not identical in intensity. But in the perceptual space of a bee, the colours of the spider and the flower are practically identical (Fig 3; the colour contrast is 0,016).

This is not the case with the yellow form of *Misumena vatia* on *S vernalis*. The spider, like the centre of the flower, is UV-absorbing (Fig 2b). However, the colours of the spider and the floral centre are not identical, although similar, to bees (Fig 3: the colour contrast is 0.065). Additionally, the spiders were observed to be non-selective in terms of its choice of position on the flower (either centre or periphery), so that the UV-absorbing abdomen often obscured UV-reflecting parts of the flowers (Fig 1). The colour contrast between these parts and spiders is pronounced (0.24).



Fig 1: A crab spider, *Misumena vatia* (Clerck 1757) [Aranida: Thomisidae], waiting for prey on a flower of *Senecio vernalis* (Linnaeus 1753) [Asteraceae].

From larger distances, or when flowers are very small, honeybees and bumblebees may not always use their colour vision for object detection and recognition. In such situations, only the signal from the bees' green receptor may be used [GIURFA & LEHRER 2001; SPAETHE et al 2001]. For this reason, it is interesting to compare the green receptor contrast that a crab spider makes with its background on *S vernalis*. As is clearly apparent from Fig 4, the green receptor signal produced by the spiders is very similar to those produced by the floral parts of *S vernalis*, including the UV-reflecting periphery.

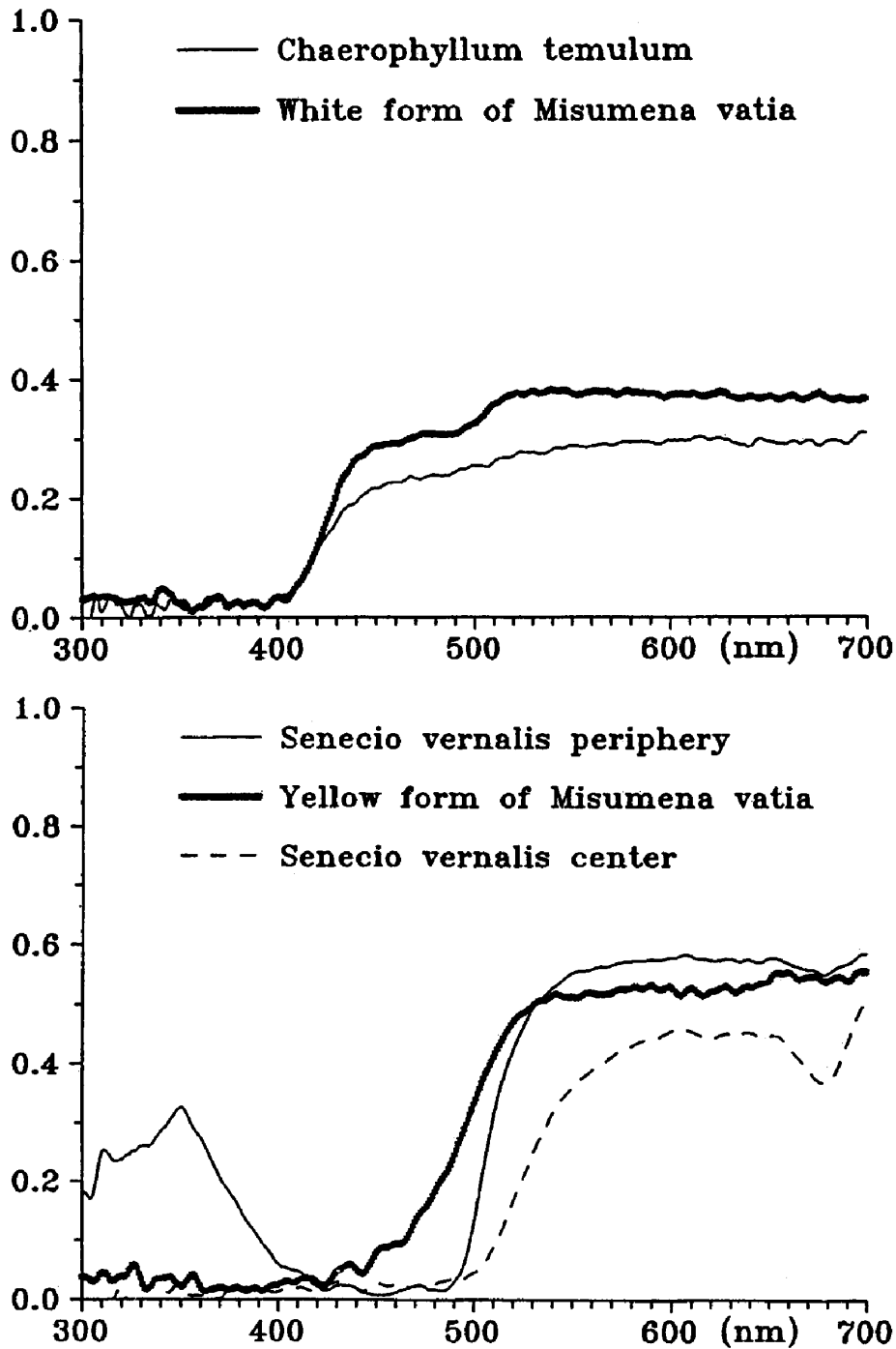


Fig 2: Spectral reflectance functions of crab spiders [Aranida: Thomisidae] and flowers, measured over the range from 300-700nm. Reflectance can vary from 0 (no reflectance) to 1 (all incident light is reflected). (a) Reflectance spectrum of white form of *Misumena vatia* (Clerck 1757), compared with the white flowers of *Chaerophyllum temulum* (Linnaeus 1753) [Apiaceae]. Both are strongly absorbing in the UV, but reflective in the human visible spectrum. (b) Yellow form of spider and the floral centre as well as peripheral petals of *Senecio vernalis* (Linnaeus 1753) [Asteraceae]. Both the centre of the flowers and the spiders absorb short wavelengths up to 450nm, and reflect long wavelength light above 520nm. The peripheral petals of *Senecio vernalis* however, produce a strong UV reflection which is not matched by the spiders.

Green contrast between spiders and flower centre is 0.089, and 0.012 between spider and floral petals. Therefore, in situations when bees use the green receptor channel for floral detection, the spiders are predicted to be cryptic even on UV-reflecting yellow flowers.

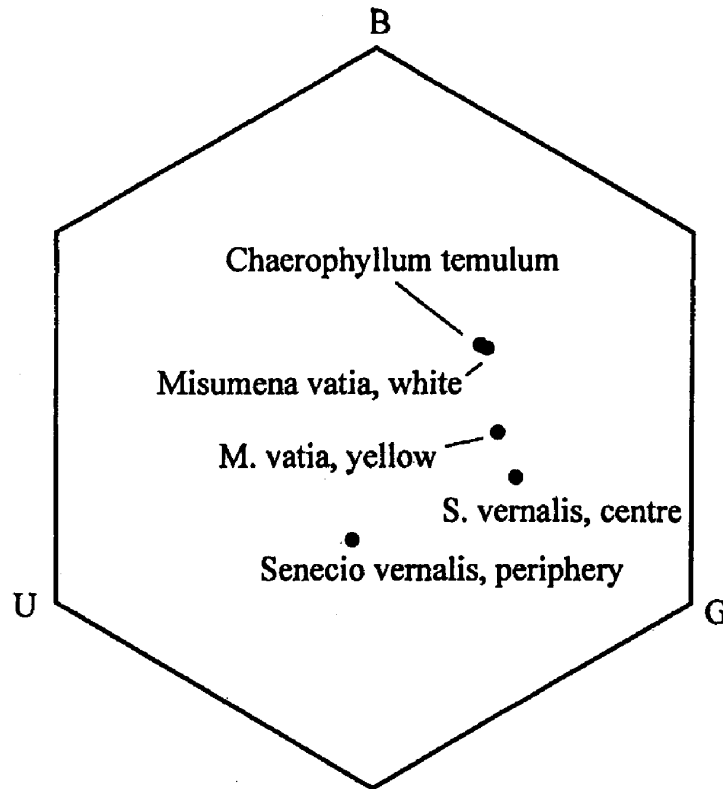


Fig 3: Colour loci of flowers and the different colour variants of spiders in a colour space for trichromatic bees, the colour hexagon. Angular position in this colour space informs about bee-subjective hue, whereas the distance between two colour loci can be used to predict their bee-subjective colour similarity [CHITTKA 1996]. The white form of *Misumena vatia* (Clerck 1757) [Aranida: Thomisidae], is nearly identical to the flowers of *Chaerophyllum temulum* (Linnaeus 1753) [Apiaceae]. The yellow form is similar, but not identical to the centre of flowers of *Senecio vernalis* (Linnaeus 1753) [Asteraceae] flowers, but differs strongly from the floral periphery.

4 Discussion

Misumena vatia spiders appear to be well matched to white flowers such as those of *C temulum* when viewed through the eyes of bees. Such flowers are almost always UV-absorbing [CHITTKA et al 1994], as are the bodies of the white form of *Misumena vatia*. Yellow flowers, however, often have UV-reflecting parts [CHITTKA et al 1994]. The spiders, even though their yellow colouration is UV absorbing, were observed to be non-selective in terms of where they positioned themselves on the flowers by previous workers [LUTZ 1924; KEVAN 1978] as well as here. Intriguingly, this may not necessarily render them highly conspicuous for pollinating bees. It has been suggested that honeybees use only their green receptors unless they are very close to the flowers [GIURFA & LEHRER 2001]. Similarly, bumblebees appear to use the same neuronal channel when they search for very small flowers [SPAETHE et al 2001]. Under such conditions, the spiders may mingle well with their floral background even if they produce a strong colour contrast to the flowers.

Additionally, it is important to consider that *Misumena vatia* does not necessarily catch prey on the very blossom on which it waits. Instead, the whole inflorescence of a plant is often thoroughly wired by silk threads which the spiders can use to move quickly from one part of the inflorescence to another in case prey is visually detected. Thus the spiders have to avoid detection at longer distances. A small colour difference between flower and spider will decrease the signal-to-noise ratio between the object to be detected and its background.

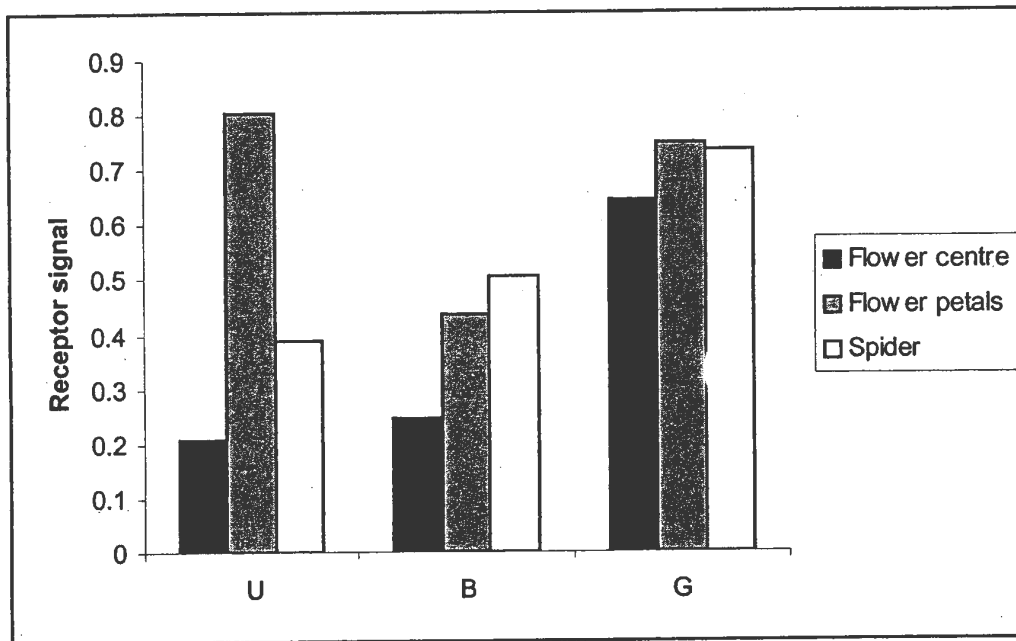


Fig 4: Receptor specific signals in a bees' UV, blue and green receptors. Signals can range from 0 (no excitation) to 1 (maximum excitation). While signals differ strongly in the UV receptor for the centre of *Senecio vernalis* flowers and *Misumena vatia* (Clerck 1757) [Aranida: Thomisidae], the signals in the green receptor of bees are very similar.

Hence, even if the colour match is not perfect, the colouration of the spiders may well blend in with the appearance of the inflorescence as a whole, as viewed from a large enough distance.

This highlights an interesting perceptual and ecological problem. Crab spiders catch insects of completely different systematic groups, such as bees, moths and flies [MORSE 1982], some of which differ in their colour vision systems [BRISCOE & CHITTKA 2001]. Additionally, the spiders should be cryptic for their own predators such as birds, which also have different colour vision [KEVAN et al 2001]. An ideal colour match of the spiders with their flowers, which would be independent of the particular viewing system, could only be achieved by a perfect match in the spectral reflectance curves.

Obviously, there are limits to the degree to which this colour match can be accomplished. First, there are constraints that result from the pigmentation possibilities of the spider [WEIGEL 1941, SCHMALHOFER 2000]. Second, the spider cannot become more similar to the flower than its own colour perception allows. It is theoretically possible that the spider finds itself perfectly matched to the colour of a blossom, but appears quite conspicuous for a flower-visitor with a different perception of colour.

This example of mimicry demonstrates that, in order to fully quantify the degree to which an imitator mimics its model, it is not only not enough to rely on human perception. It is also not sufficient to evaluate pictures taken with UV-sensitive cameras, nor even to just compare spectral measurements. One ultimately needs a model of colour perception to assess whether two colours in question are really identical, similar, or different. Future research may also reveal what role the spiders' own colour perception plays in matching its colour to the respective floral background.

5 Literature

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