

## Colouration in crab spiders: substrate choice and prey attraction

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### Summary

Australian crab spiders *Thomisus spectabilis* ambush pollinating insects, such as honeybees (*Apis mellifera*) on flowers, and can change their body colour between yellow and white. It is traditionally assumed that the spiders change their colour to match the flower colour, thus rendering them cryptic to insect prey. Here, we test this assumption combining state-of-the-art knowledge of bee vision and behavioural experiments.

In the field, yellow spiders are only found on yellow daisies (*Chrysanthemum frutescens*), whereas white spiders are found on yellow and white daisies. These field patterns were confirmed in the laboratory. When given the choice between white and yellow daisies, yellow spiders preferred yellow daisies, whereas white spiders showed only a slight but non-significant preference for white flowers. Thus, *T. spectabilis* select background colours according to their own body colour. When viewed from a distance, bees use an achromatic signal produced by their green receptors for target detection. Through this visual channel, white spiders on white flowers, and yellow spiders on yellow flowers are virtually undetectable. From a closer distance of a few centimetres, when bees evaluate colour contrast, the combination of spider colour against different flower

backgrounds affected the response of honeybees, but not in ways predicted by a classical crypsis/conspicuousness interpretation. Yellow spiders on yellow flowers are not perfectly matched when interpreted through the colour vision of a honeybee. Nevertheless, honeybees showed indifference to the presence of a spider, equally landing on vacant or spider-occupied flowers. Likewise, white spiders are poorly hidden on white flowers, as white spiders reflect ultraviolet light strongly, while white flowers do not. Surprisingly, bees are attracted to this contrast, and significantly more honeybees preferred white flowers occupied by white spiders. White spiders on yellow flowers produce the highest colour contrast and bees again preferred spider-occupied flowers. Yellow spiders on white flowers were the only pairing where bees rejected spider-occupied flowers, especially in cases where the contrast between the two was relatively strong. Thus, *T. spectabilis* select flower colours adaptively in a way that deceives honeybees, or at least does not deter them.

Key words: *Thomisus spectabilis*, *Apis mellifera*, floral signal, communication, vision.

### Introduction

In animal communication, signals elicit a specific response in a receiver or a group of receivers (Johnstone, 1997). Signals increase the fitness of the sender and are at the same time used by receivers to increase their own fitness, although the interests of signallers and receivers are often conflicting (Endler, 1999). The preconditions for signals to work are that they reach the sensory system of the receiver, that they can be processed by the receiver and that they elicit a response in the receiver (Endler and Basolo, 1998). Signals that exploit the sensory biases of receivers are selected for as they ensure signal detection (Endler, 1993; Endler and Basolo, 1998; Smith et al., 2004). Signals can only be perceived if they are distinguishable from background noise (Chittka et al., 1994; Endler, 1999). For example, the visibility of a colour signal depends on the

ambient light conditions and its contrast to the background colour (Endler, 1991, 1993; Vorobyev and Osorio, 1998; Spaethe et al., 2001; Heindl and Winkler, 2003). Animals may use behavioural means to exploit ambient light conditions to maximise the strength of the signal. For example, male birds or guppies may display their colour signal to females in habitat patches where ambient light levels maximise the signal effect (Endler, 1991; Endler and Théry, 1996; Gamble et al., 2003).

Signals are also communicated between species, with one classic example being the visual and olfactory signals used in communication between plants and pollinating insects (for review see Schaefer et al., 2004). The colours of flowers match the trichromatic visual system of pollinating insects (Briscoe and Chittka, 2001; Gumbert et al., 1999). This enables the

receiver to detect flowers and discriminate between different species of flowers during foraging (Chittka and Menzel, 1992). The signalling flowers profit through reproductive service by the receiver (e.g. Harder et al., 2001) while the pollinator benefits by accessing food resources (pollen, nectar). Thus, the colour signals created by flowers benefit both the sender and the receiver.

However, signallers can deceive, gaining a benefit at the cost of the receivers (Johnson, 2000; Heiling et al., 2003). In predator-prey systems, predators often exploit the sensory biases of potential prey to enhance foraging success. For example, female fireflies of the genus *Photuris* mimic signals of courting heterospecific fireflies (*Photinus* sp.) and thus attract males of this genus as prey (Lloyd and Wing, 1983). Sit-and-wait predators, such as many species of spiders, are excellent study objects for investigating the communication of visual signals. The success of their more or less passive hunting strategy obviously relies on how their body or their webs appear visually to approaching prey. Their lack of motion may translate into a constant visual signal that they create against a background. For example, the colourful crab spiders (Thomisidae) sit more or less motionless on flowers waiting for prey to ambush (e.g. Schmalhofer, 1999). Studies on European crab spiders revealed that, based on colour contrast, the spiders on flowers may appear cryptic to pollinating prey and bird predators (Chittka, 2001; Théry and Casas, 2002; Théry et al., 2005). We recently showed that Australian crab spiders *Thomisus spectabilis* create a visual signal by contrasting against the floral background, and that honeybees were attracted by this contrast (Heiling et al., 2003). Our study tested only the appearance of white-coloured *T. spectabilis* on one of their common substrates, a white variety of daisy, *Chrysanthemum frutescens*. Individuals of this spider species, however, can be found on differently coloured flowers, such as yellow and pink flowers. Furthermore, some crab spiders, including *T. spectabilis*, have the ability to change their colour (Oxford and Gillespie, 1998), and in the field we find both white and yellow individuals. This opens up two signalling strategies for crab spiders. They may select the appropriate floral background colours to appear cryptic to oncoming prey. Alternatively, they may be conspicuous and maximise the effect of the visual signal to oncoming prey. Both strategies depend on the spider's own colour signal, which they can change over several days, and the colour contrast they create against the flower background. Thus, we predict that spiders will select flower colours according to their own visual appearance to bees. By choosing appropriate floral backgrounds, they will either appear cryptic and therefore will not deter prey or they will deceive their prey by attracting them through colour signals. Furthermore, selection of the 'wrong' background colour, which is the colour background they are not naturally found on, will deter prey from approaching spider-occupied flowers.

#### Materials and methods

We collected *Thomisus spectabilis* Dolesch 1858

(Thomisidae) in November–January 2001–2003 in Brisbane, Australia. We noted the flower species and varieties that the spiders were found on. Spiders were transferred to the laboratory at Macquarie University, Sydney, where they were maintained in plastic cups, watered daily and fed weekly a diet of live crickets (*Acheta domestica*) and vinegar flies (*Drosophila* sp.). The temperature in the laboratory ranged from 20 to 25°C and the light was set at a 12:12 h cycle. We used honeybees (*Apis mellifera* L; Apidae), a species that was introduced to Australia about 200 years ago. These bees are a natural prey of *T. spectabilis* (A.M.H., personal observation). They came from an outdoor hive on the university campus and were trained to visit a feeding station, offering sucrose solution (about 25%), before being tested.

#### Flower choice of white and yellow *T. spectabilis*

Under natural daylight conditions, we gave adult female *T. spectabilis* a choice between two randomly selected daisies (*Chrysanthemum frutescens*, Asteraceae), which had been reared in a green house. We chose this flower species, because it is a common substrate of *T. spectabilis* in nature (Heiling et al., 2004). The petals of all flowers were cut to equalise the diameter to 30 mm and the flowers were placed in small black plastic lids. One white and one yellow daisy were presented vertically oriented in front of a black background, with a distance of 5 cm between their centres and their surfaces enclosing an angle of 90°. A yellow and a white spider were subsequently tested on the same pair of flowers in a random order. The spider was anaesthetised with carbon dioxide and placed with its carapace 5 cm away from the flower centres, heading towards the flowers. Once the spider had positioned itself on one of the two flowers, it was removed. We placed the spider onto the rejected flower for an equal amount of time to control for any olfactory cues on subsequent spider choice. The background was renewed and the same arrangement of flowers was then offered to another spider of a different colour. Each pair of flowers was tested on two spiders of different colours and each spider was used only once in the experiment.

#### Influence of spider and flower colour on honeybee choice

We performed four choice experiments using identical procedures, differing only in the colour of the flower and spider used. Honeybees were presented with one flower plus a spider, and one flower of the same colour without a spider. Three experiments using the following combinations of flower colour and spider colour were performed: a white flower occupied by a yellow spider; a yellow flower occupied by a yellow spider; and a yellow flower occupied by a white spider. Testing the fourth possible combination, a white flower occupied by a white spider, was part of a previous study (Heiling et al., 2003). The petals of the flowers were cut to equalise their diameter to 30 mm and the flowers placed in small black plastic lids. On one of the flowers, chosen randomly from the pair, we positioned an anaesthetised adult female spider, leaving the other flower vacant. The spider was placed on the petals of the daisy, according to the position of spiders on daisies in nature

(A.M.H., personal observation). The smell of flowers affects honeybee choice (Heiling et al., 2004) and therefore we covered the lids with Glad Wrap™, a foil that is permeable to all wavelengths of light above 300 nm, with less than 5% attenuation. The lids were placed in a horizontal position on a black rectangle, with a distance of 10 cm between the two flowers. Honeybees were trained to visit a feeding station, which we replaced with the rectangle containing the experimental flowers. We recorded the first visit of a honeybee on either of the two flowers and then removed the bee from the population. Due to the difficulty of obtaining yellow *T. spectabilis* in the field, the same individuals were used to test the response of honeybees to yellow spiders on white and on yellow flowers. Otherwise, each flower, spider, and honeybee was used only once in the experiment.

#### *Spectral reflectance of daisies and spiders*

The spectral reflectance (300–700 nm) of white and yellow daisy petals, and white and yellow spiders, was measured using a USB 2000 spectrometer with a PX-2-pulsed xenon light source attached to a PC running OODBase32 software (Ocean Optics, Dunedin, Florida). Six measurements were taken from each individual and the median taken for further calculations. For white and yellow spiders, and white and yellow daisies used in the experiments, we calculated the relative receptor excitation values ( $E$ ) for the photoreceptors (ultraviolet, blue and green) of honeybees (Chittka, 1996; Briscoe and Chittka, 2001). Based on the receptor excitation values, we determined the colour loci in the bee colour hexagon, a colour space based on two colour opponent processes (Backhaus, 1991). This illustrates the colour of the spiders and flowers as perceived by honeybees (Chittka, 1996). Angular position in the colour hexagon indicates bee-subjective hue, whereas the distance to the centre of the colour hexagon indicates spectral purity (or its corresponding perceptual parameter, saturation).

For each pairing of spiders and flowers used in the experiments, we calculated the colour contrast that spiders created on the floral backgrounds. Colour contrast between adjacent objects is the Euclidian distance between their colour loci in the colour hexagon (see Chittka, 1996). Note, however, that bees only use colour for object identification from a relatively close distance. An area of 15° (equivalent to 59 ommatidia of its compound eye) must be subtended for a honeybee to identify a flower by its colour (Giurfa et al., 1996, 1997; Giurfa and Lehrer, 2001). Furthermore, recent research has shown that bees are able to use a different neuronal channel with a smaller receptive field when they are further away from a flower. When a target is seen at an area subtending at least 5° (and no more than 15°), bees employ green contrast, i.e. the difference in signal provided by the green receptor between background and target, for detection (Giurfa et al., 1996, 1997; Giurfa and Lehrer, 2001; Spaethe et al., 2001). Hence we also calculated green contrast for spiders and flowers in all the colour pairings used. Moreover, we calculated the overall brightness of spiders and daisies, and the brightness contrast for each pairing of spiders and daisies,

which is the difference of signal intensity between object and background, as quantified by the differences in sums of all three photoreceptor signals (Spaethe and Chittka, 2003).

## Results

#### *Flower choice of white and yellow *Thomisus spectabilis**

In the field, yellow *Thomisus spectabilis* were found only once on white *Chrysanthemum frutescens* (6.3%); they were found predominantly on yellow ones (93.7%;  $N=16$ ). By contrast, 69% of white spiders were found on white *C. frutescens*, while 31% were found on flowers of the yellow variety of the same flower species ( $N=71$ ; Yates corrected chi-square test:  $\chi^2=18.56$ , d.f.=1,  $P<0.001$ ).

This pattern of distribution among daisies of different colours was confirmed by the choice experiment. Offering spiders the choice between a white and a yellow *C. frutescens* revealed that the distribution of spiders in the field was due to the choice of spiders, rather than to the availability of flowers. In 94.1% of the cases, yellow spiders preferred yellow flowers to white ones (5.9%; binomial  $P=0.00013$ ,  $N=17$ ). By contrast, 58.8% of white spiders chose the white daisy, while 41.2% chose the yellow one (binomial  $P=0.149$ ,  $N=17$ ). Subsequently offering a yellow and a white spider a pair of white and yellow flowers revealed that in about half of the cases (41%) the spiders chose the same flower individual from the flower pair. This indicates that spider preferences were due to reflectance properties of flowers.

#### *Analysis of spider and flower colouration*

The reflectance of yellow and white spiders differed substantially (Figs 1, 2). Yellow spiders had equally high reflectance as white spiders did above ~500 nm, but reflectance of yellow spiders fell sharply at all wavelengths below 500 nm. Conversely, white spiders reflected moderate amounts of light below 500 nm (Fig. 1). There were also differences in the colour of *Chrysanthemum* flowers. Yellow flowers reflected little UV and blue, absorbing all light below 400 nm (UV), and most light between 400 nm and 500 nm (violet to blue-green). White *Chrysanthemum* flowers strictly absorbed UV light below 400 nm, but reflected blue light above 400 nm (Fig. 1).

In the colour hexagon (Fig. 2), white flowers and white spiders lie along the same hue line, extending from the centre of the hexagon into the blue-green corner of the colour hexagon. This means that the blue and green receptors are about equally stimulated by white spiders and flowers, and white spiders and flowers are hence predicted to appear blue-green to bees. However, in correspondence with the higher UV reflectance of the white spiders, their colour loci hardly overlap with those of white flowers (Fig. 2). The colour contrast between white spiders and white flowers (mean  $\pm$  S.E.M.=0.151 $\pm$ 0.007,  $N=25$ ; Table 1) is visible by bees, where a colour distance of 0.012 hexagon units has been empirically shown to be detectable (Dyer and Chittka, 2004). Moreover, the contrast between white spiders and yellow flowers is even greater (mean  $\pm$  S.E.M.=0.486 $\pm$ 0.016,  $N=25$ ; Table 1).

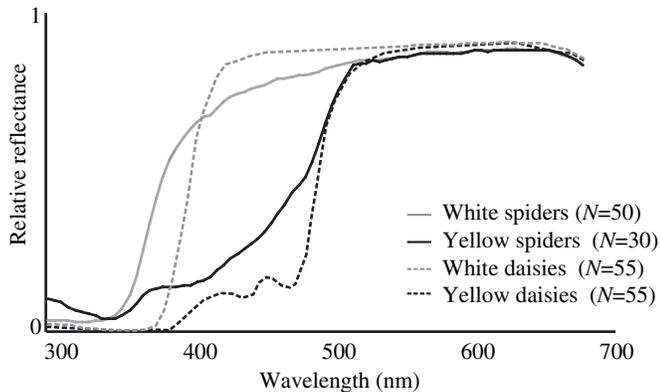


Fig. 1. Relative reflectance of white and yellow *T. spectabilis* and white and yellow *C. frutescens*, measured for the range of wavelengths relevant for bee vision.

Yellow spiders and yellow flowers stimulate the green receptor particularly strongly; therefore their colour loci come to lie in the green corner of the colour hexagon (Fig. 2). Note that the hue variability is much greater in yellow spiders and yellow flowers than it is in white spiders and white flowers. The colour contrast between yellow spiders and yellow flowers (mean  $\pm$  S.E.M.=0.291 $\pm$ 0.011,  $N=30$ ) is higher than that between white spiders and white flowers (see above; Table 1). Hence, yellow spiders on yellow flowers are predicted to be easily distinguishable. Surprisingly, in terms of colour contrast, yellow spiders are less similar to yellow flowers than they are to white flowers (mean  $\pm$  S.E.M.=0.146 $\pm$ 0.011,  $N=30$ ; Table 1).

Given an average body length of adult female *T. spectabilis* of 9.4 $\pm$ 0.2 mm (mean  $\pm$  S.E.M.,  $N=21$ ), honeybees can perceive a colour contrast between spiders on flowers only from a distance below 35.3 mm, based on the angular sensitivity of the colour channel (Giurfa and Lehrer, 2001), and provided that the colour contrast is sufficiently high. However, by using achromatic vision, honeybees can detect spiders much earlier when approaching a flower. The maximum distance that enables honeybees to perceive a green colour contrast between flower and spider is 106.5 mm, again provided that the contrast is sufficiently high. It turns out, however, that white spiders on white flowers, as well as yellow spiders on yellow flowers, are extremely well matched in terms of green contrast (Table 1).

The absolute limit of contrast sensitivity of a visual system is set by the noise level of its receptors (Vorobyev et al., 2001). These authors reported a noise standard deviation of 0.2–0.4 mV in the green receptors, where the maximum response  $V_{\max}$  was 38 mV. This corresponds to a just noticeable difference in green receptor signal of  $V/V_{\max}$  in the range of 0.0052 to 0.0105, and a green contrast of 0.016 has been shown to be behaviourally relevant (Chittka and Tautz, 2003). The green receptor signals of white spiders occupying white flowers were significantly greater than the green receptor signals of yellow spiders occupying yellow flowers (mean  $\pm$  S.E.M.=0.823 $\pm$ 0.003,  $N=25$  and mean  $\pm$  S.E.M.=0.796 $\pm$ 0.005,  $N=30$ , respectively;  $t_{45,9}=4.577$ ,  $P<0.001$ ). Nevertheless, both

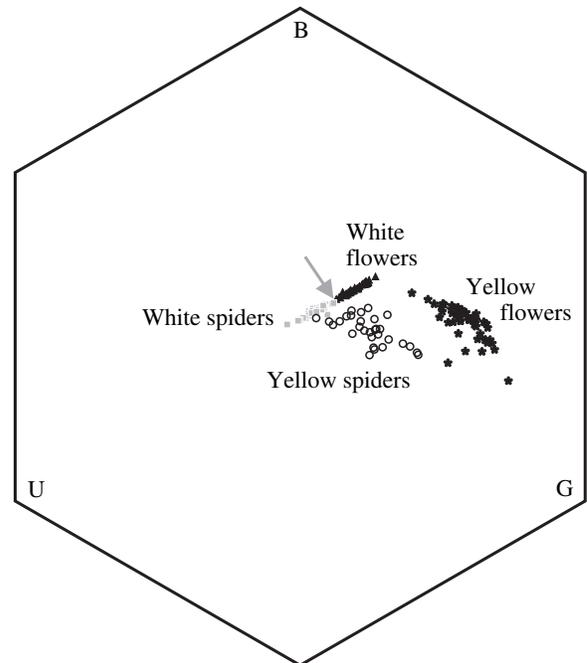


Fig. 2. The colour loci in the colour hexagon of honeybees, calculated for white spiders (grey squares,  $N=50$ ), white daisies (black triangles,  $N=55$ ), yellow spiders (white circles,  $N=30$ ) and yellow daisies (black asterisks,  $N=55$ ). The distribution of the colour loci of white flowers ends at the point indicated by the arrow. B, blue; G, green; U, UV.

the green contrasts created by white spiders on white flowers (mean  $\pm$  S.E.M.=0.017 $\pm$ 0.003,  $N=25$ ) and by yellow spiders on yellow flowers (mean  $\pm$  S.E.M.=0.024 $\pm$ 0.004,  $N=30$ ) are above the detection threshold of honeybees. Similarly, the green contrasts for white spiders on yellow flowers, as well as yellow spiders on white flowers, are above the detection threshold of honeybees (mean  $\pm$  S.E.M.=0.039 $\pm$ 0.003,  $N=25$  and 0.051 $\pm$ 0.005,  $N=30$ ; respectively). Hence, bees are predicted to be able to perceive spiders from beyond the range where colour contrast is used (>35 mm). In all of these cases, however, the green contrast is still relatively low (Table 1).

#### *Influence of spider and flower colour on honeybee choice*

Surprisingly, the presence of a white spider on a white or a yellow daisy attracted honeybees to the flower (Fig. 3). By contrast, yellow spiders did not attract honeybees on either

Table 1. Overview of the colour contrasts and green contrasts between white and yellow *T. spectabilis* and white and yellow *C. frutescens*, and the visibility of these contrasts by honeybees

Spider/flower combinations	Colour contrast	Green contrast
Yellow/yellow	Detectable (very high)	Detectable (low)
Yellow/white	Detectable (high)	Detectable (low)
White/yellow	Detectable (very high)	Detectable (low)
White/white	Detectable (high)	Detectable (low)

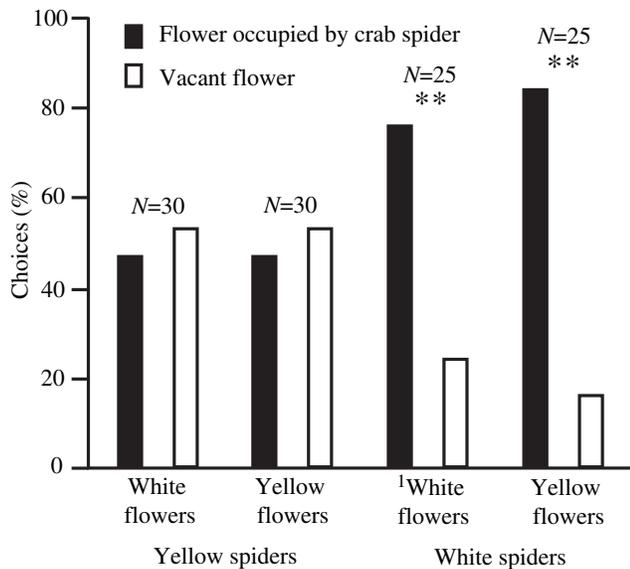


Fig. 3. The effect of spider presence on the response of honeybees, using four different combinations of spider and daisy colour. Pairs of flowers consist of spider-occupied flowers (black blocks) and vacant flowers (white blocks). \*\* $P < 0.01$ . <sup>1</sup>Results taken from Heiling et al. (2003).

white or yellow flowers (Fig. 3). We noticed, however, that there was some variation in the way bees responded to spider-occupied flowers – bees sometimes emphatically rejected such flowers, while they disregarded the presence of spiders in other cases. Because there is variation in the

colouration of individual spiders and flowers, we were especially interested to see whether these differences might be explained by the visual contrast that individual spiders made with the particular flowers they had been placed on. Therefore, we performed a post-hoc analysis of the colour contrast between spiders and flowers in cases where these flowers were visited by honeybees, and in cases where the spider-occupied flowers were rejected. For yellow spiders on white flowers, we found that colour contrast was significantly higher for spider-flower combinations that were rejected by honeybees than for combinations that were chosen (Table 2). By contrast, honeybees did not distinguish between the levels of colour contrast created by yellow spiders on yellow flowers (Table 2). The attraction of honeybees to white daisies occupied by white spiders was not influenced by the degree of colour contrast that the spiders created against the floral background (Table 2). Similarly, the degree of colour contrast created by white spiders on yellow daisies did not affect the response of honeybees (Table 2). In addition, the amount of green contrast between spiders and flowers did not affect the decision of honeybees in any of the four possible combinations of spiders and flowers (Table 3).

## Discussion

The colour of spiders serves several functions, including crypsis, aposematism, mimicry and thermoregulation (Oxford and Gillespie, 1998). For the sit-and-wait predator *Thomisus spectabilis*, it serves as a tool in signalling communication and may have other, as yet undiscovered, functions. In nature,

Table 2. Differences in colour contrast (chromatic contrast) between white and yellow *T. spectabilis* and white and yellow *C. frutescens* that were either chosen or rejected by honeybees

Spider/flower combinations	Colour contrast		Statistics
	Chosen by bee	Rejected by bee	
Yellow/white	0.12±0.0111	0.168±0.0172	$t_{25,04} = -2.347, P = 0.027$
Yellow/yellow	0.283±0.002	0.2971±0.0111	$t_{28} = -0.644, P = 0.525$
White/white	0.153±0.135, 0.174	0.139±0.115, 0.201	$U = 54, P = 0.849, N = 25$
White/yellow	0.491±0.436, 0.555	0.492±0.428, 0.508	$U = 39, P = 0.824, N = 25$

Normally distributed data are given as mean ± S.E.M. and analysed using parametric tests; otherwise, Median ± Qi, Qs are given and non-parametric tests were applied. Qi and Qs indicate lower and upper quartiles, respectively.

Table 3. Differences in green contrast (achromatic contrast) between white and yellow *T. spectabilis* and white and yellow *C. frutescens* that were either chosen or rejected by honeybees

Spider/flower combinations	Green contrast		Statistics
	Chosen by bee	Rejected by bee	
Yellow/white	0.045±0.006	0.057±0.008	$t_{28} = 1.197, P = 0.241$
Yellow/yellow	0.031±0.008	0.0181±0.003	$t_{28} = 1.555, P = 0.131$
White/white	0.015±0.005, 0.025	0.012±0.003, 0.035	$U = 55, P = 0.899, N = 25$
White/yellow	0.041±0.025, 0.051	0.044±0.041, 0.05	$U = 33, P = 0.505, N = 25$

Normally distributed data are given as mean ± S.E.M. and analysed using parametric tests; otherwise, Median ± Qi, Qs are given and non-parametric tests were applied. Qi and Qs indicate lower and upper quartiles, respectively.

yellow and white *T. spectabilis* are not distributed at random between white and yellow *Chrysanthemum frutescens* and this distribution might be due to the adaptive colour change of crab spiders (Oxford and Gillespie, 1998) and/or to the availability of flowers. However, choice experiments confirmed that *T. spectabilis* possess the ability to actively choose between flowers of different colouration, and these colour preferences correspond to the distribution of spiders in the field. While yellow spiders overwhelmingly preferred yellow flowers to white ones, white spiders showed no significant preference for either colour. Crab spiders respond to various floral cues in order to increase foraging success. For example, the condition of flowers and prey presence are used as indicators of hunting site quality in male *Misumena vatia* (Chien and Morse, 1998). In adult female *T. spectabilis*, olfactory and visual flower signals help the spiders to select flowers that are also preferred by their bee prey (Heiling and Herberstein, 2004a; Heiling et al., 2004) (A. Wignall, A.M.H., K.C. and M.E.H., manuscript submitted).

Here, we show that *T. spectabilis* do not choose flowers randomly, but respond to visual floral cues. We do not know whether *T. spectabilis* used in our study responded to the colour or the brightness of flowers, or to both. Studies on spider species of various families (e.g. De Voe, 1975; Yamashita and Tateda, 1983; Barth et al., 1993), including one species of crab spider, *Misumenops pallens* (Corronca and Teran, 2000), revealed spectral sensitivities of their eyes ranging from ultraviolet (UV) to green. However, only one study on jumping spiders *Hasarius adansoni* (Nakamura and Yamashita, 2000) provided experimental evidence that spiders are actually capable of using colour cues for their behavioural decisions. For the first time, we provide evidence that crab spiders take into account their own body colouration when deciding where to forage and that their preferences for differently coloured flowers are clearly beneficial. Yellow spiders did not affect the response of honeybees to yellow flowers. They created a similar colour contrast on the flowers, as white spiders did on white daisies. However, the green contrast between spiders and daisy petals was low, which might explain why yellow spiders neither deterred nor attracted honeybees.

The response of honeybees to the presence of yellow crab spiders on white daisies was dependent upon the degree of colour contrast. They avoided landing on spider-occupied flowers only in cases where spiders created a high colour contrast against the floral background. Flowers often display UV-absorbing markings. These markings indicate the presence of pollen (e.g. Lunau, 2000), or colour patterns that are similar to or substitute as pollen signals (e.g. Lunau, 1996), and thus attract pollinating insects to flowers. Compared with white *T. spectabilis*, yellow individuals are less reflective in the UV range. Thus, we would expect yellow spiders on white flowers to be attractive to honeybees, which was not the case. Probably the colour contrast created by the spider against the daisy petals did not match the contrast between the reproductive flower centre and the petals. Moreover, honeybees may not interpret yellow spiders that are naturally located on the petals of the

flower as a floral guide, because floral guides are typically located in the centre of a radial symmetrical flower. In any case, even though honeybees were deterred by the presence of yellow spiders on white daisies, we do not know whether they identified the spiders as potential predators. Honeybees are known for their preference for symmetrical flowers (e.g. Lehrer et al., 1995) (A. Wignall, A.M.H., K.C. and M.E.H., manuscript submitted). Therefore, spider presence might alter the shape of the flower by making it appear irregular and thus less attractive for a honeybee.

White *T. spectabilis* also change the appearance of a white daisy for a honeybee. However, previous results revealed that in contrast to yellow spiders, they attract honeybees to the flower (Heiling et al., 2003). Here, we show that honeybees are attracted to flowers occupied by white spiders, irrespective of the flower colour (white or yellow). In both cases, spiders created a pronounced colour contrast against the floral background, which obviously deceived honeybees and attracted them to the spider-occupied flower.

Yellow spiders occupying white daisies and white spiders on yellow daisies created a measurable green contrast. However, the green contrast between white spiders and white daisies, as well as between yellow spiders and yellow daisies, was low. Moreover, the green signals from white spiders occupying white daisies and from yellow spiders occupying yellow daisies were different. Thus, the spiders might adapt their body colouration in a way that minimises the green contrast against the floral background.

Unlike white daisies, white spiders are characterised by their reflectance in the UV region of the spectrum. Although UV-bright patches may indicate the location of floral food resources for insects (Silberglied, 1979), UV-reflecting objects *per se* do not attract bees (Spaethe et al., 2001). Therefore, the attraction of honeybees to the white spiders on white or yellow flowers was unlikely to be due to the green contrast between flowers and spiders, or to the reflectance of spiders in the UV range. More likely, honeybees were lured by the specific colour contrast that white spiders created on the flowers.

In contrast to European honeybees, stingless native Australian bees (*Australopebia australis*) are not deceived by white *T. spectabilis* (Heiling and Herberstein, 2004b). They can detect white spiders on flowers and avoid them. While the white colour of spiders is costly for spiders when confronted with their native prey, yellow spiders might have the advantage of being cryptic in this case. Accordingly, white spiders that choose to occupy yellow flowers might do so to change their body colouration to appear cryptic. If being white exposes spiders to their potential native prey, why do we see white spiders at all? It may be that the frequency of white *T. spectabilis* increased as a result of the increasing availability of honeybees in Australia. Colour change in crab spiders is a plastic response to background conditions. The ability of crab spiders in Australia to choose background colours that benefit them might have been selected.

Our study considered only the signalling communication between spider predators and one of their prey. From other

signalling communication systems we know that the deployment of signals may carry costs as well as benefits to the signaller. In tungara frogs, for example, male vocal signals lead to a higher risk of predation (Tuttle and Ryan, 1981). Similarly, orb-web spiders might attract both prey and predators by UV-reflecting body markings (Tso et al., 2004) or web decorations (Hauber, 1998; Bruce et al., 2001; Seah and Li, 2001). The signals generated by crab spider colouration may not only be perceived by bees and probably other potential prey, but also by potential predators. We did not have the opportunity to observe predatory attacks in the field and can only suspect that potential predators of *T. spectabilis* are wasps, mantids and birds that are found in the natural habitats of spiders. The precondition for conspicuous signals to evolve is a benefit for the sender (e.g. Krebs and Dawkins, 1984). Such a signal might persist even if it is exploited by predatory receivers that impose costs on the signaller, as long as the benefits exceed the costs (Hoffmeister and Roitberg, 1998). This evolutionary scenario might be reflected in the visual signalling communication between white-coloured *T. spectabilis* and their receivers, both potential prey and predators. In short, white spiders might trade off predation risk for prey capture success. By contrast, the yellow colouration of *T. spectabilis*, although not cryptic in the classical sense (e.g. Endler, 1991), might function primarily to conceal the spiders against predatory attacks.

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