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Floral quality signals lure pollinators and their predators

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Flowers exploit the sensory capabilities of pollinators to lure them. The crab spider *Thomisus spectabilis* benefits from this system by responding to floral signals that are intended to lure honeybees, *Apis mellifera*, which they prey upon. We investigated whether honeybees and crab spiders discriminate between flowers of *Jasminum mesnyi* plants that are either fully rewarding, with two reproductive stamens, or not. We found that both honeybees and crab spiders preferred fully rewarding flowers in the field. Moreover, honeybees preferred small flowers over larger ones, while the height above the ground and the number of petals did not influence flower choice of honeybees and crab spiders. Under experimental conditions, crab spiders showed the same choice pattern as observed in the field. This indicates that they actively search for fully rewarding flowers, which are also preferred by their potential prey. Fully rewarding *J. mesnyi* lure honeybees through visual, olfactory or a combination of these floral signals and *T. spectabilis* exploits this communication to enhance their chance of prey encounter.

Introduction

In animal communication, signals often match the sensory system of the intended receiver (Guilford & Dawkins 1991). In the interaction between plants and pollinating animals, sensory biases are being exploited, a process called 'sensory exploitation' (Basolo 1995, Johnstone 1996). The floral signals produced by plants match the inherent sensory abilities of pollinating insects they attract (e.g., Chittka *et al*. 1994, Chittka *et al*. 1999). Due to the energetic demands of pollinators, their preferences should result in a directional selection for floral cues associated with predictable pollen and nectar resources (Heinrich & Raven 1972). In fact, pollinators are attracted to pollen and anthers through gustatory (Galen & Kevan 1983, Hansen *et al*. 1998), tactile (Gack 1981), olfactory (Lunau 1992), and visual signals (Chittka & Menzel 1992, Lunau 2000).

Bees, which are probably the most extensively studied group of animals interacting with plants, are responsive to various floral characteristics that indicate the presence of food resources. For example, they discriminate amongst flowers with different sizes, preferring larger flowers (Ohara & Higashi 1994). Similarly, between flowers of the same species, they prefer flowers containing wider (Ashman *et al*. 2000) and longer (Ashman 2000) petals. Moreover, bees are attracted to symmetrical flowers (Møller &

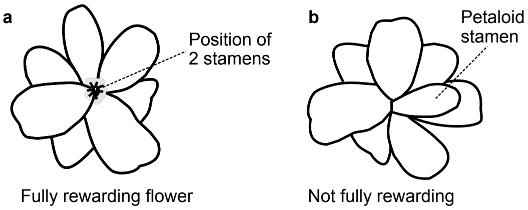

Fig. 1. Schematic representation of the two morphs of flowers in *J. mesnyi* plants. (**a**) Flower containing two stamens, i.e. these flowers are fully pollen productive, (**b**) represents the less pollen productive morph of flowers in which one stamen is converted into a petaloid.

Eriksson 1995, Møller & Scorci 1998) that also offer more food resources to pollinators than less symmetrical flowers within a species (Møller & Scorci 1998). Furthermore, odour (Galen & Kevan 1983, Wells & Wells 1985), and flower colour (Real 1981, Waser & Price 1981, Kevan & Baker 1983, Chittka & Menzel 1992) also affect flower choice in bees, whereas the brightness of objects does not seem to have any influence (Giurfa *et al.* 1995, Lunau *et al.* 1996).

Plants benefit from frequent visits of animals by reproductive service, while pollinators gain nectar or pollen resources (e.g., Harder *et al.* 2001). However, signalling systems are often manipulated or exploited, resulting in a disadvantage for either the signaller or the receiver. This situation often occurs in the communication system between predator and prey, where the predator exploits the biases of potential prey to enhance foraging success. For example, fireflies of the genus *Photuris* mimic signals of courting heterospecific fireflies (*Photinus* sp.) to attract males of this genus as prey (Lloyd & Wing 1983).

Crab spiders are predators that occupy flowers where they hunt for pollinating insects (Schmalhofer 1999). Previous studies revealed that various signalling modalities, such as olfactory (Aldrich & Barros 1995, Krell & Krämer 1998), visual and tactile ones (Morse 1988, Greco & Kevan 1994) guide them in their choice of hunting sites. Recent experimental studies on *Thomisus spectabilis* revealed that these crab spiders exploit the behaviour of their insect prey by responding to olfactory cues produced by daisies that also attracted honeybees (Heiling *et al.* 2004). Moreover, while body colour of some crab spider species matches the flower colour making them well camouflaged (e.g., Chittka 2001, Théry & Casas 2002), the Australian *T. spectabilis* is highly conspicuous against a flower background. These spiders manipulate flower signals through UV-reflecting body colouration, a novel example of deceptive signalling (Heiling *et al.* 2003).

In the present study, we extend our investigations on this predator–prey system by combining the data from field observations and experiments. Focusing our investigations on a single plant species, *Jasminum mesnyi* (Oleaceae) that shows variable pollen availability: some flowers contain two productive stamens, while other flowers on the same plant have converted one stamen into a non pollen producing petaloid stamen. We predict that honeybees preferentially visit flowers that offer a higher quantity of pollen resources and that crab spiders show the same preferences.

Methods

Study area and study organism

Field observations were carried out over 4 consecutive days in October 2001, in the urban area of Brisbane, Australia. Our choice experiment, using spiders collected in Brisbane and flowers from the Sydney area, was performed on the Campus grounds of Macquarie University, Sydney, in October 2002.

During early summer, one of the dominant flowering species in the Brisbane region is *Jasminum mesnyi* (Oleaceae), the common primrose jasmine, an evergreen shrub native to south western China. Cultivated clones mostly contain semi double, yellow flowers with 6 to 10 petals. The corolla is actinomorphic. The androecium either consists of two stamens born on the corolla tube, or one of the stamens is converted to a petal, forming the petaloid stamen (P. Hind pers. comm.; Fig. 1). In Brisbane, *J. mesnyi* is one of the hunting substrates of *Thomisus spectabilis*, the model predator in our study.

T. spectabilis (Araneae: Thomisidae) are diurnally active, anthophilous ambush predators. These spiders use their raptorial forelimbs, rather than a web, to restrain prey that land on the flowers. They either sit on or beneath the petals of jasmine flowers when hunting prey (pers. obs.). We found them preying on honeybees (*Apis mellifera*, Apidae), the model prey animal in our study.

Floral characteristics and visitation rates by crab spiders and honeybees

To investigate whether *T. spectabilis* and *A. mellifera* prefer jasmine flowers as feeding grounds that show certain characteristics, we concentrated our observations on a large shrub of *J. mesnyi* covering approximately 15 square metres. All the inflorescences on the shrub were checked for the presence of female *T. spectabilis* and the spiders were removed. We measured several parameters from these flowers ($N = 23$) including the height of the flower above the ground, the diameter of the flower, the number of petals, and whether the flower contained two reproductive stamens or petaloid stamens. The same parameters were taken from flowers that were visited by honeybees ($N = 23$). The relative frequency of inflorescences containing two reproductive stamens was ascertained from randomly selected inflorescences ($N = 48$). Here, we also measured the diameter of the corolla and the number of petals the flowers contained.

Crab spider flower preferences under experimental conditions

To investigate whether *T. spectabilis* prefer jasmine flowers containing reproductive stamens or petaloid stamens *a priori*, we offered both flower morphs to spiders in choice experiments. The crab spiders were anaesthetized with carbon dioxide and placed into the centre of a test surface, consisting of a circle of black cardboard (17 cm in diameter) within an enclosed plastic arena (height = 14.5 cm). Jasmine flowers were placed in black plastic lids (4 cm in diameter) to provide a consistent black background and the two morphs were randomly combined in pairs. The flowers were arranged vertically with a distance of 4 cm between the flower centres and their corollas enclosing an angle of 120°. Each spider was placed in front and in between the two flowers at a distance of 5 cm from the centre of the spider carapace. The spider was facing the two flowers with the two morphs assigned randomly to the left or the right side. The experiment was performed under natural daylight conditions and each spider and flower was used only once.

Reflectance properties of flowers

To examine whether the morphological differences between flowers with or without petaloid stamens also translate into differences in the reflectance properties as perceived by a honeybee, we measured the spectral reflectance (300 to 700 nm) of flowers. In both morphs, we measured the reflectance of petals in the periphery of the flowers (3 mm from the tip of the petals). To measure the centre of fully reproductive flowers, we considered an area within a radius of 3 mm from the flower centre. In flowers with converted stamens we measured the lower side of the petaloid stamens that are visible to oncoming honeybees and cover the flower centre (*see* Fig. 1). Each morph ($N = 23$, respectively) was measured six times, using a USB 2000 spectrometer with a PX-2-pulsed xenon light source attached to a PC, running OODBase32 software (Ocean Optics Inc., Dunedin, Florida). We took the median values from the six measurements from each area (centre and periphery) and calculated the receptor excitation values (E) for the photoreceptors (ultraviolet, blue and green) of honeybees (for methods *see* Chittka 1996). The calculations produce the proportion of maximum potential excitation in the UV, the blue and the green. These values refer to the visual system of honeybees, as the calculations incorporate the spectral sensitivity functions of photoreceptors, which are only available for honeybees but not for crab spiders. With the excitation values we calculated the colour loci in the bee colour hexagon. From the colour coordinates in the colour hexagon we calculate the euclidean distances between the flower periphery and flower centre. This is the colour contrast as perceived by the honeybee (Chittka 1996). This approach takes into con-

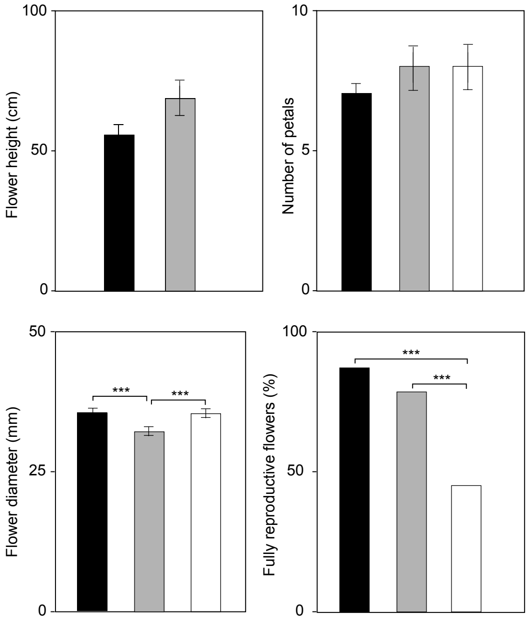

Fig. 2. Characteristics of *J. mesnyi* flowers occupied by spiders (N = 23; black bars), visited by honeybees (N = 23; grey bars), and randomly selected flowers (N = 48; white bars). The data are given as means (± SE) or percentages. *** $P < 0.001$.

sideration the colour opponent processes that influence how the bee brain integrates a colour signal (Chittka 1996). Moreover, we calculated the overall brightness, defined as the sum of the excitation values of the three receptor types, for petals and flower centres (Chittka 1996).

Statistical analyses

All data were tested for normal distribution (Kolmogorov Smirnov test) and analysed accordingly. We used http://vassun.vassar.edu/~lowry/VassarStats.html for calculating the exact binomial probabilities and SPSS version 11 software for all other analyses.

Results

Floral characteristics and visitation rates by crab spiders and honeybees

On *J. mesnyi*, the height of flowers ranged from 15 cm above the ground to 170 cm but there was no difference in height above the ground of flowers occupied by crab spiders and visited by honeybees ($t_{44} = -1.42$, $P = 0.162$; Fig. 2). The flowers visited by honeybees were significantly smaller (ANOVA: $F_{2,92} = 9.14$, $P < 0.001$; Fig. 2) than those occupied by crab spiders (post hoc Scheffè: $P = 0.004$) and randomly selected flowers (post hoc Scheffè: $P < 0.001$). By contrast, size did not differ between spider-occupied and random flowers (Post hoc Scheffè: $P = 0.997$; Fig. 2). Furthermore, there was no difference in the size of flowers with and without petaloid stamens ($t_{61.1} = -0.661$, $P = 0.551$). Flowers visited by bees, occupied by spiders, and randomly

Table 1. Mean (± SE) receptor excitations (E) in the ultraviolet, the blue and the green receptors of honeybees, ranging from 0 (no excitation) to 1 (maximum excitation) and brightness of *J. mesnyi* flowers. Flower centre and periphery of flowers containing two intact stamens differ in colour (UV, blue and green), while there is no such difference in flowers with the androecium covered by a converted stamen (N = 23, respectively).

Reflectance properties	Flowers containing		Significance Paired t, P
	Reproductive stamens	Petaloid stamens	
Periphery of the flower			
E_{uv}	0.86 ± 0.02	0.85 ± 0.02	1.05, 0.30
E_{blue}	0.54 ± 0.05	0.53 ± 0.06	1.04, 0.31
E_{green}	0.84 ± 0.01	0.84 ± 0.01	–1.82, 0.08
Brightness	2.24 ± 0.07	2.22 ± 0.09	0.94, 0.36
Centre of the flower			
E_{uv}	0.12 ± 0.01	0.84 ± 0.01	–24.15, < 0.001
E_{blue}	0.22 ± 0.08	0.57 ± 0.03	–11.89, < 0.001
E_{green}	0.81 ± 0.01	0.84 ± 0.01	–11.39, < 0.001
Brightness	1.15 ± 0.02	2.24 ± 0.01	–20.14, < 0.001

selected flowers did not differ in the number of petals they contained (Kruskal-Wallis: $\chi^2 = 3.13$, df = 2, $P = 0.209$; Fig. 2). Analysing the data of randomly selected flowers, we found that the plant contained the same numbers of flowers with and without petaloid stamens. Interestingly, 78% of the bees and 87% of spiders were found on flowers without petaloid stamens, deviating significantly from the frequencies to be expected from random samples ($\chi^2 = 38.55$, df = 1, $P < 0.001$ and $\chi^2 = 64.23$, df = 1, $P < 0.001$, respectively; Fig. 2).

Choice experiment

In the laboratory choice experiments, we considered the spider to have made a choice if it approached and touched a flower, often positioning itself in the petals. From the 32 spiders tested in this choice experiment, 9 tried to escape the arena after they woke up, remained motionless for more than 30 minutes, or found their way to one of the flowers by a detour route. These were not considered in our analyses. In 16 out of the 23 remaining cases, the spiders chose flowers with two reproductive stamens over flowers containing petaloid stamens (exact binomial $P = 0.029$, two-tailed). *T. spectabilis* clearly perceived the two flowers before they came to their decision. They lifted the frontal part of their body, with the forelimbs stretched out, remained motionless for a few seconds and then moved to one of the flowers, this whole process taking them between 45 and 680 seconds.

Reflectance properties of flowers

A calculation of the excitation (E; Table 1) of the ultraviolet, the blue and the green receptors of honeybees by the innermost and the outermost parts (petals) of the jasmine flowers revealed a difference between the two morphs. The outermost parts did not differ in their reflectance properties between flowers with and without petaloid stamens (Table 1). However, there is a pronounced difference between the morphs with regard to the reflectance properties of the flower centre. The centre of flowers without petaloid stamens reflects less light in each region of the light spectrum relevant for bee vision (UV, blue and green), making the flower centre a contrasting mark to the approaching honeybee (euclidean distance in colour space = 0.617 ± 0.024 (mean ± SE), $N = 24$). However, the brightness of flowers was not related to their size ($R_p = -0.074$, $P = 0.628$, $N = 46$). When present, the petaloid stamens cover the flower centre and the whole surface of flowers reflects equally (euclidean distance in colour space = 0.076 ± 0.011 (mean ± SE), $N = 24$; Table 1). To visualise the colour contrast in the bee colour space, we plotted the contrasts for periphery and centre in flowers with and without petaloid stamens (Fig. 3). Therefore the presence or absence of petaloid stamens in a jasmine flower can also be perceived by *A. mellifera* due to differences in the contrast within each type of flower.

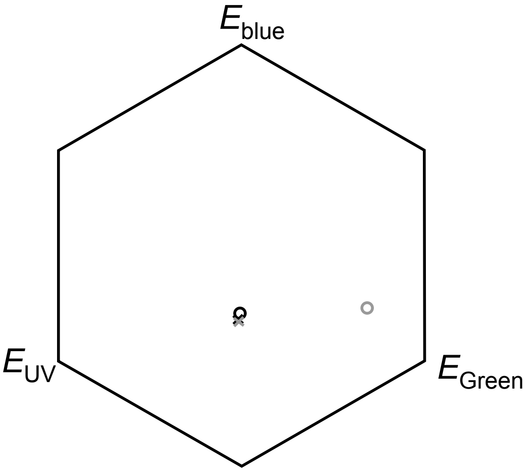

Fig. 3. The mean colour loci of flower periphery (crosses) and flower centre (circles) measured from *J. mesnyi* flowers that contained two stamens (grey cross & circle, $N = 24$) or one stamen and one petaloid (black cross & circle, $N = 24$).

Discussion

Our results on flower choice of pollinating insects and their predators add to previous work illustrating that crab spiders *Thomisus spectabilis* respond to floral signals in the same manner as honeybees *Apis mellifera* do, thus exploiting the communication between flower and pollinator (Heiling *et al.* 2004). In the field, both spiders and honeybees showed an inherent preference for *Jasminum mesnyi* flowers with two stamens that are full pollen productive and thus offered a greater pollen resource. In the other, less preferred morph of *J. mesnyi* one stamen is converted into a petaloid stamen.

Pollinating insects recognize pollen located in the inner corolla of flowers through various sensory modalities, including olfactory, visual, tactile and gustatory signals (for review *see* Lunau 2000). In our study, spiders and bees preferred flowers with a visible androecium over flowers where the inner corolla was covered by petaloid stamens. If the inner corolla is not visible, at least the visual signals will be obscured for the approaching flower visitors. The colour contrast between pollen and corolla is probably the most common colour pattern in flowers (Lunau 2000). In *J. mesnyi*, there is a pronounced colour contrast between the inner part of the corolla, if not covered by petaloid stamens, and the surrounding petals. It is likely that the honeybees based their choice of flower on this, but we did not test this directly.

With the stamens exposed, flowers may be easier to handle for a honeybee as compared with flowers with the stamen covered by petaloid stamens. Furthermore, as *J. mesnyi* flowers neglected by honeybees and spiders produce less pollen as compared with those containing two intact stamens, we cannot exclude that these flowers also produce weaker olfactory signals, which in turn might influence the response of pollinators to these flowers. It may be that our estimate of flower choice observed in the field has been biased by the proximity between flowers, which we did not measure. Bee visitation rates may be higher to areas that contain more flowers, thus minimising travelling effort for the honeybees. Our field observations however, could not detect any distribution patterns of flowers with one or two stamens. Both types of flowers seem to be distributed evenly throughout the plant.

A visual-olfactory synergism determines the flower choice of bees (e.g., Lunau 1992), which means that this choice is not determined by signals of a single modality but that bees perceive their foraging grounds as multimodal sensory entities (e.g., Gegear & Laverty 2001). In bumblebees (*Bombus terrestris*), olfactory signals facilitate colour discrimination and memory formation (Kunze & Gumbert 2001). However, in the absence of olfactory signals, these animals also visit odourless artificial flowers (e.g., Chittka *et al.* 2001). Similarly, in our system, honeybees may utilise a suit of signals and cues to perceive and assess flower quality.

Honeybees preferred *J. mesnyi* flowers with a diameter below the average. Our results contrast other studies, which revealed that within plant species, the duration and frequency of plant visits by pollinating insects increase with the size of flower corollae (Stanton & Preston 1988) and the number of flowers the plant contains (Morse & Fritz 1982, Morse 1986, Ohara & Higashi 1994). The two morphs of *J. mesnyi* used in our study did not differ in size, nor was there any relationship between corolla diameter and the brightness of flowers. Therefore, the decision of honeybees was unlikely affected by these visual characteristics. It may be that in *J. mesnyi* the size of flowers is linked to odour characteristics as a factor influencing the choice of honeybees, but we have no direct evidence for this. While crab spiders are able to perceive and respond to traits associated with pollen productivity of flowers, they obviously fail to exploit floral cues in terms of floral size aimed to attract honeybees in *J. mesnyi*, which might affect encounter rates to the benefit of bees. Alternatively, crab spiders may require a minimum size flower to position themselves on.

In the field, *T. spectabilis* was more frequently found on *J. mesnyi* that offered higher pollen resources and attracted higher numbers of honeybees. These results support previous findings on *Misumena vatia*, another species of crab spiders, showing that the quality of flowers (either nectar-producing or senescent), affects the probability of spider visits (Morse & Fritz 1982). Given the choice between two flowers containing one reproductive stamen and the other two reproductive stamens, the crab spiders preferred the fully rewarding flower. The results support our previous studies, which showed that *T. spectabilis* do not arrive at flowers by chance, but utilise odour signals to identify high quality flowers

(Heiling *et al.* 2004). However, studies on the visual system of various diurnal orb-web spider species revealed that the spectral sensitivity of their receptors ranged from green to ultraviolet (e.g., Yamashita & Tadeda 1976, Yamashita & Tadeda 1983, Barth *et al.* 1993). From studies on jumping spiders (Nakamura & Yamashita 2000) and our studies (A. M. Heiling & M. E. Herberstein unpubl. data) we know that spiders not only perceive colours but that they have the sensory capacity to visually discriminate between them. Thus, given the pronounced differences in the reflectance properties between the two morphs of *J. mesnyi*, the choice of *T. spectabilis* may have been guided by visible flower patterns. However, as we did not exclude odour in our experimental set up, we cannot dismiss the possibility that *T. spectabilis* also utilised olfactory differences between the two types of flowers.

The notion of flower quality in *T. spectabilis* obviously corresponds to that of honeybees, which may result in an increased chance of prey capture for these spiders. Thus, crab spiders greatly benefit from exploiting floral cues aimed to attract honeybees through increased prey encounter rates and ultimately higher growth rates and higher reproductive success (Fritz & Morse 1985). It is unlikely that the spiders used in our experiments based their flower choice on previous experience on jasmine flowers. For one, the spiders have been maintained in the laboratory for about eight months before being used in the experiment. Additionally, the spiders have been collected from a variety of flowers such as daisies, *Lantana* and other species of jasmine.

The presence of predators on flowers may impose selective pressures on their prey to avoid occupied flowers and perhaps even selection on flowers as these predators may reduce pollination. It is unlikely that the selective pressure imposed by crab spiders is sufficient to evoke counter adaptation by their prey or by the plants they occupy. Crab spider occupied flowers only make up a minute subset of flowers visited by pollinators. In fact, it is in the interest of signal exploiters to remain at low density relative to rewarding signals and avoid the evolution of counter strategies (Grafen 1990, Hasson 1994).

In conclusion, our study shows that crab spiders do not select floral hunting substrates randomly, but select them according to the presence of fully pollen producing stamens. This corresponds to the foraging choices of honeybees that also prefer flowers with two functional stamens. Thus the flower choice of spiders may increase their rate of prey encounter.

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