

Predator–prey coevolution: Australian native bees avoid their spider predators

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Australian crab spiders *Thomisus spectabilis* manipulate visual flower signals to lure introduced *Apis mellifera*. We gave Australian native bees, *Austroplebia australis*, the choice between two white daisies, *Chrysanthemum frutescens*, one of them occupied by a crab spider. The colour contrast between flowers and spiders affected the behaviour of native bees. Native bees approached spider-occupied flowers more frequently. However, native bees avoided flowers occupied by spiders and landed on vacant flowers more frequently. In contrast to honeybees that did not coevolve with *T. spectabilis*, Australian native bees show an anti-predatory response to avoid flowers occupied by this predator.

Keywords: *Thomisus spectabilis*; *Austroplebia australis*; predator–prey coevolution; floral signal

1. INTRODUCTION

Animal communication works through signals that elicit a specific response in a receiver or a group of receivers (Guilford & Dawkins 1995). Signals may evolve to mimic a cue that a receiver is pre-evolved to respond to, which is referred to as sensory exploitation (Johnstone 1997). For example, colourful flowers exploit the inherent sensory abilities of pollinating insects by attracting them (Chittka *et al.* 1994). In this system, pollinating insects benefit from nectar or pollen, while plants gain a reproductive service (Harder *et al.* 2001).

Signalling systems are often exploited or even manipulated, whereby either the signaller or the receiver does not benefit from the signal (Johnson 2000). Sensory exploitation and manipulation occur in the interaction between spiders and their prey. Orb-web spiders exploit the sensory biases of their prey by attracting them via ultraviolet (UV)-reflecting body colour (Craig & Ebert 1994) or UV-reflecting silk (see Herberstein *et al.* (2000) for a review). Similarly, nocturnal orb-web spiders construct their webs at artificially lit sites, thereby capturing numerous prey attracted to the light (Heiling 1999).

Crab spiders ambush pollinating insects on flowers and occupy sites where a high foraging success can be expected. They are attracted by flower odours (Aldrich & Barros 1995) and use visual and tactile cues for selecting hunting sites (Chien & Morse 1998). The Australian crab spider, *Thomisus spectabilis*, exploits the communication between flowers and European honeybees (*Apis mellifera*

by responding to the same floral signals as these honeybees do (Heiling & Herberstein 2004; Heiling *et al.* 2004). Furthermore, it manipulates visual floral signals. While European crab spiders appear camouflaged on flowers (Chittka 2001; Théry & Casas 2002), *T. spectabilis* produces a strong colour contrast in the UV range of the light spectrum, attracting honeybees (Heiling *et al.* 2003). This is in line with empirical data showing that bees are attracted to strongly contrasting marks on flowers (Lunau *et al.* 1996).

European honeybees did not coevolve with *T. spectabilis* but were introduced to Australia *ca.* 200 years ago. By contrast, native Australian bees that are also captured by *T. spectabilis* coevolved with this species. We test our prediction that native Australian bees evolved anti-predatory behaviour to avoid their predators, unlike the naive European honeybees.

2. MATERIAL AND METHODS

Thomisus spectabilis were collected in suburban areas of Brisbane, Australia. Females reach a body length of *ca.* 1 cm. Female coloration varies and we used only white ones in our experiments. Native bees (*Austroplebia australis*) that were kept in an outdoor hive at the University grounds were transferred into a growth house and trained to visit a feeding station (*ca.* 30% sucrose solution).

The experiments were performed in a growth house, covered on all sides with Perspex panels. The Perspex panels were permeable to all wavelengths, stimulating the three receptor types of bees (UV, blue and green) at similar levels compared with natural light (receptor excitation values: $E_{UV} = 0.73$ versus 0.75, $E_{blue} = 0.85$ versus 0.89, $E_{green} = 0.86$ versus 0.88, respectively). The E -values measure the physiological receptor voltage signals for each photoreceptor in the visual system of the hymenopterans (UV, blue and green) and do not carry a unit. They refer to the visual system of European honeybees (*A. mellifera*) only (for methods see Chittka 1996), as the spectral sensitivity functions for Australian native bees are not known.

We used fully developed white daisies *Chrysanthemum frutescens* (variety ‘Summer Angel’) and cut their petals to equalize the diameter of flowers to 4 cm. Each flower was placed into a black plastic lid and the pair of flowers arranged against a black background, with a distance of 10 cm between the flower centres. This experimental arrangement replaced the feeding station of the native bees. An anaesthetized *T. spectabilis* was placed on the petals of a randomly selected flower. We noted the number of native bees approaching the two flowers within a distance of 4 cm for a period of 4 min. We recorded the first visit by a native bee on either flower. These procedures were repeated using plastic foil covering each black plastic cup to exclude olfactory cues. The foil transmitted all light above 300 nm, with less than 5% attenuation. No spider and flower was used more than once.

We measured the spectral reflectance of all crab spiders and daisies 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, FL, USA). We averaged the six measurements and calculated the receptor excitation values. Using these E -values, we calculated the position of flowers and crab spiders within the honeybee visual colour hexagon, which is a projection of the three-dimensional photoreceptor signal space, and calculated the contrast created by crab spiders against the white petals of daisies (Chittka 1996).

3. RESULTS

The bee receptor excitation values of daisy petals for ultraviolet, blue and green varied (range of $E_{UV} = 0.657$ – 0.759 , $E_{blue} = 0.899$ – 0.917 , $E_{green} = 0.876$ – 0.882), with a difference between chosen and rejected flowers of less than 1% in each range of the spectrum. Thus, the choice of Australian native bees was not affected by the visual signals of daisies. *Thomisus spectabilis* created a colour contrast against *C. frutescens* (mean Euclidian distance \pm s.d. = 0.15 ± 0.03 ; figures 1 and 2), which did not differ between the two experiments. The colour contrast is caused by crab spiders reflecting more light in the UV range of the light spectrum than daisies (Heiling *et al.* 2003).

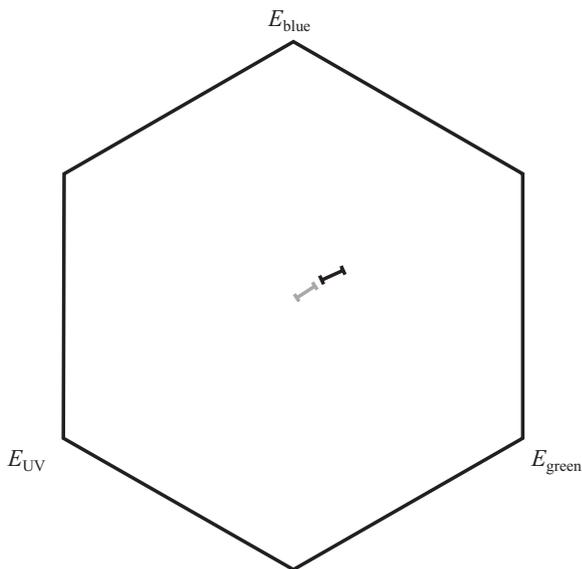


Figure 1. The range of colour loci of flower petals (black line; $n = 57$) and crab spiders (grey line; $n = 57$), calculated for the colour hexagon of honeybees.

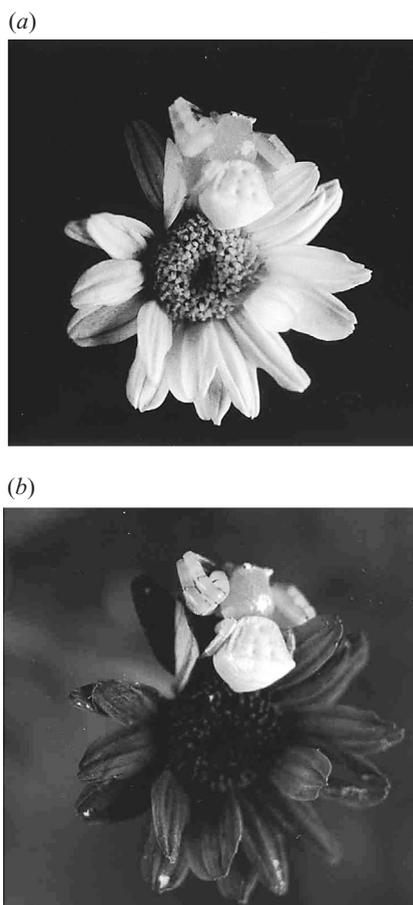


Figure 2. (a) The crab spider *Thomisus spectabilis* on a white daisy, photographed using light visible to humans. (b) The same animal photographed using only UV light to create an image that might resemble that perceived by honeybees.

The presence of white crab spiders on the petals of daisies strongly affected the response of native bees in the absence and presence of smell (figure 3). When smell was

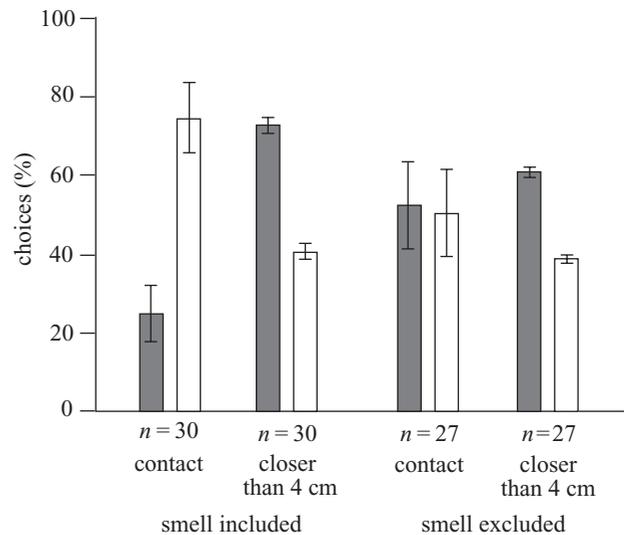


Figure 3. The effect of spider presence on the reaction of Australian native bees. Percentage of bees visiting flowers and bees coming closer than 4 cm to flowers occupied by crab spiders (filled bars) and vacant flowers (open bars) in the presence and absence of smell.

included, native bees approached spider-occupied flowers more frequently (Wilcoxon $Z = -4.636$, $p < 0.001$, $n = 30$; figure 3), but fewer bees landed on spider-occupied flowers, preferring vacant flowers (paired $t_{29} = -3.635$, $p = 0.001$). When smell was excluded, significantly more bees approached spider-occupied flowers (Wilcoxon $Z = -4.544$, $p < 0.001$, $n = 27$; figure 3). However, there was no difference in the number of bees landing on the foils covering vacant and spider-occupied flowers (paired $t_{26} = 0.28$, $p = 0.782$).

4. DISCUSSION

Predation is a key selective force that shapes the adaptation of prey, ranging from morphological to behavioural traits (Lima & Dill 1990). The interaction between predators and prey is dynamic: natural selection will favour prey with improved defensive capabilities at the same time as favouring more efficient predators (Vermeij 1994). Selection for anti-predatory traits will partly depend on the duration and intensity of the interaction. In our system, we tested for the presence of anti-predatory adaptations by comparing naive prey with prey that has presumably undergone selection to reduce or avoid predation.

We show that the coevolved *A. australis* perceive and avoid their spider predators, *T. spectabilis*. Unlike introduced European honeybees (Heiling *et al.* 2003), they were less likely to land on spider-occupied flowers. Nevertheless, both the naive and coevolved prey were attracted to spider-occupied flowers. *Austroplebia australis* visually perceive the contrast created by *T. spectabilis* against the daisies. We know nothing about the visual capabilities of *A. australis*. However, the photoreceptor sensitivities of stingless bees fall within the scatter of other Apidae (Chittka *et al.* 2001). Honeybees can distinguish colour differences down to a contrast of 0.01 (F. Bock, A. G. Dyer and L. Chittka, unpublished data), far lower than the colour contrast in our study. By creating a colour

contrast, crab spiders may appear as nectar guides, which are known to attract pollinating insects (Lunau *et al.* 1996).

Unlike introduced prey, coevolved prey did not land on the spider-occupied flower. We do not know how native bees discriminate the predator. They may take longer to inspect the flower, allowing them to identify the spider. We tested if they use olfactory cues from the spider to detect their presence. Excluding smell did not affect the rate of flower approach, but the rate of landings. However, we are not confident that these results identify the predator recognition mechanism because the plastic foil simply reduced the rate of landings on occupied and vacant flowers in Australian native bees, which was not the case when we used European honeybees.

Honeybees are renowned for their excellent learning capabilities (Menzel *et al.* 1993; Giurfa *et al.* 1999) as are Australian native bees (Nieh *et al.* 2000). However, we can exclude any learning effect in our experiment, as the beehive was kept for several months prior to the experiment without any exposure to crab spiders.

In the coevolutionary arms race between crab spider and native pollinator, it appears that the native pollinator currently has the upper hand and it may be that spiders, in turn, will respond to this predator-avoidance adaptation by reducing conspicuousness or by exploiting a different sensory modality to attract native prey. It is tempting to speculate how non-social native bees respond to crab spiders, as the fitness cost of a successful predatory attack would be higher on a reproducing female compared to a worker bee. We predict even greater anti-predatory efficiency under this scenario.

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