

sioning is low and their period of parental care is the longest of any bird². Their low reproductive rate and high life expectancy (more than 30 years) make them exceptional even among long-lived birds¹⁰ and, combined with their unusual morphology and foraging strategy, are examples of extreme adaptations to poorly provisioned tropical waters.

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Pollinator attraction

Crab-spiders manipulate flower signals

Some European species of crab-spider match the colour of the flower on which they lie in wait to ambush insect pollinators, a tactic that is presumed to camouflage them from their intended prey and from predators^{1,2}. Here we show that the coloration of an Australian species of crab-spider, *Thomisus spectabilis*, which is cryptic on the white daisy *Chrysanthemum frutescens* to the human eye, is highly conspicuous to ultraviolet-sensitive insect prey — but that, instead of repelling foraging honeybees (*Apis mellifera*) as might be expected, the contrast of the spider against the petals makes the flowers more attractive. The spider is apparently exploiting the bee's pre-existing preference for flowers with colour patterning.

Visual signals communicated at ultraviolet wavelengths, which are invisible to humans and are therefore more difficult to analyse^{3,4}, may be used by ambush predators to manipulate their prey's behaviour and increase capture success. We have

investigated how *T. spectabilis* interferes with floral signals, and the effect of its visibility on the attractiveness of the flower to pollinating insects.

Under natural light conditions, we presented honeybees with pairs of randomly selected white daisies, one of which carried an anaesthetized spider, and recorded which of the two flowers the bee visited first. We then repeated the experiment using a plastic foil covering on each flower and spider; the cover blocked olfactory cues but was transparent to light of wavelengths greater than 300 nm.

Compared with empty flowers, the presence of white crab-spiders on the petals of daisies evidently attracted honeybees more, in both the presence and absence of olfactory cues (Fig. 1a). This indicates that the bees must have been guided by visual signals alone, and that the visual signal generated by the spider renders the flower more inviting to bees.

To identify this signal, we measured the spectral reflectance from 300 to 700 nm of the flower petals and of the spiders' abdomens. We calculated the colour contrast⁵ of the spiders against the flower petals and

computed the euclidean distances in the colour space of hymenopterans². We found that, compared with the flowers, white spiders reflect a considerable amount of ultraviolet light.

There was also a pronounced difference in the honeybee receptor-excitation values generated by spiders and flowers at ultraviolet wavelengths (Tukey-tests, $P < 0.001$ and $P < 0.001$, respectively), but not in the blue and green regions of the spectrum (ANOVA, $F_{2,74} = 136.8$, $P < 0.001$; Fig. 1b), where receptor excitation is comparable for both (Tukey test, $P = 0.901$). Consequently, instead of being cryptic, as they are to humans, the spiders produce a strong colour contrast that is detectable by their hymenopteran prey (mean euclidean distance in colour space \pm s.e., 0.14 ± 0.01 ; $n = 25$). The values for colour contrast are well above the detection threshold of 0.05 (ref. 2; one-sample t -test, $t_{24} = 7.6$, $P < 0.001$).

We conclude that *T. spectabilis* uses quite the opposite signalling strategy to that known to be used by other crab-spiders^{1,2}. *T. spectabilis* is difficult to perceive from far away, when bees use only their green-receptor signal to detect objects⁶, but is highly conspicuous in the insect visual spectrum when seen at close quarters. Because ultraviolet-reflecting white flowers are extremely rare in nature⁵, the spider will contrast strongly with almost any natural flower.

T. spectabilis will also be just as conspicuous to other flower visitors, as all known pollinating insects, including stingless bees⁷ (which are the spider's most likely Australian native prey), perceive ultraviolet light. We propose that the presence of spiders on flower petals creates a colour pattern that is particularly effective because bees have a pre-existing bias towards it — an idea that is consistent with empirical data showing that bees innately prefer flowers with strongly contrasting markings⁸.

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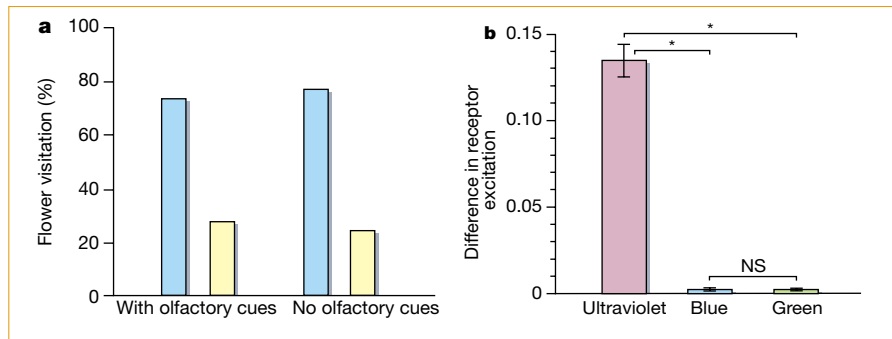


Figure 1 The effect of the presence of the crab-spider *Thomisus spectabilis* on the white daisy (*Chrysanthemum frutescens*) on flower visitation by honeybees (*Apis mellifera*). **a**, Proportion of bees that visit vacant daisies (yellow bars) and daisies occupied by spiders (blue bars) in the presence (binomial test, $n = 33$, $P = 0.0045$) and absence ($n = 25$, $P = 0.0053$) of olfactory cues. All spiders, flowers and bees were used only once. **b**, Difference in honeybee colour-receptor excitation values (mean \pm s.e.; for methods, see ref. 2) between spiders' abdomens and daisy petals at different wavelengths (ultraviolet receptors, $\lambda_{\text{max}} = 345$ nm; blue receptors, $\lambda_{\text{max}} = 440$ nm; green receptors, $\lambda_{\text{max}} = 535$ nm; ref. 7). Tukey test, asterisk denotes $P < 0.001$; NS, not significant.

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