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Foraging at a safe distance: crab spider effects on pollinators

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Abstract. 1. The ability of pollinating insects to discover and evade their predators can affect plant–pollinator mutualisms and have cascading ecosystem effects. Pollinators will avoid flowers with predators, but it is not clear how far away they will move to continue foraging. If these distances are relatively small, the impact of predators on the plant–pollinator mutualism may be lessened. The plant could continue to receive some pollination, and pollinators would reduce the time and energy needed to search for another patch.

2. A native crab spider, *Xysticus elegans*, was placed on one cluster in a small array of *Baccharis pilularis* inflorescence clusters, and the preferred short-range foraging distances of naturally visiting pollinators was determined.

3. Nearly all pollinator taxa (honey bees, wasps, other Hymenoptera, and non-bombyliid flies) spent less time foraging on the predator cluster.

4. The key result of this study is that inflorescences within 90 mm of the crab spider were avoided by visiting honey bees and wasps, which spent three- and 18-fold more time, respectively, foraging on more distant flower clusters.

5. Whether honey bees can use olfaction to detect spiders was then tested, and this study provides the first demonstration that honey bees will avoid crab spider odour alone at a food source.

Key words. Crab spider, foraging, honey bee, olfaction, pollination, predation, public information.

Introduction

The ability of prey to detect and avoid predators plays a major role in structuring ecosystems, in part by altering the spatio-temporal distribution of prey within a landscape (Laundré *et al.*, 2010; Wirsing *et al.*, 2010). Prey decision-making is affected by information about predator location and should be tuned to allow prey to forage in a dangerous world (Krupa & Sih, 1998). For prey that are pollinators, such decisions have a broad importance, because pollination is a key ecosystem service (Fisher & Turner, 2008). Predators can disrupt the plant–pollinator mutualism by deterring pollinator visitation, resulting in reduced seed set (Suttle, 2003), fruit production (Dukas, 2005; Hanna *et al.*, 2012) and fruit biomass (Antiqueira & Romero, 2016). However, in some cases, predators can attract pollinators and thereby increase seed weights (Welti *et al.*, 2016)

or increase the plant's reproductive success (fruit and seed set) by deterring less effective pollinators (González *et al.*, 2013). Thus, the ability of pollinators to detect predators and fine-tune where and for how long they forage has complex, cascading ecosystem effects (Knight *et al.*, 2006).

In general, predator presence decreases the rate of pollinator visitation (Elliott & Elliott, 1994; Dukas & Morse, 2003; Suttle, 2003; Dukas, 2005; Gonçalves-Souza *et al.*, 2008; Jones & Dornhaus, 2011) because insect pollinators usually avoid inflorescences occupied by predators (Romero *et al.*, 2011; Antiqueira & Romero, 2016). For example, crab spiders (Thomisidae) are common ambush predators that prey upon a wide variety of insect pollinators (Lovell, 1915; Nentwig, 1986). Insect pollinators therefore decrease visitation when crab spiders are on inflorescences of milkweed (Dukas & Morse, 2003), slickspot peppergrass (Robertson & Maguire, 2005) or other plant species (Reader *et al.*, 2006). Visitation rates are important because they influence the probability of pollination (Kearns & Inouye, 1993). In addition, the duration of pollinator visitation can be positively correlated with pollinia removal (Fishbein & Venable, 1996) and with increased pollen deposition on stigmas (Thomson, 1986).

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The distances at which this predator avoidance occurs are not clear. A study by Miller *et al.* (2014) showed that grasshoppers adapted the distances they moved in order to avoid spider predators by appropriately reducing their motion levels. We hypothesize that insect pollinators can detect the predator and determine a safer foraging distance that will decrease the probability of predation. The extent of this safe foraging distance is important. If pollinators can tolerate foraging at short distances from a spider, the spider-hosting plant could continue to receive some pollination and pollinators would be able to reduce the time and energy expended in searching for another patch. To the best of our knowledge, no studies have explicitly tested this hypothesis by providing insect pollinators with an array of choices at different distances from the predator and testing the effect of distance. For example, it is not known whether the fine-scale space use of pollinating insects is altered by the presence of spiders.

A separate, but closely related, question is how pollinators detect predators. Prey use multiple modalities to identify predators, and vision and olfaction are among the most important information channels (Kats & Dill, 1998; Weissburg *et al.*, 2014). Of these two senses, pollinator visual detection of predators, particularly crab spiders, has received the most attention. Crab spiders can engage in crypsis by colour matching with their floral backgrounds to hide from pollinators (Defrize *et al.*, 2010; Anderson & Dodson, 2015). Bees that have co-evolved with such spiders can usually see and avoid them (Heiling & Herberstein, 2004). In this evolutionary arms race, spiders have innovated with UV patterns that heighten their conspicuousness against the background and thereby attract bees (Tso *et al.*, 2004; Herberstein & Gawryszewski, 2012), exploiting their innate preferences for floral UV patterns (Heiling *et al.*, 2003). Moreover, some crab spiders may regulate their degree of UV reflectiveness to better entice prey (Llandres *et al.*, 2011b). Spiders can therefore use multiple visual strategies – web colour, web ornaments, body colour and body movements – to assist prey capture (Théry & Casas, 2009).

Somewhat surprisingly, far less is known about the ability of pollinators to detect and avoid spider odours, although bees have excellent olfactory abilities (Gadenne *et al.*, 2016) and can use this ability to avoid predators. For example, bees avoid the visual and olfactory cues of ants (González & Rodríguez-Gironés, 2013). Ant odours reduce bumble bee pollination of artificial flowers (Cembrowski *et al.*, 2014). Honey bees can avoid the odour trails of predatory ants (Li *et al.*, 2014), ant odour cues (Sidhu & Wilson Rankin, 2016) and a potential by-product of predation, honey bee haemolymph (Goodale & Nieh, 2012).

Although multiple studies have demonstrated that bees can see and avoid (or be attracted to) crab spiders, no studies to date have directly tested whether honey bees can detect and avoid crab spider odour alone. Reader *et al.* (2006) suggested that honey bees could avoid spider odour: bees avoided flowers upon which a spider had walked and may have deposited spider odour. We know that honey bees can sense and avoid a freshly dead crab spider (Dukas, 2001) or a dried spider (Brecht *et al.*, 2010). Thus, predator motion or another aspect of a living predator is not necessary to elicit avoidance. However, both of these dead

spider treatments provided olfactory and visual cues. Can bees avoid spider odour alone?

We thus tested the ability of pollinators to avoid a crab spider predator and their preference for safer inflorescences at relatively short-range distances from this predator. The first two experiments tested whether pollinators from various taxa would spend less time on an inflorescence with a predator (Experiment 1) and whether they would forage further away from the predator (Experiment 2). We chose a common native angiosperm species, coyote bush (*Baccharis pilularis* de Candolle; Fig. 1), a dioecious perennial shrub that is abundant in California coastal sage scrub (Rudgers & Whitney, 2006), that hosts crab spiders (Bolger *et al.*, 2008) and that is visited by a wide variety of insect pollinators (Fig. 2). For our predator, we used a native crab spider, *Xysticus elegans* Keyserling (Araneae: Thomsidae), which is a generalist ambush predator (Riechert & Lawrence, 1997) and which we commonly found on *B. pilularis*. These small spiders are among the most common and widespread *Xysticus* species in North America, are brown in colour (Fig. 1) and have a carapace that is approximately 2.7 mm long (Turnbull *et al.*, 1965).

Because our experiments showed that honey bees (Hymenoptera: Apidae: *Apis mellifera* Linnaeus), among other pollinators, could avoid crab spiders, we were inspired to test honey bee avoidance of crab spider odours. Visual avoidance probably played a role. Honey bees may recognize crab spider appearance (Gonçalves-Souza *et al.*, 2008; Romero *et al.*, 2011). However, visual detection alone may be insufficient because crab spiders can hide in blossoms and may be cryptically coloured (Morse, 1981). Selection should therefore favour the ability to detect and recognize crab spider odour. We therefore tested whether the odour of *X. elegans* is sufficient to elicit honey bee avoidance (Experiment 3).

Methods and materials

Field sites

We used two coastal sage scrub sites in southern California (bee foraging region 3; Ayers & Harman, 1995) that provide habitat for native and introduced pollinators and their spider predators: the Scripps Coastal Reserve (32°52'32"N, 117°14'52"W) and the coastal sage scrub area surrounding the UCSD Biological Field Station (BFS, 32°53'13"N, 117°13'48"W). Permits were obtained from the UCSD Natural Reserve System. Each field season (Experiments 1 and 2), we conducted 2-h-long trials for 30 h per field site for 60 observation-hours year⁻¹ and 120 h total over 2 years.

Experiment 1: Do predators influence pollinator foraging duration decisions?

We tested whether pollinators would spend less time foraging on an inflorescence cluster with a crab spider present (the dangerous cluster). To obtain spiders and avoid disturbing our field site, we sweep-netted *B. pilularis* at other locations to obtain *X. elegans* spiders. Although this species is sexually dimorphic (Turnbull *et al.*, 1965), most of the spiders that we

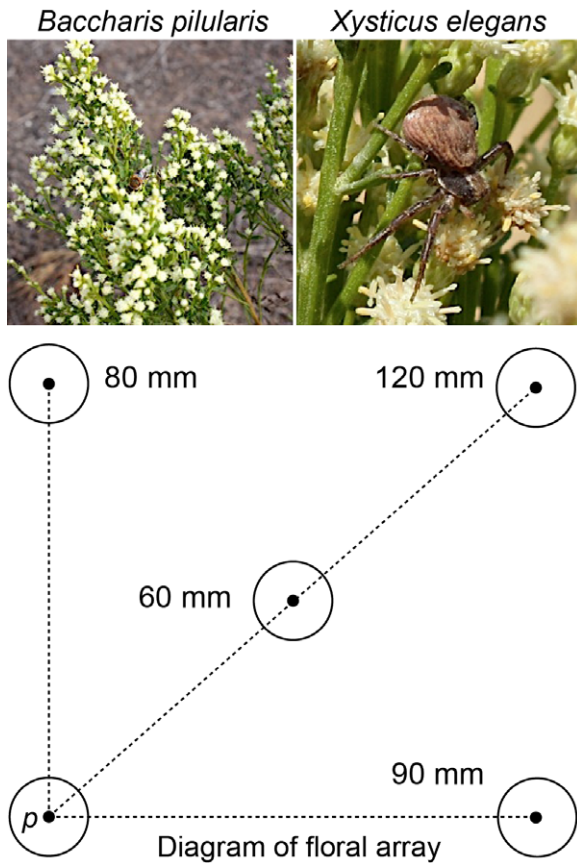


Fig. 1. The study plant (*Baccharis pilularis* with a foraging *Apis mellifera* in the centre of the image), a crab spider (*Xysticus elegans*) and the rectangular foraging array. The predator (*p*) was randomly placed at one of the corner locations (the dangerous inflorescence cluster). Distances to each of the safer inflorescence clusters are shown. Because of the symmetry of this design, distances between the safer inflorescences and the dangerous inflorescence are the same, regardless of which corner was chosen for the predator. [Colour figure can be viewed at wileyonlinelibrary.com].

used were of similar size (2.5–3 mm carapace) and probably, based upon our random sampling, a mixture of males and females. Each spider was maintained in good condition in a plastic container on a diet of three crickets week⁻¹. We used a different crab spider per trial. After each trial, spiders were recaptured to avoid introducing new predators to the field sites. In total, we used 40 adult crab spiders over 40 trials.

At each field site, we randomly chose a large inflorescence patch (approximately 2 m²) that was being visited by pollinators, randomly selected and harvested five fresh inflorescence clusters from within this patch (~20 inflorescences per cluster) that had no predators based upon careful visual inspection, and placed each cluster into a 15 ml conical centrifuge tube with 7 ml of water to prevent wilting. We then immediately presented the fresh inflorescences to pollinators. To ensure that the inflorescences did not differ, on average, in pollen content or nectar sugar concentration from the focal patch or from the general foraging available to bees at the research site, we did not bag

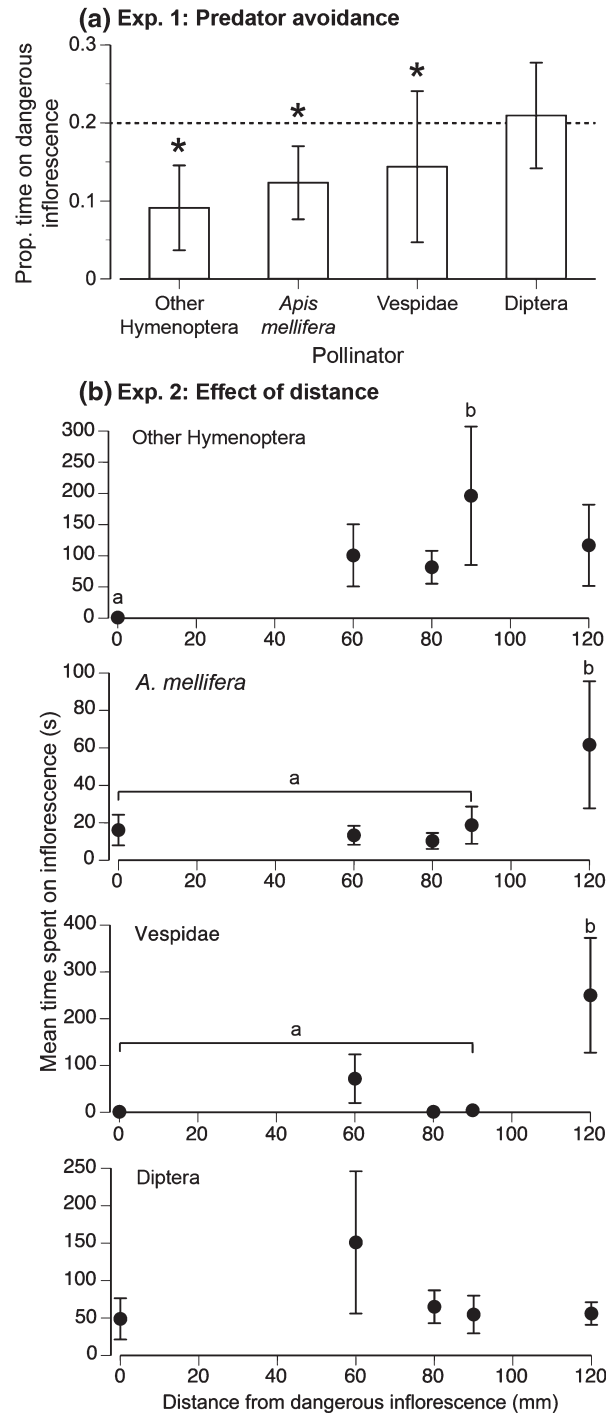


Fig. 2. (a) Effect of predator on the proportion (prop.) of time spent by pollinators on the dangerous inflorescence cluster. Stars indicate which pollinator type spent significantly less time than predicted (dashed line). (b) Effect of distance from the dangerous inflorescence on the visitation time spent by each pollinator type. Standard error bars are shown. Different letters indicate significant differences. There was no significant effect of distance upon Dipteran visits.

them the previous night. The collected inflorescences should therefore have contained approximately the same quantity and concentrations of pollen and nectar that were available, on average, in the patch and field site. Each trial used a different inflorescence patch.

To create an array of inflorescence clusters, we placed one tube in the centre and four in the corners of a rectangular tray (Fig. 1). The dangerous cluster was always at one of the four corners, yielding four distances between the dangerous cluster and the safer ones: 60, 80, 90 and 120 mm (Fig. 1). Because of the radial symmetry in this array, we could place the predator at any corner and maintain the same distances to the safer inflorescences. We attached this tray to a wooden rod and placed it 1 m away from and at the same height as the floral patch. Observers sat 1 m away from the tray.

We used a wood stick to gently place a crab spider on one randomly selected corner cluster in our array, taking care to not harm the spider or inflorescences. We did not allow the spider to move to a different cluster. During the trials, spiders rarely attempted to leave their assigned cluster. In those few cases when a spider left its cluster, it usually dropped down the stem, but did not try to move to a different cluster. When this happened, we used a stick to carefully move the spider back to its assigned cluster.

We observed the individual behaviour of naturally foraging pollinators. We did not train pollinators or otherwise enhance their natural rate of visitation. To avoid altering pollinator behaviour, we did not mark or capture them. The nectar provided by flowers was not supplemented, and thus individuals were unlikely to return to our small array after visiting it because the much larger natural patch was only 1 m away. However, because of potential revisitation, we included trial as a factor in our analyses (see later). We did not include the choices of pollinators that arrived when other pollinators were on the array to avoid potential social facilitation effects (Avarguès-Weber *et al.*, 2015), but such overlapping visits occurred very rarely. Each cluster was visited an average of 1.1 times h^{-1} by a pollinator, which spent a median time of 10 s foraging.

We visually classified pollinators into six groups: *A. mellifera*, Vespidae, other Hymenoptera (largely consisting of halictine and augochlorine bees) and Diptera. Honey bees were a special focus of our study because they were the most frequent visitors to our array (33.6% of all visits). We recorded the total amount of time that each pollinator spent on a safe or dangerous inflorescence cluster, summing the times spent on these cluster types when a pollinator visited multiple clusters in a single trip to the array. For example, a pollinator that visited two safe clusters for 5 s each during a single foraging trip would be recorded as visiting safe clusters for 10 s. Pollinators chiefly collected nectar.

Experiment 2: Do predators influence pollinator spatio-temporal foraging decisions?

Our array was designed to simulate a small patch of inflorescences, and we did not expect pollinators to discriminate between the close distances within the array. We therefore did not record the distances at which pollinators foraged in Experiment 1. However, by the end of Experiment 1, we noticed that

pollinators spent more time on clusters farther away from the predator cluster. In our second field season, we therefore conducted Experiment 2, which was identical to Experiment 1, except that we measured the time spent by each pollinator at each cluster distance (0, 60, 80, 90 and 120 mm; Fig. 1) from the dangerous cluster.

Experiment 3: Testing honey bee avoidance of spider odour

The crab spider, *X. elegans*, is a small brown spider that can be rather inconspicuous. Given the results of Experiments 1 and 2, we tested the hypothesis that honey bees could use spider odour to detect and avoid this predator. We used two-feeder choice tests (methods of Goodale & Nieh, 2012) to test whether honey bees would avoid spider odour. The feeder was a 4-cm-diameter Petri dish painted pink on its exterior base to facilitate forager orientation, filled with 5 ml of 2.5 M unscented sucrose solution, and centred in a Petri dish (9 cm diameter) painted white. We placed the feeder on a 20-cm-diameter white circular platform atop a 1-m-high tripod. Bees were trained to a training feeder (methods of von Frisch, 1967) located 40 m from the focal colony. To begin the 30 min trial, we covered the training feeder with an opaque plastic cylinder, causing bees to choose between the test feeders. We then set out two identical test feeders, each on a separate tripod and spaced 30 cm apart, equidistant from the focal colony and 60 cm from the training feeder. Test feeders were empty.

We prepared an extract of crab spider odour (Allan *et al.*, 2002) by gently agitating frozen spiders for 72 h in reagent-grade hexane (1 spider $100 \mu\text{l}^{-1}$ hexane). The experimental feeder consisted of 100 μl of odour extract (one spider equivalent) pipetted onto the centre of a 2.5-cm-diameter circle of filter paper weighted down with a 1.3-cm-diameter metal disc and placed under the 4-cm-diameter feeding dish. The control feeder was identical, but we used 100 μl of pure hexane instead of the odour extract.

We swapped test feeder tripod positions every 5 min to prevent potential site bias from affecting our results. We defined a choice as a bee landing within the white Petri dish, as they normally would to feed. We then immediately captured the bee with a snap-cap plastic vial placed over the bee and changed the white Petri dish to remove potential bee-deposited odour marks. We only counted choices made in the absence of other bees near the feeders to ensure independent choices. At the end of each trial, captured bees were chilled, marked with acrylic paint on their thoraces, and released so that their choices would not be recounted. We then carefully washed all equipment with laboratory detergent and ethanol, fully drying it in the sun before reuse. All experimenters wore clean, disposable vinyl gloves to avoid contaminating items with scent. We conducted these experiments at the BFS site with four *A. mellifera* colonies, running nine trials and conducting only one trial day^{-1} .

Statistics

For Experiment 1, we calculated the proportion of time that pollinators spent on the predator inflorescence cluster and use

two-tailed Wilcoxon signed-rank (WSR) tests to determine if the mean was significantly different from the null expectation of equal visitation to all five clusters (20%).

To determine if pollinators spent more time foraging on clusters further away from the dangerous one (Experiment 2), we used a generalized linear model (GLM) with an exponential distribution, log link and maximum likelihood estimation to test the effect of pollinator type and distance from the dangerous cluster upon the time spent at each inflorescence cluster. We included trial in this model to account for potential multiple visits by the same individual, although only 3.3 pollinators visited our array per 2 h trial and dozens visited the adjacent floral path. Including trial in the model also allowed us to deal with the potential lack of data independence due to similar conditions, such as weather, during a trial. We then used *post hoc* contrast tests to analyse differences based upon inspection of the data (Fig. 2b). All analyses were conducted with (JMP v10, Cary, North Carolina). To analyse honey bee avoidance of spider odour (Experiment 3), we conducted χ^2 tests with Microsoft EXCEL v14.5.5.

Results

Over both field seasons (Experiments 1 and 2), pollinators foraged for 6.13 h during 60 observation-hours with foraging time divided as follows: *A. mellifera* (18.4%), Vespidae (14.1%), other Hymenoptera (35.3%) and Diptera (32.2%). Out of 331 pollinator visits to our arrays in both seasons, spiders successfully captured only a single forager, a bombyliid fly: 0.3% overall pollinator capture rate (successful captures/total number of pollinator visitations to the array) and 1.1% Diptera capture rate (successful captures/total number of dipteran visitations to the array). In calculating these capture rates, we considered a pollinator that landed on multiple inflorescences within the array as making a single overall visit to the array because the array covered a relatively small area.

Experiment 1: Hymenoptera spent less time foraging on the dangerous inflorescence cluster

If pollinators did not avoid the predator, they should have spent 20% of their time on each of the five inflorescence clusters in the array (Fig. 1). However, Hymenoptera (*A. mellifera*, Vespidae and other Hymenoptera) spent a significantly smaller proportion of time on the dangerous cluster (WSR tests: *A. mellifera*, $W_{36} = -143.5$, $P = 0.018$; Vespidae, $W_{12} = -32.5$, $P = 0.006$; and other Hymenoptera, $W_{25} = -123.5$, $P < 0.0001$). Diptera did not avoid the dangerous cluster ($W_{33} = -53.5$, $P = 0.34$; Fig. 2a).

Experiment 2: Hymenoptera preferred to forage farther away from the predator

In this experiment, we tested the effects of distance from the dangerous cluster. There were significant effects of pollinator type (GLM, $\chi^2_3 = 12.68$, $P = 0.005$), distance (GLM, $\chi^2_1 =$

8.78, $P = 0.003$) and the interaction pollinator type \times distance (GLM, $\chi^2_3 = 13.40$, $P = 0.004$) because Diptera did not avoid the dangerous cluster (Fig. 2b).

Specifically, *A. mellifera* and Vespidae spent significantly more time foraging on the farthest cluster from the predator (0 vs. 120 mm: contrast_{*A. mellifera*} L-R $\chi^2_1 = 4.59$, $P = 0.03$, contrast_{Vespidae} L-R $\chi^2_1 = 11.95$, $P = 0.0005$). Other Hymenoptera similarly preferred a farther cluster (0 vs. 90 mm: contrast_{Other Hymenoptera} L-R $\chi^2_1 = 5.71$, $P = 0.016$).

Experiment 3: Honey bees avoided spider odour

Bees strongly avoided the odour of *X. elegans* (Fig. 3). On average, $88 \pm 3\%$ of foragers chose the feeder without spider odour ($N = 391$ bees from four colonies). Bees from each tested colony avoided spider odour in each of the nine trials ($\chi^2 \geq 5.83$, $P \leq 0.016$). Bees from all colonies showed a similarly strong aversion (per colony, 78%, 89%, 94% and 96% avoided the spider odour).

Discussion

We tested the foraging preferences of native insect pollinators and honey bees on inflorescences and showed that pollinators (Vespidae, *A. mellifera* and other Hymenoptera) spent significantly less time foraging on the inflorescence with a crab spider predator, *X. elegans* (Fig. 2a). Honey bees and wasps spent an average of four- and 13-fold more time, respectively, on the inflorescence cluster furthest away from the crab spider (120 mm) as compared with time spent on inflorescences at distances of 0–90 mm from the spider. Other Hymenoptera spent three-fold more time on the 90 mm cluster as compared with clusters closer to the spider (Fig. 2b). Pollinators may have avoided the spider, in part, based upon its odour. In a separate experiment, honey bee foragers showed a seven-fold preference for a control feeder over a feeder with crab spider odour (Fig. 3).

These results have implications for pollination. *Baccharis pilularis* is dioecious and a single plant typically has inflorescences of the same sex spread out over diameters of approximately 2.0 m, (Rudgers & Whitney, 2006). A 120 mm distance is thus well within the area of flower clusters produced by a single plant of these species, and the presence of a single crab spider should not, therefore, exclude all pollination of a female plant or the collection of pollen from a male plant. In general, crab spider density on plants was relatively low. We collected crab spiders by sweep-netting the same species of plants, and <10% of *B. pilularis* plants had a crab spider. Typically, there was no more than one crab spider per plant. Dukas and Morse (2003) showed that crab spiders were similarly rare, occurring on only 1.1% of milkweed inflorescences. Modelling suggests that, even at such a low density, ambush predators can have a strong impact on the populations of solitary bees (Rodríguez-Gironés, 2012), but what about the other half of this mutualism? Our results suggest that a single crab spider per plant can alter pollinator behaviour but should not completely disrupt the pollinator–plant mutualism because pollinators would forage just 90–120 mm away from the dangerous inflorescence.

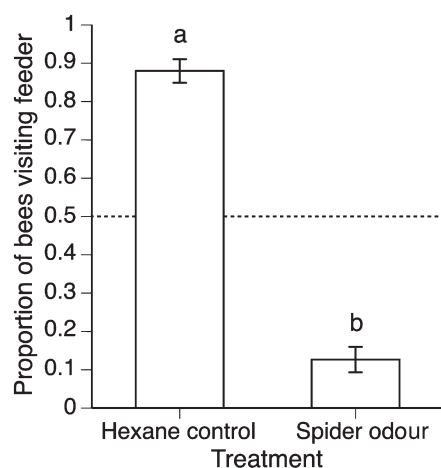


Fig. 3. Effect of spider odour on honey bee choices in a paired-choice foraging test. The dashed line shows the null hypothesis expectation. Standard error bars are shown. Different letters indicate significant differences.

Predator avoidance

Predation risk reduces pollinator floral visitation and the time that pollinators spend on flowers (Romero *et al.*, 2011). However, it was not clear whether pollinators prefer to forage further away from predators within a rewarding patch. Demonstrating such a distance effect provides an insight into pollinator foraging strategies: how pollinating insects gauge risk and determine an acceptable safe distance. In retrospect, it would have been beneficial to conduct replicate trials with arrays that had no spiders at all on the same days and times as the spider array trials and measure visitation. This control may have shown a higher overall foraging rate on inflorescences without spiders than on an array with a single spider. However, with our design, we were still able to show a significant and somewhat surprising effect with an inflorescence separation of only 120 mm.

Pollinator visit sequence could also be important. However, our results show that there was an overall effect of the dangerous inflorescence on pollinator choices: crab spider presence decreased the amount of time that some pollinators (Vespidae, *A. mellifera* and other Hymenoptera) spent on inflorescences (Fig. 2a).

Our goal was to provide pollinators with the same average rewards that they would naturally encounter within a *B. pilularis* patch, and thus we did not bag inflorescences before testing. Our inflorescences, like ones in the larger adjacent patch, therefore probably had variation in nectar concentration and quantity, but these were not pre-selected and were therefore probably randomly distributed. This should not have affected our experimental results.

The effects of prior pollinator visitation on subsequent pollinators were probably minor. The median time that a pollinator spent on a cluster was 10 s and each cluster was visited an average of 1.1 times h^{-1} by a pollinator. This low rate and duration of visitation meant that the majority of flowers in our array were unvisited by pollinators during a trial. Even if the nectar depleted slightly over the trial, it should not account for

the longer time spent foraging on the more distant inflorescence cluster.

Crab spiders can prey upon honey bees (Morse, 1986) and wasps (Lovell, 1915) and both groups spent the most time foraging at the inflorescence cluster furthest away (120 mm) from the predator inflorescence cluster (Fig. 2b). Honey bees and wasps evidently found this distance acceptable, even though they had far more choices 1 m away in the natural patch of inflorescences. Other Hymenoptera similarly preferred a more distant cluster (90 mm), although not the 120 mm cluster, perhaps because of high variation in durations spent on the furthest cluster (Fig. 2b).

Honey bees may have preferred the 120 mm cluster because, at this distance, their ability to see the predator was minimized. They may have chosen an inflorescence at which there was no visible predator nearby. Including legs, each crab spider was approximately 10 mm in diameter. Giurfa *et al.* (1996) demonstrated that honey bee can detect green-contrasting stimuli that subtend a visual angle of approximately 5° . Thus, honey bees may only have been able to detect a 10-mm-diameter spider within a distance of 90–110 mm. At the 120 mm inflorescence, the spider should have been difficult to see. It would be interesting to examine this hypothesis in future studies.

It is unclear why Diptera did not avoid the predator. However, Diptera have exceptionally fast motor escape skills (Card & Dickinson, 2008). In line with our results, Llandres *et al.* (2011a) found that honey bees were more susceptible to crab spider predation than flies. For Diptera, a larger floral array may have revealed distance preferences. However, we wished to determine if the presence of a spider on one inflorescence within a naturalistic patch of inflorescences would alter forager time allocations in the patch. Significantly larger gaps between inflorescences did not occur in natural patches at our field site.

Our 0.3% rate of successful predation is similar to the 0.7% reported by Morse (1986) for successful predation attempts by crab spiders on milkweed inflorescences. Like us, he found that spiders had the greatest success capturing Diptera as compared with taking other insect pollinators (Morse, 1979). We fed our spiders with crickets to keep them in good condition and this may have decreased their motivation to hunt. Nonetheless, our spiders significantly altered spatio-temporal visitation by pollinators, demonstrating that successful predation is not required for predators to exert significant effects (Lima, 1998).

Predator detection

Honey bees detected and avoided crab spider odour at a food source (Fig. 3). Honey bees may not always avoid crab spider odour, particularly when the spider provides an attractive UV pattern (Heiling *et al.*, 2003). However, we showed that spider odour alone could provide public olfactory information about predation that flows between predators (crab spiders) and prey (honey bees). These data reinforce the importance of olfaction in the ecology of information, influencing how pollinators obtain food and how plants are pollinated. Prior research has demonstrated that bee pollinators learn to avoid nectar-depleted flowers by recognizing the odour of cuticular

hydrocarbons deposited by previous visitors (Goulson *et al.*, 2000; Leadbeater & Chittka, 2007; Yokoi & Fujisaki, 2008; Witjes & Eltz, 2009). Our results suggest that we should also consider a broader olfactory landscape that includes detection of predators and predation events, all of these cues weighing in to influence floral visitation and, ultimately, pollinator and plant fitness. Given that pollinators can, in some cases, visually detect pollinators, there may be a complex interplay, perhaps even an arms race, between pollinator detection skills and spider crypsis. It is unclear which modality, visual or olfactory, will be more important for spider detection, but it would be interesting to test for olfactory crypsis.

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