

REPORT

Effects of perceived danger on flower choice by bees

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Abstract

Studies on animal–flower interactions have mostly neglected the third trophic level of pollinators' predators, even though antipredatory behaviour of pollinators may affect patterns of pollinator visitation, pollen transfer and floral traits. In three experiments, it was found that honeybees showed sensitivity to perceived danger at flowers by preferring apparently safe flowers over equally rewarding alternatives harbouring either a dead bee or a spider, and avoiding revisitation of a site where the bees had escaped a simulated predation attempt. These results suggest that bees, like other animals, take antipredatory measures, which may have far reaching effects on animal–flower interactions.

Keywords

Bees, flowers, pollination, predation, spiders.

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INTRODUCTION

Most pollination studies neglect the possible effects of predation on flower visitors; various authors have even claimed that predation is too infrequent to influence pollinator behaviour (Pyke 1979; Miller & Gass 1985; Morse 1986; Schmid-Hempel 1991). Recent research, however, indicates that assertions about the irrelevance of predation are commonly falsified when closely examined: animals, including short-lived arthropods, have been observed to take considerable measures in response to perceived predation risk. Such measures include altering diurnal patterns of activity; choice of diet, habitat, food patches and food type; ways of handling food items; social organization; choice of nest sites and various physiological factors such as diurnal and seasonal levels of fat reserves and respiration patterns (Lima & Dill 1990; Nonacs & Dill 1990; Lima 1998a; Ydenberg 1998). These antipredator measures taken by animals affect fitness, life history and interactions among species (Stamps & Bowers 1991; Peckarsky *et al.* 1993; Scrimgeour & Culp 1994; Werner 1994; Martin 1995; Schmitz *et al.* 1997; Peacor & Werner, 2000).

Many researchers seem to assume that predators avoid bees, the most commonly observed pollinators, due to their sting. This belief is in disagreement with the long list of species that prey on bees, most notably, bee eaters (Meropidae) (Fry 1983), Old and New World flycatchers (Muscicapidae and Tyrannidae) (Ambrose 1990), bee-

wolves (*Philanthus* spp.) (Evans & O'Neill 1988), some social wasps (Evans & Eberhard 1970; De Jong 1990), crab spiders (Thomisidae) (Morse 1981; Morse 1986), predacious bugs (Hemiptera) (Balduf 1939; Greco & Kevan 1995) and praying mantids (Mantidae) (Caron 1990). Another common assertion is that the nonreproducing workers of social bees should ignore predation risk because worker predation would not affect colony reproduction. This idea, however, has been refuted by theoretical analyses, which indicate that the workers should consider predation risk while making foraging choices, albeit to a lesser degree than solitary bees (Clark & Dukas 1994; Dukas & Edelstein-Keshet 1998). Finally, field data indicate that predation rates on pollinators are sufficiently high for maintaining strong antipredatory adaptations (reviewed in Dukas, *in press*).

Research in other systems, a long list of bee predators and formal theory all suggest that bees and other pollinators should show antipredatory behaviour, which may affect pollinator–plant interactions (Dukas, *in press*). However, little data on the effect of predation risk on pollinators exist. As a first step in addressing this issue, I conducted experiments with honeybees to test how information about potential danger at flowers affects bees' flower choice. Specifically, I asked the following questions: first, would bees prefer a plain, apparently safe, flower over a flower with potential danger, as indicated by the presence of either a dead bee or a spider? Second, would bees avoid a site where they have experienced a predator attack?

METHODS

General

All experiments were carried out at a meadow at Simon Fraser University on sunny days in the summer of 2000. A two-frame observation hive containing approximately 4000 honeybees (*Apis mellifera*) was placed under a 3 × 4 m tarpaulin, which protected the hive from direct sunlight and rain. The bees originated from apiaries at Simon Fraser University consisting of an unspecified racial mix dominated by the ‘‘Italian’’ race, *A. m. ligustica*. The bees were trained to visit a feeder located 15 m south of the hive using standard techniques (von Frisch 1967). The feeder consisted of a 250-mL glass jar placed upside down on a Plexiglas circle, 8 cm in diameter, outfitted with eight 1 × 1 × 10 mm grooves (see fig. 18 in von Frisch 1967). The feeder contained 0.5 M sucrose solution (approximately 17% weight by volume) scented with anis (6 µL per 100 mL). Usually, 5–10 bees were sipping syrup at the feeder simultaneously. Note that, although honey bees avoid real flowers currently or recently visited by another bee, they are attracted to feeders and artificial flowers visited by nest-mates, a behaviour mediated by pheromones (Free 1987, page 109).

At the start of each trial, I lured a bee arriving in the feeder to a small piece of Plexiglas containing a drop of anis-scented sugar syrup of a higher concentration than in the feeder (2 M in Experiments 1 and 2 and 0.675 M in Experiment 3). Once the bee was sipping syrup, I transferred her to the test arena 5 m west of the feeder (and 15 m south–south–west of the hive). The bee typically conducted a reorientation flight upon departure and returned within a few minutes for a successive visit, during which I applied a unique colour marking to her thorax and/or abdomen using fabric writers. At the end of the trial, the bee was captured and not used further. That is, a bee was used only once in the experiments.

Experiment 1

In this experiment, I tested whether bees would avoid a flower harbouring a freshly killed bee. Such a setting may be associated with the presence of an ambush predator such as a crab spider, praying mantid or predacious bug. Each experimental trial consisted of a short training period followed by a test. In the training period, I trained a single, individually marked bee at a time to visit an artificial flower consisting of a Plexiglas circle 4 mm thick and 8 cm in diameter painted with 6 blue petals, which contained a 100-µL drop of anis-scented 2 M sucrose syrup at its centre. This syrup volume is about twice as large as the honeybee’s loading capacity (von Frisch 1967). The flower was placed at the centre of a 30 × 30 × 30 cm Plexiglas

box covered with yellow cardboard. After the focal bee had visited the flower, I replaced it with a new identical flower.

After the second visit of the focal bee, I prepared the test arena consisting of two new flowers identical to the ones used for training. One of the two flowers also contained a freshly killed bee 1 cm from its centre; the bee was killed by pressing it gently inside a test tube. The two flowers were placed side-by-side, 20 cm apart on the same Plexiglas box, equidistant from where the training flower had been located. The third visit of the focal bee was the test, during which I recorded the bee’s behaviour from her arrival until she settled on one flower and initiated feeding, at which point I captured her and terminated the trial. I then washed the flowers and initiated another trial with a new focal bee. Overall, I conducted 2 blocks of 10 trials each. On each block, the flower containing the dead bee was on the right side on 5 randomly chosen trials and on the left side on the other 5 trials.

Experiment 2

In this experiment, I tested whether bees would avoid a flower with an immobile spider, which represented the general shape and colour of a potential ambush predator. I used the same general setup and training procedure as in Experiment 1: in all trials, a focal, individually marked bee visited twice an artificial flower with 100 µL of 2 M sugar syrup and then, on her third visit, was presented with a choice test between two alternative flowers. This experiment had two treatments, spider and white cylinder. On trials of the spider treatment, a bee had to choose between a plain flower and a flower with a spider (*Argiope* sp.) placed horizontally 1 cm from the centre of the flower. The spider, which had been frozen to death before the experiment, was 15 mm in total length and 7 mm long without the legs. To control for the possibility that bees merely avoid novel objects rather than the shape and colour of a potential predator, I conducted the white cylinder treatment, in which a bee had to choose between a plain flower and a flower with a white plastic cylinder approximately the volume of the spider (11 mm in diameter and 5 mm tall). In either treatment type, the two flowers, which were 20 cm apart, contained 100 µL of sugar syrup at their centres and the object (spider or plastic cylinder) was placed beside the syrup drop.

Overall, there were four types of trials: spider on the left side, spider on the right, cylinder on the left, and cylinder on the right. Each of the four trials was carried out once in random order within a block of four trials. Every six blocks (24 trials) consisted of a session, and I conducted a total of 2 sessions (48 trials).

Experiment 3

The previous two experiments addressed whether bees would choose between flowers based on existing danger. Experiment 3 went a step further by asking whether bees would avoid returning to a site where they have experienced a predator attack. I used the same general setup and training procedure except that the test arena contained a circular grooved Plexiglas dish identical to the one used in the feeder instead of an artificial flower. The eight grooves contained large drops (~200 μ L) of 0.675 M syrup, which were refilled as necessary after the bee left for the hive. As in the previous experiments, I applied individual colour marking to the bee upon her first visit to the test arena. The marked bees typically returned for a second visit within a few minutes (mean \pm 1 SD: 2.8 \pm 1.6 min, n = 20 bees) except for two bees designated for the attack treatment and two bees designated for the control treatment, which did not return and hence were replaced with other bees.

On test trials of the attack treatment, when the marked bee arrived on her second visit, she experienced a simulated spider attack. I used a 25-mm long black model spider made of flexible rubber and connected to a 30-cm long metal wire. I attempted to hit the bee's lateral side with the spider, but there was some variation among trials (e.g. a bee flew just before the spider's strike). After that initial attack, I placed the spider on the Plexiglas dish and moved it short distances in varying directions. Following this simulated attack, the bee left the test arena either for the hive or the feeder. From that moment of departure, I monitored whether the bee returned to the test arena within 10 min. If the bee did not return by the end of this test period, I searched for her at the feeder and the hive to verify that she was alive and uninjured.

On test trials of the control treatment, the second bee visit to the test arena was a regular one consisting of the bee sipping syrup and then leaving to the hive. From the moment of the bee's departure, I recorded whether she returned to the test arena within 10 min. Overall, I conducted two blocks of 10 trials each. Five attack trials and five control trials were carried out in random order on each block.

RESULTS

Experiment 1

Most bees arriving in the test arena behaved in a similar manner: they first approached the flower with the dead bee and flew in zigzag motion close to the dead bee for several seconds, then inspected the surrounding area focusing their close zigzag-motion flights on prominent objects. Following this inspection, six bees left the arena altogether. Three of the six bees failed to return and hence were substituted by

additional bees so that the analysis would contain 20 bees that have made a flower choice. The other three bees that left the arena returned shortly and made further close inspections of the dead bee. Overall, 19 out of the 20 bees landed on the flower with no dead bee (χ^2 = 16.2, P < 0.001, d.f. = 1, Fig. 1). The effects of flower side and block were nonsignificant.

Experiment 2

In trials of the spider treatment, some bees behaved as bees in Experiment 1, conducting inspection flights very close to the spider culminating with a rejection of that flower and landing on the other. Neither such inspection flights nor rejections were observed in trials of the white-cylinder treatment. Overall, the type of object significantly affected flower choice, with 25% of bees landing on the flower with spider and 75% on the plain alternative in spider trials, and 54% of bees landing on the flower with white cylinder and 46% on the plain alternative in white cylinder trials (log-linear model, χ^2 = 4.35, P < 0.05, d.f. = 1, for the effect of object, P > 0.3 for the effects of session, object side, and object-side interaction, Fig. 1).

Experiment 3

Following the simulated spider attack, most bees initiated inspection flights near the spider and the surroundings of

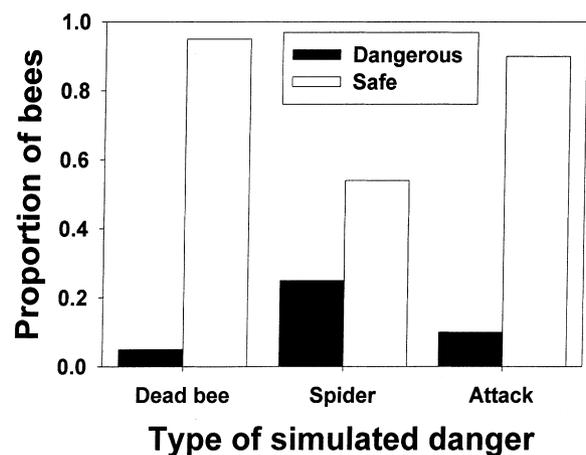


Figure 1 The proportion of bees that (i) landed on a flower with (left dark bar) or without (left white bar) a freshly killed bee (n = 20 bees); (ii) chose a flower with an immobile spider over a plain flower (centre dark bar, n = 24) or chose a flower with a white plastic cylinder over a plain flower (centre white bar, n = 24); and (iii) returned to a feeder for a successive visit after a simulated spider attack (right dark bar), or after a regular visit (right white bar, n = 20). Within an experiment, differences in landings between the two treatments were statistically significant (P < 0.05; see text for details).

the test arena and then left either to the hive or feeder. Only 10% of the test bees returned to feed at the test arena within 10 min following the simulated attack on their second visit. In contrast, 90% of the control bees returned to the test arena within 10 min after their second visit (log-linear model, $\chi^2 = 14.7$, $P < 0.001$, d.f. = 1, for the difference between test and control, $P > 0.8$ for block effect, Fig. 1). On average, the control bees returned for their third visit 2.0 ± 0.9 min ($n = 9$) after the second visit. Of the test bees that did not return to the test arena, all but one were observed at the feeder within 1 h after the simulated attack and the remaining bee was seen at the feeder on the following morning.

DISCUSSION

The opinion that predation in many systems is rare and can be ignored has dramatically changed over the past decade (Lima & Dill 1990; Lima 1998b; Dukas, in press). First, because of its potentially lethal outcome, animals, including short lived insects, should possess antipredatory adaptations even if predation levels are low. Clark & Dukas (1994) provide a formal analysis of this argument for bees foraging on flowers while facing realistically low predation levels. Second, because animals take various antipredatory measures, the actual observed predation rates may be low; even so, predation can have strong indirect effects on animal traits and fitness (reviewed in Lima 1998a). An intuitive example would be to claim that pedestrians should ignore danger from automobiles because accidents are rare. It is indeed true that accidents are rare, but this is mostly due to extensive safety measures taken by people, which include partitioning of activity in space (roads vs. sidewalks) and time (lights at pedestrian crossings), and strong behavioural avoidance (see Lima & Dill 1990). Finally, it is widely agreed that many pollinators do possess antipredatory traits such as stings in bees and noxiousness in butterflies, which are accompanied with aposematic colouration and extensive complexes of Mullerian and Batesian mimicry (Plowright & Owen 1980; Gilbert 1983; Schmidt 1990). This indicates that selection by predators has been sufficiently high to maintain sophisticated antipredatory adaptations.

Bees' response to perceived danger

When given a choice between a safe flower and a potentially dangerous alternative, bees showed significant preference for the safe flower. In Experiment 1, the indication of potential danger was a freshly killed bee. The distinctive response of focal bees to the presence of the recently dead bee suggests that they smelled and responded to alarm pheromone(s) emitted by the dead bee. At the hive,

honeybees' alarm pheromone provokes other bees to engage in colony defence activity characterized by search for and attack of intruders (Free 1987). Away from the hive, alarm substances from the mandibular glands and sting chamber seem to be deterring (Free 1987; Balderrama *et al.* 1996). Experiment 1 suggests that, during foraging, honeybees regard an injured or dead bee as indication of potential nearby danger which should be avoided. Note that the bees had foraged on a feeder visited concurrently by several other bees, so the possibility that they avoided the artificial flower with the dead bee to stay away from competition is very unlikely. On the contrary, honey bees show preference for artificial flowers visited by nest-mates over empty controls, a behaviour mediated by pheromones (Free 1987, p. 109).

Similarly, bees in Experiment 2 showed significant avoidance of an immobile spider. That behaviour was probably in response to the colour and shape of the spider rather than to novelty, because the bees did not avoid a white cylinder of similar volume. The spider in this experiment was conspicuous, while ambush predators in natural settings may be well camouflaged. Indeed, Morse (1986) observed neither avoidance nor earlier departure of honeybees and bumblebees from milkweed umbels containing nonattacking crab spiders compared to umbels with no spiders, a result suggesting that the bees did not perceive the presence of the cryptic spiders. Nevertheless, Experiment 2 indicates that bees are sensitive to the presence of potential predators and avoid them when detected. It is, of course, expected that predators would attempt to minimize detection by potential prey (Craig *et al.* 1996), but this would only diminish rather than eliminate the utility of antipredatory behaviour.

Even if bees have difficulty detecting ambushing predators, they can still respond to either a failed predation attempt or successful capture of another bee by subsequently avoiding the hazardous location. It is relevant to possess an ability to respond to failed attacks because reported success rates of bee predators range between 10 and 40% (reviewed by Dukas, in press). Experiment 3 indeed indicates that bees are sensitive to location-specific attack. Note that a predator attack in Experiment 3 as well as in nature has two effects, the most significant of which is the perceived danger, while the other is reduced level of nectar intake due to the abrupt departure from the flower. Experiment 3 did not distinguish between these proximate effects because I focused on the ultimate outcome, avoidance of the attack site.

Because I was able to monitor the behaviour of focal bees following the simulated predator attack, I could reject the alternative that the bees stopped foraging altogether due to injury. Rather, the bees selectively avoided the test arena but returned to the safe feeder they had previously visited even though that feeder offered a lower quality of sucrose

solution (0.5 vs. 0.675 M). Bees may also adopt a milder response to evidence of danger by showing heightened alertness expressed as inspection of a food source before landing, and fleeing in response to nearby moving objects. I observed these behaviours during my experiments but have not quantified them.

It is essential to distinguish between the proximate and ultimate mechanisms of responding to perceived danger. When bees avoid a flower (i) with a freshly killed bee, (ii) with a predator-like object or (iii) where they have been attacked (the proximate mechanisms), they effectively avoid elevated mortality risk at flowers (the ultimate outcome). It does not matter whether these proximate mechanisms are generalized danger-avoidance responses or specific antipredator adaptations expressed only at flowers. The fact that bees possess such proximate danger-avoidance mechanisms means that they can consider perceived danger in addition to economic factors while choosing among flowers.

Previous data in bees and hummingbirds

My results, which explicitly addressed honeybees' responses to perceived danger, are in agreement with a few studies indicating that bees attempt to avoid danger. Gould trained honeybees to avoid visiting artificial flowers associated with a puff of compressed air (Gould 1986), and to selectively avoid landing on the five out of six petals of a mechanical flower that flicked forward and hit a bee upon landing (Gould 1987). Abramson (1986) trained honeybees to avoid locations associated with formic acid and electric shock, and Smith *et al.* (1991) trained honeybees to avoid extending their proboscis in response to odour associated with electric shock. Two field studies have also suggested that the presence of predators at flowers has a negative effect on pollinator visitation (Louda 1982; Willmer & Stone 1997). Finally, after harmless interceptions, stingless bees learned to bypass spider webs placed in front of syrup feeders (Craig 1994).

My results are also in agreement with two sets of experiments suggesting that hummingbirds feeding on artificial flowers that obstruct view of their surroundings often interrupt feeding to engage in antipredatory vigilance, and that hummingbirds prefer food sources farther from the ground, probably because of danger posed by terrestrial predators (Lima 1991; Blem *et al.* 1997).

Cultivated honeybees vs. wild bees

It is worth noting that my experiments, as well as many others, involved honeybees. One reason I used honeybees is that they are somewhat docile. Indeed the prevalent

worldwide commercial use of the "Italian" honeybees, *A. m. ligustica*, is due in part to their gentle behaviour on the comb and lesser tendency to sting compared to other honeybee races (Ruttner 1988; Crane 1999). It is possible that docility on the comb and at flowers are genetically correlated traits. If this is the case, one would expect to find stronger antipredatory behaviours in wild bees. Furthermore, solitary bees are expected to exhibit stronger antipredatory behaviour than social bees (Clark & Dukas 1994; Dukas & Edelman-Keshet 1998). Hence, the most promising research program evaluating the effect of predation on bees and flowers would be one conducted in habitats currently and historically dominated by wild, solitary pollinators.

Relevance for pollination ecology

Research on flower-pollinator interactions has been conducted almost exclusively within a framework of two trophic levels (but see Louda 1982; Lima 1991; Wasserthal 1993; Willmer & Stone 1997; Wasserthal 1998). Recent studies in other ecological systems illustrate, however, that it is useful to consider predators and address interactions at three trophic levels (Price *et al.* 1980; Martin 1988; Bernays 1989; Werner 1994; Turlings & Benrey 1997; Dicke 1998). As illustrated in my experiments, honeybees also are sensitive to perceived danger at flowers. The danger-avoidance behaviour of bees and other pollinators may, at the least, affect patterns of pollen transfer in time and space. This would be the case if pollinators avoid plant patches or species more frequented by predators due to either the proximity of these plants to the predators' nest aggregations or some other resource, or interplant variation in the ease of capturing prey (see Geitzbauer & Bernays 1996). Furthermore, pollinators' antipredatory behaviours may have had some influence on the evolution of various floral traits such as flowering time, nectar availability and floral morphology (Dukas, in press). Future studies may evaluate whether variation in predation risk among plants is correlated with pollinator visitation rate and pollen transfer, and whether predation on pollinators has had indirect evolutionary effects on floral traits.

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