

Predation risk makes bees reject rewarding flowers and reduce foraging activity

Emily I. Jones · Anna Dornhaus

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Abstract In the absence of predators, pollinators can often maximize their foraging success by visiting the most rewarding flowers. However, if predators use those highly rewarding flowers to locate their prey, pollinators may benefit from changing their foraging preferences to accept less rewarding flowers. Previous studies have shown that some predators, such as crab spiders, indeed hunt preferentially on the most pollinator-attractive flowers. In order to determine whether predation risk can alter pollinator preferences, we conducted laboratory experiments on the foraging behavior of bumble bees (*Bombus impatiens*) when predation risk was associated with a particular reward level (measured here as sugar concentration). Bees foraged in arenas containing a choice of a high-reward and a low-reward artificial flower. On a bee's first foraging trip, it was either lightly squeezed with forceps, to simulate a crab spider attack, or was allowed to forage safely. The foragers' subsequent visits were recorded for between 1 and 4 h without any further simulated attacks. Compared to bees that foraged safely, bees that experienced a simulated attack on a low-reward artificial flower had reduced foraging activity. However, bees attacked on a high-reward artificial flower were more likely to visit low-reward artificial flowers on subsequent foraging trips. Forager body size, which is thought to affect vulnerability to capture by

predators, did not have an effect on response to an attack. Predation risk can thus alter pollinator foraging behavior in ways that influence the number and reward level of flowers that are visited.

Keywords *Bombus impatiens* · Bumble bees · Foraging · Non-consumptive effects · Pollination · Predation risk

Introduction

Acquiring resources is necessary for survival, yet increased foraging effort often results in a higher risk of predation (Verdolin 2006). While predation events may be rare, they impose an extremely high fitness cost when they do occur. Consequently, selection can favor foraging strategies that sacrifice foraging gains in order to decrease the risk of predation (reviewed in Bednekoff 2007; Brown and Kotler 2007). Such “non-consumptive effects” of predators on forager behavior lead to trait-mediated indirect effects on other community members that may be even larger than the effects of actual prey death (Preisser et al. 2005).

Trait-mediated indirect effects can weaken all forager interactions (i.e., by reducing overall foraging effort) or change the profile of forager interactions (i.e., by changing habitat use due to habitat-specific predation risk; Schmitz et al. 2004). The habitat-specific predation risk depends on habitat characteristics that increase the chance of prey concealment or escape (e.g., light, habitat complexity, and availability of refugia Bednekoff 2007), as well as on the habitat preferences of the predators themselves. Predator-prey foraging games predict that predators should prefer to hunt in patches that are high quality for their prey (Hugie and Dill 1994; Sih 1998), resulting in a tradeoff for the prey between foraging gains and predation risk.

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E. I. Jones (✉)
School of Biological Sciences, Washington State University,
Pullman, WA 99164, USA
e-mail: eijones@wsu.edu

A. Dornhaus
Department of Ecology and Evolutionary Biology,
University of Arizona,
Tucson, AZ 85721, USA

This preference for higher quality foraging patches has been observed in crab spiders (Thomisidae), which are ambush predators of important pollinators, including honey bees and bumble bees. Crab spiders will move to flowers receiving more pollinator visits (e.g., Morse and Fritz 1982; Morse 1988), as well as to flowers with cues that they provide more or better resources, both within (Heiling and Herberstein 2004) and between (Schmalhofer 2001) plant species. These cues, which are preferred by both pollinators and crab spiders, include floral symmetry (Møller 1995; Wignall et al. 2006), odor (Andersson 2003; Heiling et al. 2004), and age (Chien and Morse 1998; Higginson et al. 2006). Thus, depending on how crab spiders change pollinator foraging behavior, they could have trait-mediated indirect effects on plant communities by reducing overall pollination or by altering phenotype-specific and species-specific pollination rates.

Previous studies have found that bees avoid crab spiders (Dukas 2001a; Dukas and Morse 2003; Robertson and Maguire 2005; Reader et al. 2006; Gonçalves-Souza et al. 2008) and flowers where either they have experienced simulated predation attempts or encountered dead conspecifics (Dukas 2001a; Abbott 2006). Furthermore, bees will avoid locations that are more likely to harbor crab spiders; after experiencing a simulated attack on a flower with a camouflaged predator model, bees are more likely to falsely reject similar-appearing flowers without a predator model (Ings and Chittka 2008; Ings and Chittka 2009). However, in all these studies, safe and dangerous flowers provided equal rewards or reward levels were not controlled. Therefore, while it has been predicted that pollinators should optimize their lifetime foraging success by switching their preference to low-reward flowers when ambush predators are present (Jones 2010), this prediction has not been empirically tested.

Here, we examine the response of bumble bee (*Bombus impatiens*) foragers to simulated predator attacks when artificial flowers differ in reward level. We measured whether predation risk affects foraging activity and preference for flower type and patch. Furthermore, as the strength of pollinator response is predicted to increase with the pollinator's vulnerability to capture by the predator (Jones 2010), we investigated whether there is any interaction between response to predation risk and forager body size, a potential determinant of vulnerability to capture by crab spiders (Morse 1979). Foragers were given access to two foraging arenas, representing separate flower patches, each provisioned with one high-reward and one low-reward artificial flower, which could be distinguished by the color of the flower. Given this setup, an attacked forager could avoid the flower on which it was attacked by (1) continuing to visit the same flower type, but switching to a new resource patch, or (2) switching to the other flower type.

Switching patches, but not flower type, suggests that bees associate the experience of danger with an individual flower, not the flower type. Alternatively, switching flower types suggests that danger is associated with flower type, not just an individual flower.

Methods

Setup and training

Two *B. impatiens* colonies (obtained from Koppert Biological Systems, MI, USA), containing approximately 150 to 200 workers each, were housed in wooden nest boxes (39×23×8 cm). All bees were marked with colored, numbered plastic tags for individual identification. Each colony was connected to three wooden foraging arenas (each 24×20×8 cm) by transparent PVC tubes 152 cm long (Fig. 1). Nest boxes and foraging arenas had transparent acrylic covers to allow viewing, and foraging arenas had trap doors on the

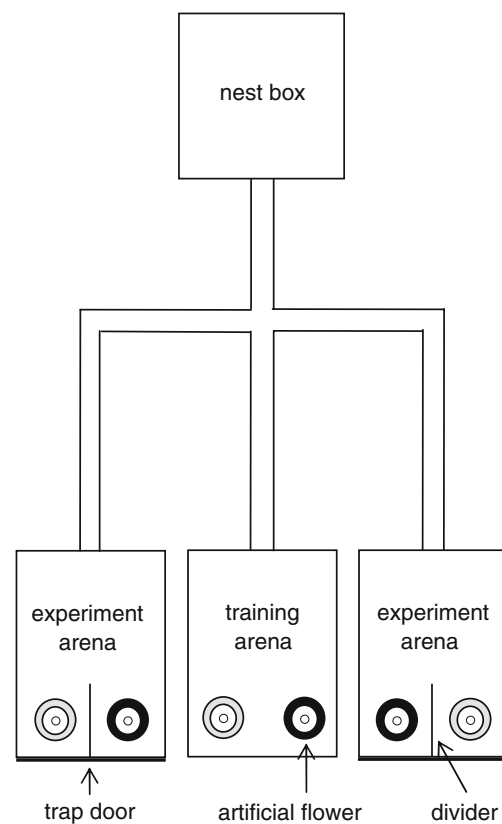


Fig. 1 Experimental setup. Artificial flowers consisted of a colored foam circle (outermost circle) beneath a Petri dish (large white circle) filled with sugar solution that could be reached through a small hole in the lid (innermost circle). The position (left or right) of the low-reward and high-reward artificial flowers (light and dark backgrounds) was randomized in each box for each training day and during each trial. The experimental arenas were accessible to bees at all times, but were empty except during test periods

rear wall to allow for simulated predator attacks (described below). These laboratory foraging conditions allowed us to control the bees' foraging options and to monitor all foraging trips within the experimental trials. While foraging under laboratory conditions is restricted, previous laboratory experiments on bumble bee foraging response to predation risk (e.g., Ings and Chittka 2008; Ings and Chittka 2009) have found behavior similar to that observed in the field.

Bees were given ground pollen daily and, except for training and trials, were provided with a low-concentration sugar solution in artificial flowers placed in the center foraging arena. The sugar solution was 25% *v/v* "Beehappy" in water solution (Koppert Biological Systems) in colony 1 and 20% *w/w* sucrose solution in colony 2. The artificial flowers were constructed from Petri dishes (4 cm diameter \times 1 cm) sealed with hot glue, with a slit drilled through the top, and placed on top of a gray foam (Crafters Square) circle (Fig. 1).

Training of all active foragers took place for 24 h before experimental trials were carried out. During training, a low-reward artificial flower on a yellow foam circle and a high-reward artificial flower on a blue foam circle were put in the center foraging arena. In colony 1, "low" and "high" sugar solutions were 25% and 50% *v/v* "Beehappy" in water, respectively; in colony 2, "low" and "high" sugar solutions were 20% and 40% *w/w* sucrose, respectively. These sugar concentrations span a typical range found in bumble bee visited flowers (Cruden et al. 1983), and honey bees have been shown to discriminate against sucrose solutions that are 50% lower than the alternative (Bachman and Waller 1977). Furthermore, during training, a strong preference for the high-reward flower was observed. In the "Beehappy" trials of colony 1, bees had additional olfactory cues for reward level compared to sugar solution trials of colony 2; however, data were combined after no significant difference was found between the two colonies.

Testing

During experimental trials, artificial flowers were removed from the center (training) arena and pairs of new, clean artificial flowers were placed in the experimental arenas (which had not previously contained food). Each pair included one low-reward artificial flower (as described above) on a yellow foam circle and one high-reward artificial flower on a blue foam circle. Trials lasted between 2 and 4 h, during which every forager visit was recorded by forager identity, flower visited, and time. Simulated predator attacks were modeled after crab spider attacks, in which the spider grabs the bee with its raptorial forelimbs (Morse 2007). We simulated this type of attack by lightly squeezing the bee's abdomen with forceps for approximately

2 s before releasing the bee. Our simulated predator attacks are similar in effect to those of Ings and Chittka (2008, 2009), who simulated attacks by squeezing bees between pads attached to robotic arms. Additionally, previous investigation has shown similar responses to flowers where a forager encountered either a dead bee or a dead spider, or had been attacked by a model spider (Dukas 2001a), suggesting that forager responses are not specific to particular cues of crab spider presence.

Within each trial, we systematically attacked every second bee that was making its initial foraging trip. However, foragers were not attacked if there was another forager present on or near the artificial flower; instead, the next bee making its initial foraging trip would be attacked. The forceps used in the simulated attacks were immediately removed from the foraging arena following an attack to restrict the cue of predation risk to the forager that was attacked. This may have led to a lower estimate of predation risk than if a spider model had been present; several bees searched the area around the artificial flower after being attacked and resumed feeding after failing to encounter further danger (personal observation). After all trials were completed, the thorax widths of foragers were measured with digital calipers as a measure of body size (Goulson et al. 2002; Jandt and Dornhaus 2009).

Statistical analyses

We hypothesized that experiencing an attack would make foragers less likely to return to forage, slower at returning to forage, and less likely to return to the same flower type and box. Thus, we used one-tailed statistical tests reflecting these hypotheses in analyses of the effect of an attack on foraging behavior. The reward level of the first flower visited greatly affected the response to an attack, so these analyses were split by first flower type. Two-tailed tests were used on analyses of the effects of body size on foraging behavior as we did not have a clear prediction of how size would affect vulnerability. Morse (1979) found that crab spiders were more successful in capturing smaller pollinator species; however, in that study, captured bumble bees were not significantly smaller than the general population of foraging bumble bees. Larger individuals could be more difficult for the predator to handle, but might also differ in maneuverability. The mass of foragers has been found to decrease their flight performance, which Dukas (2001b) has suggested could increase their vulnerability to capture. The reward level of the first flower visited did not interact with forager body size, so these analyses simply compare attacked and non-attacked foragers. The times to the first return foraging trip were exponentially distributed, and consequently were log-transformed for analysis with parametric tests. Analyses of

proportions of return visits to the original foraging arena or to the original flower type included only those bees that had had the opportunity to visit all arenas or flowers within the given time period (i.e., those that had made at least two or four return trips, respectively).

Results

Simulated attacks did change foraging behavior, but the type of response depended on the reward level of the flower on which the attack occurred. For bees that first visited a high-reward artificial flower, there was no significant difference between bees that were attacked and those that were not attacked in the likelihood to return to forage at all in the hour after the first foraging trip (χ^2 test, $n=90$, $\chi^2=0.645$, $p=0.422$; Fig. 2a) or, for those bees that did return to forage, in the rate of return visits (Mann–Whitney U test, $n_1=52$, $n_2=22$, $U'=575$, $z=0.0296$, $p=0.489$; Fig. 3a). However, for bees that first visited a low-reward artificial flower, bees that were attacked were significantly less likely to return to forage in the hour after the attack (χ^2 test, $n=72$, $\chi^2=4.35$, $p=0.0369$; Fig. 2a) and, if they did return to forage, had a significantly lower rate of return visits (Mann–Whitney U test, $n_1=30$, $n_2=22$, $U'=426$, $z=1.769$, $p=0.0385$; Fig. 3a) than those bees that were not attacked. On the other hand, for those bees that were not attacked, whether the first visit was to a low-reward or high-reward artificial flower did not significantly affect the rate of return visits (two-tailed Mann–Whitney U test, $n_1=30$, $n_2=52$, $U'=920$, $z=1.343$, $p=0.179$; Fig. 3a). Larger bees took less time to return to forage, though this relationship was significant only for those bees that were not attacked (linear regression, attacked, $n=39$, $p=0.510$, $R^2=0.012$; not attacked, $n=70$, $p=0.0171$, $R^2=0.0807$; Fig. 3b). However, bee size did not alter the time to return after an attack (comparison of regression coefficients, $t=-0.858$, $p=0.393$) and, for the bees that had experienced an attack, body size did not affect whether the bees returned to forage within an hour of the attack (unpaired t test, $n=56$, $t=-0.0646$, $p=0.949$).

While those foragers that were attacked on a high-reward flower did not reduce their foraging activity, their foraging preferences did change. These bees were significantly less likely to return to the same type of flower on the second foraging trip than bees that were not attacked (χ^2 test, $n=76$, $\chi^2=12.2$, $p=0.000482$; Fig. 2b). Foragers attacked on a high-reward flower also made a smaller proportion of their return foraging trips to high-reward flowers during their first hour of foraging (Mann–Whitney U test, $n_1=10$, $n_2=20$, $U'=142$, $z=1.88$, $p=0.0304$; Fig. 4a). On the other hand, foragers that were attacked on a low-reward flower were not significantly less likely to return to a low-reward

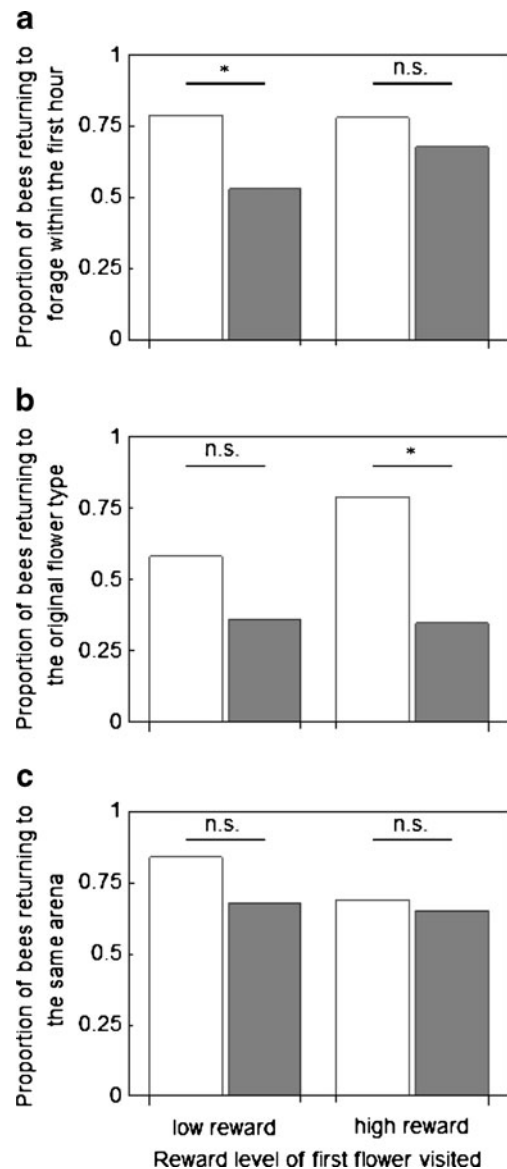


Fig. 2 The proportion of bees that **a** returned to forage within an hour of their first foraging trip, **b** returned to the same flower type on their second foraging trip, and **c** returned to the same arena on their second foraging trip. On the first foraging trip, bees either went to a low- or high-reward artificial flower and either foraged safely (white bars) or were attacked (gray bars)

flower on the second trip (χ^2 test, $n=56$, $\chi^2=1.89$, $p=0.170$; Fig. 2b) or to make a smaller proportion of their return foraging trips to low-reward flowers during their first hour of foraging (Mann–Whitney U test, $n_1=8$, $n_2=16$, $U'=55$, $z=-0.596$, $p=0.724$; Fig. 4a) compared to foragers that were not attacked. After the first hour of foraging, there was no longer a significant difference in preference for flower type for bees that were attacked either on a high-reward flower (Mann–Whitney U test, $n_1=7$, $n_2=18$, $U'=59.5$, $z=-0.0764$, $p=0.531$) or on a low-reward flower (Mann–Whitney U test, $n_1=7$, $n_2=12$, $U'=45$, $z=0.224$, $p=0.411$).

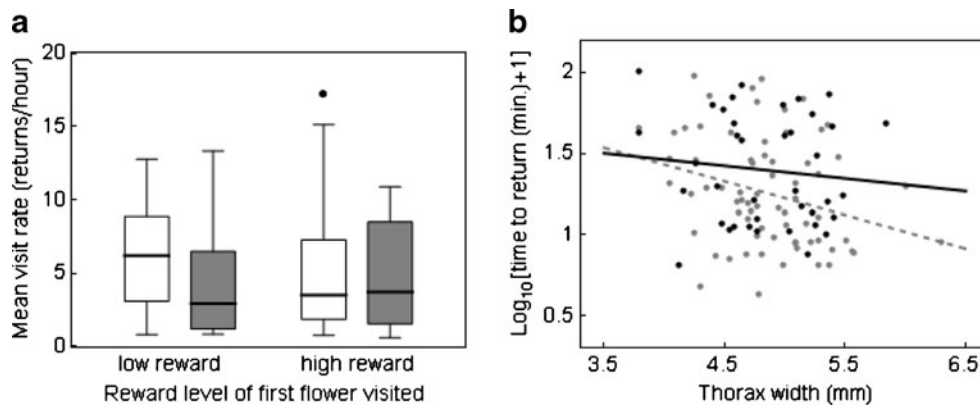


Fig. 3 **a** The effect of artificial flower reward level and simulated predator attacks on the mean rate of bees returning to forage (visits/hour). On the first foraging trip, bees either went to a low- or high-reward artificial flower and either foraged safely (*white boxes*) or were attacked (*gray boxes*). *Boxes* show the median and interquartile range, with *whiskers* spanning the entire range, except for outliers (*black circles*) that fall beyond 1.5

Overall, 28.4% of bees switched foraging arenas between the first and second foraging trips. However, switching between arenas did not appear to be a response to perceived predation risk. Bees that had experienced an

times the interquartile range from the 25th or 75th percentile. **b** The relationship between forager body size and the time between first and second flower visits for bees that were attacked (*black circles*, *black regression line*, $y = 1.774 - 0.078x$) and not attacked (*gray circles*, *dashed gray regression line*, $y = 2.260 - 0.207x$) on their first foraging trip

attack were not significantly more likely to switch between arenas (χ^2 test, first visit to high-reward flower, $n=78$, $\chi^2=0.00464$, $p=0.946$; first visit to low-reward flower, $n=56$, $\chi^2=1.17$, $p=0.280$; Fig. 2c). Similarly, an attack did not decrease the proportion of return trips to the original arena during the first hour of foraging (Mann–Whitney U test, first visit to a high-reward flower, $n_1=20$, $n_2=39$, $U'=419.5$, $z=0.494$, $p=0.311$; first visit to a low-reward flower, $n_1=15$, $n_2=24$, $U'=225$, $z=1.37$, $p=0.0855$; Fig. 4b).

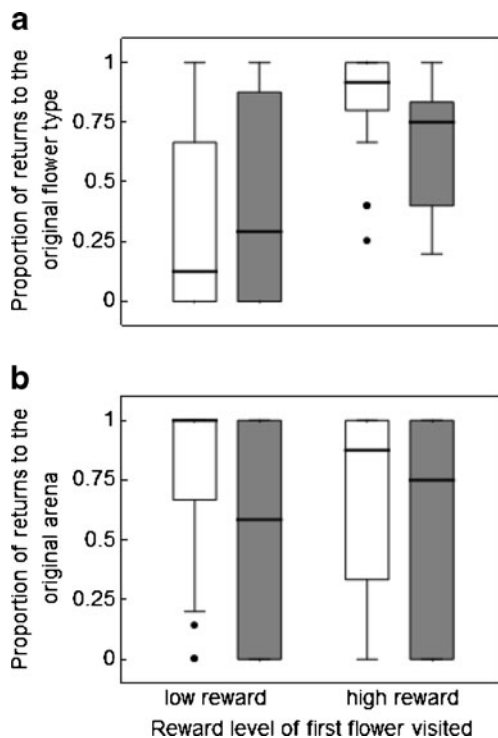


Fig. 4 The effect of artificial flower reward level and simulated predator attacks on **a** the proportion of return visits to a forager's first flower choice during the first hour of foraging and **b** the proportion of return visits to a forager's first arena choice during the first hour of foraging. On the first foraging trip, bees either went to a low- or high-reward artificial flower and either foraged safely (*white boxes*) or were attacked (*gray boxes*). *Boxes* show the median and interquartile range, with *whiskers* spanning the entire range, except for outliers (*black circles*) that fall beyond 1.5 times the interquartile range from the 25th or 75th percentile

Discussion

In our experiments with *B. impatiens*, we found that simulated predator attacks affected either the foraging activity or the foraging preferences of the bees. The behavioral response to predation risk was dependent on the reward level of the flower where the attack occurred. Bees attacked on a low-reward artificial flower spent more time in the nest between flower visits and were less likely to return to forage within an hour of the attack. Bees attacked on a high-reward artificial flower were more likely to switch flower types on subsequent foraging trips, even though that meant switching to an inferior resource; however, this change in preference decayed within about 1 h.

By avoiding dangerous flowers, foragers may be able to increase their lifespan and therefore lifetime resource gain. From data synthesized by Dukas (2001b), we estimated that, even in areas with relatively low crab spider densities, between 20% and 47% of bumble bee forager losses each day could be attributed to predation by crab spiders. Therefore, avoiding crab spiders may be adaptive despite a cost to short-term resource gain.

Since a single crab spider attack is unlikely to be successful in capturing a bumble bee (Morse 1979, 1981),

bumble bees may be able to use unsuccessful attacks to inform their future foraging behavior. Given the positive relationship between flower reward level and crab spider presence that has been observed (Chien and Morse 1998; Schmalhofer 2001; Heiling et al. 2004; Heiling and Herberstein 2004; Wignall et al. 2006), foragers may be able to infer crab spider densities, and thus optimal foraging strategies, through limited encounters with crab spiders. Predation risk may also be communicated; honey bees have been found to reduce waggle dance recruitment to patches with predators (Abbott and Dukas 2009), and bumble bees can copy the flower preferences of more experienced foragers (Baude et al. 2008).

Theory predicts that a forager encountering a crab spider on a high-reward flower is likely to be able to increase its lifetime foraging gains by switching to lower-reward flowers (Jones 2010), the forager response we observed here. This prediction is independent of the number of flower phenotypes present, but further research will be required to determine whether pollinators generalize predation risk to high-reward flowers that differ in appearance from the one where a predator was encountered. If, instead, a forager encounters a crab spider on a low-reward flower, it is likely that there is a high crab spider density and that the forager may be better off searching for another patch. We did not find support for this prediction here: foragers were not more likely to switch between arenas after an attack. Given the small scale of the foraging arenas, the two patches in our experiment may not have been considered sufficiently independent by the foragers; thus, further experiments are required to fully test this prediction.

Pollinator vulnerability is also expected to play a role in the response to predation risk (Jones 2010). However, while we found that smaller foragers generally took longer to forage (as has been reported previously, see Spaethe and Weidenmüller 2002), changes in foraging rate after an attack did not depend on forager body size. Previous studies have found differences in the crab spider capture success of pollinator species of different sizes (Morse 1979, 1981), though not in bumble bee individuals of different sizes. While bumble bee foragers do vary greatly in size, it is possible that all are too large for further increases in size to affect their vulnerability. Alternatively, advantages of increased size might be associated with tradeoffs. For example, increased mass can decrease flight performance, which has been suggested to lead to increased vulnerability to capture (Dukas 2001b). Behaviors such as vigilance (e.g., Yokoi and Fujisaki 2009) and avoidance learning could potentially compensate for smaller size, but our results and those of Ings and Chittka (2008) suggest that this is not the case in bumble bees.

Solitary pollinator species may react even more strongly to predation risk than what we show here for bumble bees,

due to both greater vulnerability and greater loss of fitness resulting from predation. Solitary species, which tend to be smaller than the bumble bees we studied, have been found to be more vulnerable to capture by crab spiders (e.g., Morse 1979, 1981). Furthermore, the cost of predation is higher for solitary species. Social insects have been predicted to be less risk averse than solitary species (Clark and Dukas 1994) because a worker's investment into the colony is not lost at its death (Queller 1989; Gadagkar 1990). Indeed, pollinators such as solitary bees and syrphid flies have been observed to have stronger avoidance of crab spiders than honey bees and bumble bees (Brechtbuhl et al. 2010a; Brechtbuhl et al. 2010b).

The results of our experiments, that predation risk does significantly alter bumble bee behavior, both in terms of foraging activity and foraging preferences, suggest that anthophilous (flower inhabiting) ambush predators could indirectly reduce overall pollination and alter the plant phenotypes and species that receive the most pollination. The bees in our study appeared to generalize predation risk across flowers with a similar phenotype to those where an attack had been experienced. It has been demonstrated previously that this generalization of predation risk is especially strong when the predator is camouflaged (Ings and Chittka 2009), as it was in our study. However, we have shown for the first time that avoidance of flowers more likely to harbor a predator occurs even when it reduces foraging gains.

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References

- Abbott KR (2006) Bumblebees avoid flowers containing evidence of past predation events. *Can J Zool* 84:1240–1247
- Abbott KR, Dukas R (2009) Honeybees consider flower danger in their waggle dance. *Anim Behav* 78:633–635
- Andersson S (2003) Foraging responses in the butterflies *Inachis io*, *Aglais urticae* (Nymphalidae), and *Gonepteryx rhamni* (Pieridae) to floral scents. *Chemoecology* 13:1–11
- Bachman WW, Waller GD (1977) Honeybee responses to sugar solutions of different compositions. *J Apic Res* 16:165–169
- Baude M, Dajoz I, Danchin E (2008) Inadvertent social information in foraging bumblebees: effects of flower distribution and implications for pollination. *Anim Behav* 76:1863–1873
- Bednekoff PA (2007) Foraging in the face of danger. In: Stephens DW, Brown JS, Ydenberg RC (eds) *Foraging: behavior and ecology*. The University of Chicago Press, Chicago, pp 305–329

- Brechbuhl R, Casas J, Bacher S (2010a) Ineffective crypsis in a crab spider: a prey community perspective. *Proc R Soc B Biol Sci* 277:739–746
- Brechbuhl R, Kropf C, Bacher S (2010b) Impact of flower-dwelling crab spiders on plant–pollinator mutualisms. *Basic Appl Ecol* 11:76–82
- Brown JS, Kotler BP (2007) Foraging and the ecology of fear. In: Stephens DW, Brown JS, Ydenberg RC (eds) *Foraging: behavior and ecology*. The University of Chicago Press, Chicago, pp 437–480
- Chien SA, Morse DH (1998) The roles of prey and flower quality in the choice of hunting sites by adult male crab spiders *Misumena vatia* (Araneae, Thomisidae). *J Archnol* 26:238–243
- Clark CW, Dukas R (1994) Balancing foraging and antipredator demands—an advantage of sociality. *Am Nat* 144:542–548
- Cruden RW, Hermann SM, Peterson S (1983) Patterns of nectar production and plant–pollinator coevolution. In: Bentley B, Elias T (eds) *The biology of nectaries*. Columbia University Press, New York
- Dukas R (2001a) Effects of perceived danger on flower choice by bees. *Ecol Lett* 4:327–333
- Dukas R (2001b) Effects of predation risk on pollinators and plants. In: Chittka L, Thompson JD (eds) *Cognitive ecology of pollination*. Cambridge University Press, Cambridge, pp 214–236
- Dukas R, Morse DH (2003) Crab spiders affect flower visitation by bees. *Oikos* 101:157–163
- Gadagkar R (1990) Evolution of eusociality—the advantage of assured fitness returns. *Philos Trans R Soc Lond B Biol Sci* 329:17–25
- Gonçalves-Souza T, Omena PM, Souza JC, Romero GQ (2008) Trait-mediated effects on flowers: artificial spiders deceive pollinators and decrease plant fitness. *Ecology* 89:2407–2413
- Goulson D, Peat J, Stout JC, Tucker J, Darvill B, Derwent LC, Hughes WOH (2002) Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? *Anim Behav* 64:123–130
- Heiling AM, Cheng K, Herberstein ME (2004) Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behav Ecol* 15:321–326
- Heiling AM, Herberstein ME (2004) Floral quality signals lure pollinators and their predators. *Ann Zool Fenn* 41:421–428
- Higginson AD, Gilbert FS, Barnard CJ (2006) Morphological correlates of nectar production used by honeybees. *Ecol Entomol* 31:269–276
- Hugie DM, Dill LM (1994) Fish and game—a game-theoretic approach to habitat selection by predators and prey. *J Fish Biol* 45:151–169
- Ings TC, Chittka L (2008) Speed–accuracy tradeoffs and false alarms in bee responses to cryptic predators. *Curr Biol* 18:1–5
- Ings TC, Chittka L (2009) Predator crypsis enhances behaviourally mediated indirect effects on plants by altering bumblebee foraging preferences. *Proc R Soc B Biol Sci* 276:2031–2036
- Jandt JM, Dornhaus A (2009) Spatial organization and division of labour in the bumblebee *Bombus impatiens*. *Anim Behav* 77:641–651
- Jones EI (2010) Optimal foraging when predation risk increases with patch resources: an analysis of pollinators and ambush predators. *Oikos* 119:835–840
- Møller AP (1995) Bumblebee preference for symmetrical flowers. *Proc Natl Acad Sci USA* 92:2288–2292
- Morse DH (1979) Prey capture by the crab spider *Misumena calycina* (Araneae, Thomisidae). *Oecologia* 39:309–319
- Morse DH (1981) Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. *Am Midl Nat* 105:358–367
- Morse DH (1988) Cues associated with patch-choice decisions by foraging crab spiders *Misumena vatia*. *Behaviour* 107:297–313
- Morse DH (2007) *Predator upon a flower: life history and fitness in a crab spider*. Harvard University Press, Cambridge
- Morse DH, Fritz RS (1982) Experimental and observational studies of patch choice at different scales by the crab spider *Misumena vatia*. *Ecology* 63:172–182
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509
- Queller DC (1989) The evolution of eusociality—reproductive head starts of workers. *Proc Natl Acad Sci USA* 86:3224–3226
- Reader T, Higginson AD, Barnard CJ, Gilbert FS (2006) The effects of predation risk from crab spiders on bee foraging behavior. *Behav Ecol* 17:933–939
- Robertson IC, Maguire DK (2005) Crab spiders deter insect visitations to slickspot peppergrass flowers. *Oikos* 109:577–582
- Schmalhofer VR (2001) Tritrophic interactions in a pollination system: impacts of species composition and size of flower patches on the hunting success of a flower-dwelling spider. *Oecologia* 129:292–303
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett* 7:153–163
- Sih A (1998) Game theory and predator–prey response races. In: Dugatkin LA, Reeve HK (eds) *Game theory and animal behavior*. Oxford University Press, Oxford, pp 221–238
- Spaethe J, Weidenmüller A (2002) Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insect Soc* 49:142–146
- Verdolin JL (2006) Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. *Behav Ecol Sociobiol* 60:457–464
- Wignall AE, Heiling AM, Cheng K, Herberstein ME (2006) Flower symmetry preferences in honeybees and their crab spider predators. *Ethology* 112:510–518
- Yokoi T, Fujisaki K (2009) Hesitation behaviour of hoverflies *Sphaerophoria* spp. to avoid ambush by crab spiders. *Naturwissenschaften* 96:195–200