

# Bumblebees avoid flowers containing evidence of past predation events

K.R. Abbott

**Abstract:** Bees are at risk of predation from flower-dwelling ambush predators. Since these predators tend to be cryptic, bees trying to mitigate predation risk may need to make use of indirect cues of the predator's presence. For example, they may use cues of past predation events as indirect cues of current predation risk. I conducted a series of experiments that examined how bumblebees (genus *Bombus* Latreille, 1802) respond to cues of past predation events. In two field experiments, I found that wild rose (genus *Rosa* L.) flowers containing a freshly killed bumblebee, or the scent of a freshly killed bumblebee, received fewer bumblebee visits than control flowers. To test the possibility that bumblebees in the first two experiments were avoiding cues of competition risk rather than cues of predation risk, captive-reared bumblebees were given a choice between two artificial flowers — one containing a freeze-killed bumblebee (relatively more similar to a live foraging bee) and the other containing a crush-killed bumblebee (relatively more similar to a bee killed by a predator). Most bumblebees chose the flower containing the freeze-killed bee, supporting the hypothesis that the bumblebees in the first two experiments were attempting to avoid predation.

**Résumé :** Les abeilles courent un risque de prédation de la part des prédateurs qui se tiennent en embuscade dans les fleurs. Puisque ces prédateurs ont tendance à être cryptiques, les abeilles qui essaient de réduire les risques de prédation doivent peut-être utiliser des signaux indirects de la présence des prédateurs. Par exemple, elles peuvent se servir de signes d'épisodes passés de prédation comme signes indirects du risque actuel de prédation. Une série d'expériences m'ont permis d'examiner comment les bourdons (genre *Bombus* Latreille, 1802) réagissent aux signaux d'événements de prédation du passé. Dans deux expériences de terrain, des fleurs de la rose sauvage (genre *Rosa* L.), qui contiennent un bourdon fraîchement tué ou l'odeur d'un bourdon fraîchement tué, reçoivent moins de visites de bourdons que les fleurs témoins. Afin de vérifier la possibilité que, dans les deux premières expériences, les bourdons évitent les signaux de risque de compétition plutôt que les signaux de risque de prédation, des bourdons élevés en captivité ont été placés devant un choix de deux fleurs artificielles — l'une contenant un bourdon tué par gel (relativement plus semblable à un bourdon vivant en train de butiner) et l'autre un bourdon écrasé (relativement plus semblable à un bourdon tué par un prédateur). La plupart des bourdons choisissent la fleur contenant le bourdon tué par gel, ce qui appuie l'hypothèse selon laquelle les bourdons dans les deux premières expériences cherchent à éviter la prédation.

[Traduit par la Rédaction]

## Introduction

There is a recent and growing appreciation that pollinators, such as bees, may face considerable predation risk from predators that hunt on flowers (Dukas 2001b). There is also recent evidence that these predators can reduce the pollinator visitation rates at flowers (Elliott and Elliott 1994; Dukas and Morse 2003; Suttle 2003; Muñoz and Arroyo 2004; Dukas 2005; Dukas and Morse 2005; Robertson and Klemash Maguire 2005; but see Morse 1986; Elliott and Elliott 1991; Wilkinson et al. 1991; Dukas et al. 2005). However, relatively little is currently known about what cues, if any, pollinators use to assess the predation risk associated with a flower. Similarly, little is known about how bees respond when encountering a cue of predation risk.

One simple cue that pollinators could use in assessing the

predation risk associated with a flower is the observed presence of a predator. Dukas (2001a) found that honeybees (*Apis mellifera* L., 1758) avoid artificial flowers containing a conspicuous predator (a frozen spider). Ambush predators that hunt pollinators on flowers, however, are generally cryptic and difficult for pollinators to detect (Balduf 1939; Morse 1979, 1986; Elliott and Elliott 1991; Chittka 2001; Théry and Casas 2002; Heiling et al. 2005a). For example, the ambush bug *Phymata americana* Melin, 1930 remain still while waiting for prey to approach, hide between flowers (Balduf 1939), and may have a tendency to hunt on flowers on which they are camouflaged (Balduf 1939; Elliott and Elliott 1991). Similarly, some crab spiders (family Thomisidae Sundevall, 1833) reversibly change their colour between yellow and white to match their current background (Chittka 2001; Théry and Casas 2002; Heiling et al. 2005a), remain still while waiting for prey to approach (Morse 1979, 1986), have a tendency to choose to hunt on flowers on which they are more easily camouflaged (Greco and Kevan 1994), and may hide among flowers (Morse 1986). In some cases, crab spiders may even have an appearance that exploits the sensory biases of pollinators, causing them to be attracted to the flower containing the predator (Heiling et al. 2003, 2005b; but see Heiling and Herberstein 2004). A

Received 9 March 2006. Accepted 19 July 2006. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 10 October 2006.

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more conspicuous, and possibly more useful, cue of predation risk associated with a flower might be the presence of a dead pollinator or any other sign that another pollinator was killed on the flower recently. For example, Dukas (2001a) showed that presence of a dead conspecific reduced the likelihood that honeybees would choose to land on an artificial flower.

If pollinators can detect these cues of predation risk, then there is the possibility that they can respond to reduce this risk. There are a number of behavioural responses that pollinators could make in the presence of a cue of predation risk (for a full discussion see Dukas 2001b). The most obvious are for individual pollinators to avoid landing on high-risk flowers (Elliott and Elliott 1994; Dukas 2001a; Suttle 2003; Muñoz and Arroyo 2004; Robertson and Klemash Maguire 2005) or to spend less time foraging on any given high-risk flower (Elliott and Elliott 1991, 1994; Suttle 2003; Muñoz and Arroyo 2004). It should be noted that if most pollinators avoid a risky flower, the competition at that flower would be reduced and the amount of available resources would be increased. Thus, it is possible that pollinators landing on a high-risk flower would actually spend more time on that flower than they would on a low-risk flower.

To fully understand the effects of predators on pollination systems, it is important to understand both what cues pollinators use to detect predation risk and how they respond to these cues. Therefore, I conducted a series of laboratory and field experiments to study whether, and how, bumblebees (genus *Bombus* Latreille, 1802) respond to evidence of past predation events. In the first experiment, I examined whether the presence of a dead bumblebee on a flower affected the number and duration of visits by wild bumblebees.

## Experiment 1: Bumblebee response to the presence of a dead bee on wild rose

### Methods

Data collection occurred in an old field at the Darling Marine Center, Lincoln County, Maine (described in Morse 2000), in 2004 and on the Hamilton Harbour Waterfront Trail in Hamilton, Ontario, in 2005. The 2005 data were collected, as the sample size and power of the 2004 data were low. As the two data sets were collected at different sites with different bee and flower populations (see below), they were analysed separately.

In both 2004 and 2005, data were collected early in the day when bumblebees were most active on wild rose (genus *Rosa* L.). Pairs of flowers were selected that were as close together as possible while still being comparable on the following dimensions: size, colour, degree to which the petals were open, and degree to which they were accessible to bumblebees. One flower was randomly assigned to be the experimental flower and the other to be the control flower. A freshly killed stimulus bumblebee was pinned to the edge of a lower petal of the experimental flower. These stimulus bumblebees were killed by crushing them inside a vial (Dukas 2001a). While every effort was made to shape these crushed bees into a naturalistic form, they did tend to look abnormal. In particular, the crushed bees generally looked flatter and wetter (from leaked body fluids) than live bees

and had disarrayed wings and hair. These crushed bees were pinned so that their ventral side was in contact with the flower petal and their dorsal side faced away from the petal. To control for effects of the pin and petal damage, the edge of the lower petal of the control flower was pierced with a pin. Observers watched the pairs of flowers for 30 min and recorded the time to the nearest second that each bumblebee visitor arrived and departed (leaving the flower and immediately returning without visiting any other flowers was not considered a departure). As the data conformed to the assumptions of parametric tests, two-tailed paired *t* tests were used to test whether there were any differences between experimental and control flowers in the number of bees that landed on the flower and the mean visit duration. Only trials where both flowers received at least one visitor were included in the analysis of visit duration. On trials where a flower received multiple visitors, the mean duration of these visits was used as the measure of visit duration for that flower.

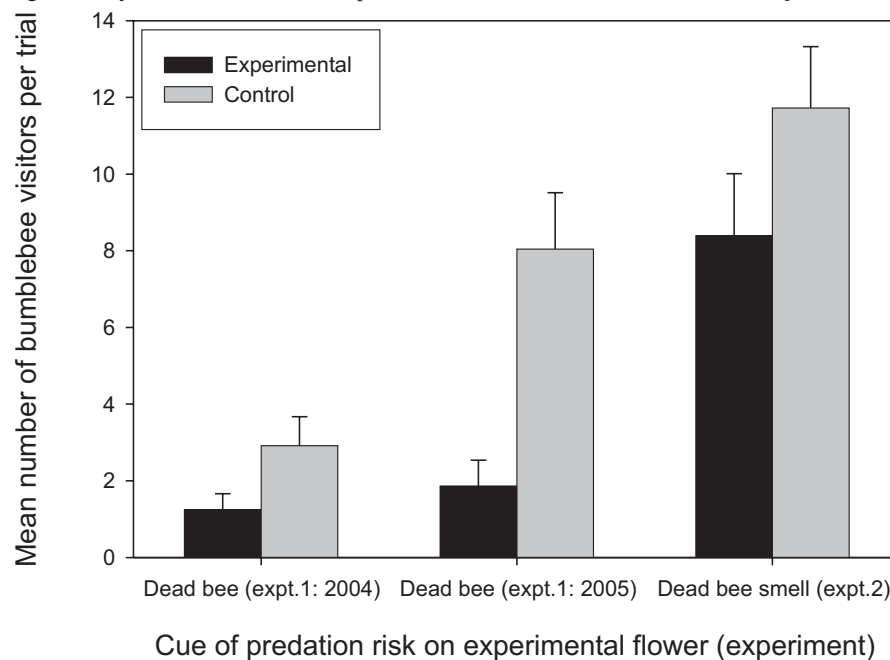
In 2004, data were collected from 16 to 18 July between 0900–1400 on 12 pairs of pasture rose, *Rosa carolina* L., flowers (30–60 cm apart). Stimulus bumblebees were *Bombus vagans* Smith, 1854 workers captured while foraging on flowers less than 1 km from the study site. *Bombus vagans* was the only bumblebee species observed at these flowers.

In 2005, data were collected from 25 to 30 June between 0700–1130 on 22 pairs of wild rose flowers (10–50 cm apart). The predominant rose species that was in bloom during this time was Virginia rose (*Rosa virginiana* P. Mill.). *Rosa rugosa* Thunb. and *R. carolina* bushes were also present. All three wild rose species were used, but each trial involved only a single rose species. Several bumblebee species (*Bombus griseocollis* (DeGeer, 1773), *Bombus impatiens* Cresson, 1863, and *Bombus rufocinctus* Cresson, 1863) were observed foraging on these flowers. Because discriminating between similar looking bumblebee species while simultaneously recording visitation data would have been very difficult, the species of bumblebee workers visiting the experimental and control flowers was not recorded. The dead stimulus bee placed on the experimental flower was always a *B. impatiens* worker collected while foraging on wild rose bushes at least 3 km from the Hamilton Harbour Waterfront Trail.

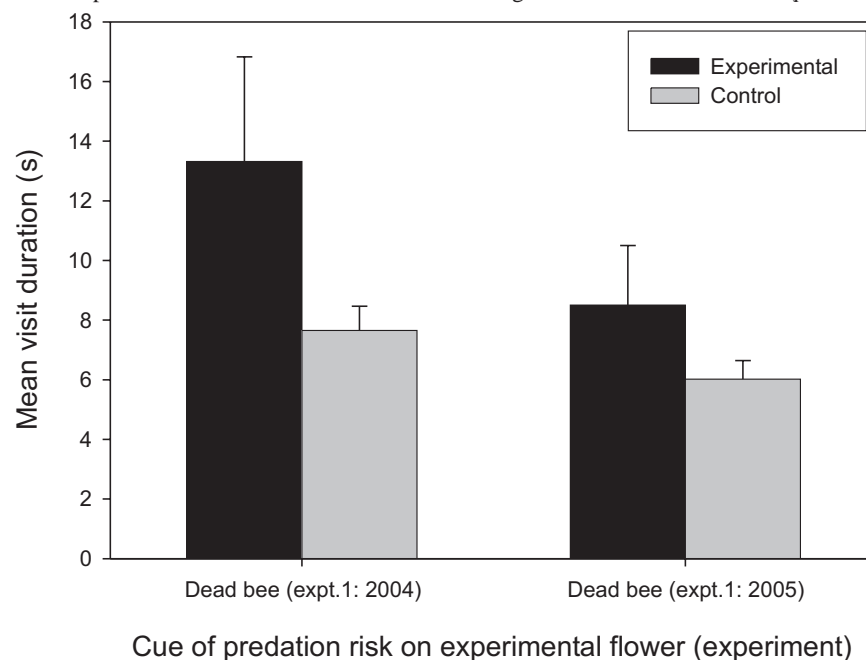
### Results

For both 2004 and 2005 data sets, there were significantly fewer visitations to experimental flowers than to control flowers (2004: two-tailed paired *t* test,  $t_{[11]} = -2.54$ ,  $p = 0.027$ ; left set of bars in Fig. 1; 2005: two-tailed paired *t* test,  $t_{[21]} = -5.64$ ,  $p < 0.0001$ ; centre set of bars in Fig. 1). For both 2004 and 2005 data sets, mean visit duration was not significantly different between experimental and control flowers (2004: two-tailed paired *t* test,  $t_{[6]} = 1.41$ ,  $p = 0.21$ ; left set of bars in Fig. 2; 2005: two-tailed paired *t* test,  $t_{[10]} = 1.18$ ,  $p = 0.27$ ; centre set of bars in Fig. 2). Note that the sample size for the tests of mean visit duration is much smaller than that for the tests of number of visitations because a difference score for mean visit duration could not be calculated on trials where one, or both, of the flowers in a pair received no visitations. This resulted in low power for

**Fig. 1.** The mean ( $\pm$ SE) number of bumblebee (genus *Bombus*) visitations at experimental and control flowers per trial for experiments 1 (2004 data set: leftmost pair of bars; 2005 data set: centre pair of bars) and 2 (rightmost pair of bars). In experiment 1, the experimental flower contained a freshly killed bumblebee. In experiment 2, the experimental flower was rubbed with a freshly killed bumblebee to transfer the scent to the flower. Trials for experiment 1 were 30 min long, whereas trials for experiment 2 were only 15 min long. For all three experiments, there were significantly fewer visitations at experimental flowers than at control flowers ( $p < 0.05$ ; see text for details).



**Fig. 2.** The mean ( $\pm$ SE) duration of bumblebee visitations at experimental and control flowers for experiment 1 (2004 data set: leftmost pair of bars; 2005 data set: rightmost pair of bars). In this experiment, the experimental flower contained a freshly killed bumblebee. The differences in visit duration between experimental and control flowers were not significant for either data set ( $p > 0.2$ ; see text for details).



the test of mean visit duration, particularly for the 2004 data set. To illustrate, for the 2004 data set the overall mean visit duration, calculated for all visits to experimental and control flowers, was 10.48 s. However, there were visits to both the experimental and control flowers on only 7 of the 12 trials. Thus, even if the mean difference in visit

duration between experimental and control flowers was as high as 75% of the overall mean visit duration ( $0.75 \times 10.48 = 7.86$  s), the probability of detecting this difference would have only been about 52%. In the 2005 data set, only 11 of the 22 trials were useable for the mean visit duration test and the overall mean visit duration was

7.26 s. Using the same analysis as for the 2004 data set, the probability of detecting a difference in mean visitation duration between experimental and control flowers that was 75% of the overall mean visit duration ( $0.75 \times 7.26 = 5.44$  s) would have been about 74%. It should be noted that it may be unrealistic to expect such a large mean difference in visit duration between experimental and control flowers.

## Experiment 2: Bumblebee response to the scent of a dead bee on wild rose

### Rationale

Although experiment 1 suggests that the presence of a dead bumblebee is a potential cue of predation risk, it is unclear to which aspect of this stimulus the live bumblebees were responding. Foraging bees rely heavily on scent (e.g., Dobson et al. 1999). In particular, honeybees are repelled or attracted to feeders containing various sting-gland components (Free 1987, pp. 142–143). Therefore, it is possible that the smell emitted by the dead stimulus bumblebees is what caused the avoidance response. Experiment 2 further studies the cues of predation risk to which bumblebees respond by examining whether the scent of a dead bumblebee is sufficient to cause the avoidance response seen in experiment 1.

### Methods

Experiment 2 was similar to experiment 1 with the following exceptions. Experiment 2 was conducted from 11 to 15 July 2005 between 0630–1000 at LaSalle Park in Burlington, Ontario. This experiment was conducted on two large adjacent prairie rose (*Rosa setigera* Michx.) bushes. The bumblebee species seen on these rose bushes were the same as reported for the 2005 data set in experiment 1, with the addition of *B. vagans*. As in experiment 1, visitations by all bumblebee workers, but not species identity, were recorded. For 18 separate trials, stimulus bumblebees (*B. impatiens* worker individuals collected while foraging on wild rose at least 8 km from LaSalle Park) were killed as in experiment 1; however, instead of being pinned to the experimental flower, they were cut open along the medial axis and rubbed on the petals of the experimental flower. This was done to transfer the smell of these freshly killed bees to the experimental flowers. The control flowers were rubbed for a comparable length of time with a clean piece of paper towel to control for any effects of disturbance or of human odours. The distance between experimental and control flowers varied from approximately 10 to 40 cm. Because the visitation rates at this site were much higher than in experiment 1 (see Fig. 1), 15 min trials instead of 30 min trials were used. In addition, the high visitation rates made recording arrival and departure times unreliable, so data on mean visit duration were ignored and only data on the number of bees landing on experimental and control flowers were analysed.

### Results

Relative to control flowers, there were fewer visitations to experimental flowers (two-tailed paired *t* test,  $t_{17} = -3.28$ ,  $p = 0.004$ ; right set of bars in Fig. 1). On 9 of the 18 trials, rubbing the stimulus bee on the experimental flower caused

small dark smudges on the petals. Removing these trials from the analysis made the results marginally nonsignificant (two-tailed paired *t* test,  $t_{18} = -2.06$ ,  $p = 0.07$ ). The mean difference between the number of visits on control and experimental flowers (where positive numbers indicate more visits on control flowers and therefore greater apparent avoidance of experimental flowers), however, is lower for trials with smudging (3.11) than for trials with no apparent smudging (3.56), making it unlikely that the significant difference in the number of visitations was caused by this discoloration.

## Experiment 3: The presence of a dead bee as a cue of predation risk or competition risk

### Rationale

Experiments 1 and 2 suggested that the presence of a dead bumblebee is a cue of predation risk that affects the foraging behaviour of other live bumblebees. There is, however, a non-mutually exclusive alternative explanation. It is possible that the dead bumblebee (or the smell of a dead bumblebee) is viewed as a cue of competition, rather than predation, risk. Although Dukas (2001a) and I (experiments 1 and 2) interpreted avoidance of crushed bees as evidence of avoidance of predation risk, Somers (2004) interpreted avoidance of flowers containing freeze-killed bees as evidence of competition avoidance. It is plausible that the way in which the stimulus bees were killed affected how they were perceived by foraging bumblebees. Specifically, a bee comparing freeze-killed and crush-killed bees will likely perceive the freeze-killed bee as relatively more like a live foraging competitor (cue of competition risk) and the crush-killed bee as relatively more like a dead bee killed by a predator (cue of predation risk). Crushing bees damages the exoskeleton, which may cause damage-specific odours. In addition, it is possible that, like honeybees (Balderrama et al. 1996), bumblebees emit a distinctive smell when alarmed, such as when being crushed inside a vial. Freshly crushed bumblebees do emit a strong detectable odour (personal observation). It is likely that at least some of these odours are emitted by bees being attacked or killed by a predator. In contrast, a freeze-killed bee will not emit damage specific odours and may not emit any alarm-related odours.

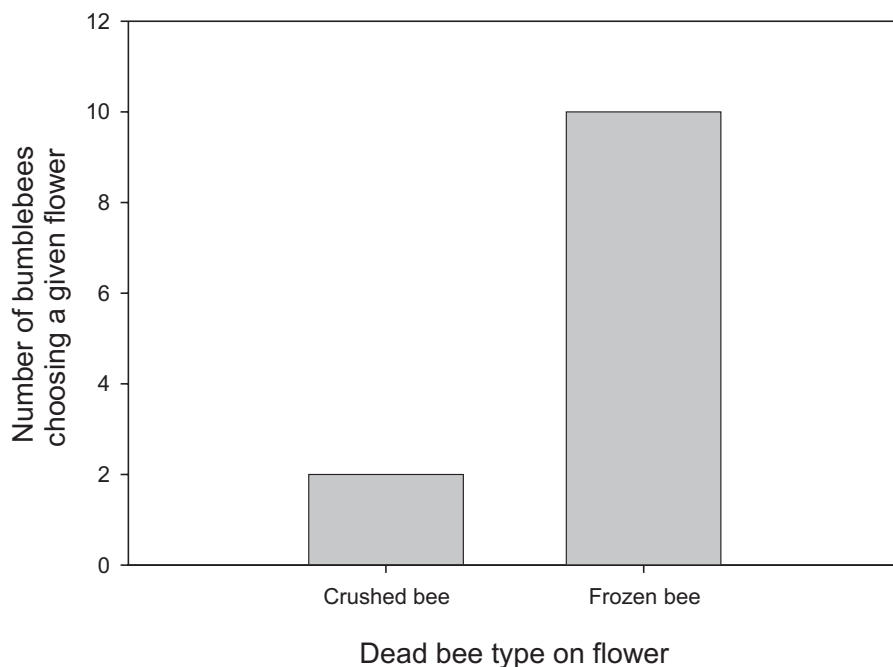
Given the uncertainty of the cause of the avoidance response seen in experiments 1 and 2, experiment 3 tested whether at least some component of that response could be attributed to avoidance of cues of predation risk. This was done by determining whether bumblebees avoid artificial flowers containing a crush-killed bumblebee relative to ones containing a freeze-killed bumblebee.

### Methods

This experiment was conducted in the laboratory from 14 October to 5 November 2005 using workers from two captive-reared *B. impatiens* colonies foraging on artificial flowers in a flight cage (54 cm long  $\times$  54 cm wide  $\times$  17 cm high wooden box with a transparent plastic top) attached to the colony. Twelve individuals were trained to forage on a single artificial flower (a 9 cm diameter purple disk with a 1.5 mL centrifuge vial with the lid removed inserted in



**Fig. 3.** Number of bumblebees choosing to land and drink from either an artificial flower containing a freshly crush-killed bumblebee or one containing a thawed freeze-killed bumblebee. Significantly more bees chose the flower with the freeze-killed bee ( $p = 0.021$ ; see text for details).



the centre to hold sucrose solutions). During initial training, the flower contained 50% (*m/m*) sucrose solution with honey added for scent. Towards the end of training, the honey was removed so that there would be no scent emitted from the flower except that from the stimulus bumblebees. Over the course of training, the single artificial flower was moved from near the entrance to the back of the flight cage. At all times, the training flower was in the centre of the flight cage (in the right-left dimension from the perspective of a bumblebee entering the cage). Training trials were run until the bumblebee reliably flew directly to, and drank from, a single artificial flower at the back of the cage containing the unscented sucrose solution.

For test trials, the single artificial flower at the centre of the back of the cage was replaced with two identical artificial flowers located 7 cm to the left and right of centre at the back of the cage. Each of these artificial flowers contained unscented sucrose solution. In every test trial, one randomly selected flower contained a crush-killed bee and the other contained a freeze-killed bee. These dead stimulus bees (also captive-reared *B. impatiens* workers) were placed on the edge of the flower closest to the entrance of the cage. Crush-killed bees were killed as in experiments 1–3. Because it was important that the live bumblebees did not perceive the freeze-killed bumblebees as being predator-killed bumblebees (at least relative to crush-killed bumblebees), the freeze-killed bumblebees were handled in such a way as to minimize the release of potential alarm-related odours. Rather than being captured in a vial like the crush-killed bees, freeze-killed bees were collected in a 473 mL clear plastic container attached to their colony. To minimize visual disturbance to the freeze-killed bees, this container was then enclosed in a cardboard box and placed in a freezer overnight. The following day, the container with the now

dead bumblebees was removed from the cardboard box and left uncovered in the freezer for at least another day to allow any scents (e.g., alarm-related odours) to dissipate. Freeze-killed bees were removed from the freezer 15 min before the start of test trials, as preliminary work indicated that this length of time allowed the internal temperature of the bee to thaw to ambient temperature (24 °C).

Foraging bees were allowed to choose between the two flowers. The identity of the flower that they chose to land on and drink nectar solution from was recorded. No bees drank from both flowers in any given trial. Flowers were cleaned with rubbing alcohol between trials to remove odours.

## Results

A significant majority of bees chose the flower containing the freeze-killed bee rather than the one containing the crush-killed bee ( $\chi^2$  test,  $\chi^2 = 5.33$ ,  $p = 0.021$ ; Fig. 3). One trained bumblebee refused to accept the unscented solution, so the test trial was run with the scented solution. The results were statistically significant even when this bee was removed from the analysis.

## Discussion

My results demonstrate that, in at least two different locations with different wild rose and bumblebee species, the presence of a dead bumblebee reduced the number of visitors that a flower received (experiment 1). I was, however, unable to detect an effect of the presence of a dead bumblebee on visit duration, but the power of this test was small (especially in the 2004 data set in experiment 1). More work on this problem is warranted because the possibility that cues of predation risk, especially in the absence of an

actual predator, may actually increase the amount of time individual visitors spend on a flower has interesting implications for how predators of pollinators affect plant fitness (Somers 2004). Note that previous studies have found that the presence of an ambush predator has either no (Morse 1986) or negative (Elliott and Elliott 1991, 1994; Suttle 2003; Muñoz and Arroyo 2004) effects on mean visit duration. The high-risk flowers or plants in those studies contained an actual predator. Aggressive movements by those predators may have startled the pollinators and reduced the length of the average pollinator visitation.

Additionally, these results suggest that a component of the cue that elicited this avoidance response was olfactory (experiment 2). There were numerous cues, olfactory and otherwise, that could have elicited a response from the bumblebees. For example, they could have been responding to the smell of a dead bee (Visscher 1983), the smell of an alarmed bee (Balderrama et al. 1996), the smell of a damaged bee (Grostal and Dicke 1999), or the sight of a non-moving bee. Although experiments 2 and 3 suggested that olfactory cues, particularly cues related to damage or alarm, were important, future studies should be done to determine what exactly elicits the avoidance response.

Furthermore, experiment 3 supports the hypothesis that at least some component of the avoidance response observed in experiments 1 and 2 was related to avoidance of predation risk rather than just avoidance of competition risk. There are, however, other potential explanations for the avoidance response seen in all three experiments. The two most obvious alternate hypotheses have to do with (1) neophobia and (2) repellent scent marks. These are discussed below.

It is possible that the bumblebees were simply avoiding a novel object in experiment 1, a novel smell in experiment 2, and the most novel of two objects in experiment 3. Even though previous work on honeybees (Dukas 2001a) and bumblebees (Somers 2004) have failed to find any avoidance of novel, but neutral, objects, it is difficult to conclusively rule out neophobia as an explanation for avoidance of cues of past predation events. In particular, it is possible that the neutral novel object used in Dukas (2001a) and Somers (2004) were less salient than the cues of past predation event used in the current study. A sophisticated psychophysical experiment would likely be required to conclusively discount neophobia as an explanation for the results presented here. It should be noted that the neophobia and predation-avoidance hypotheses are not mutually exclusive. Given that bees are at risk of predation from a wide variety of predators (Dukas 2001b), neophobia could be a proximate mechanism that promotes the generalized avoidance of situations with elevated predation risk. There are, however, other reasons why neophobia could have evolved. For example, neophobia could help bees avoid damaged flowers that may contain less nectar or pollen (Krupnick et al. 1999).

Bumblebees are known to avoid flowers that have been recently visited by other bumblebees (Goulson 2003, pp. 115–121 and references therein). In bumblebees, the primary source of the repellent scent marks that cause this avoidance is thought to be the tarsal glands (Goulson 2003). It is not clear to what extent crushing bumblebees would release chemicals from the tarsal glands. It does seem, however, that more chemicals would have been released from glands

in the thorax and abdomen where most of the crushing-induced damage occurred. Additionally, cutting the bumblebees along the medial axis, as in experiment 2, would not have affected the release of tarsal gland chemicals. Nonetheless, extracts from the cuticle of bumblebees have been found with a chemical composition similar to that of extracts from the tarsal glands (Goulson 2003). It therefore remains a possibility that the behaviour of the bumblebees in the current study was affected by residual scent marks on the stimulus bees. It is also possible that avoidance of cues of past predation events and avoidance of recently visited flowers are mediated by the same chemical cues. Note that avoiding recently visited flowers would reduce competition for resources, but it differs from the type of competition that was dealt with in experiment 3. The competition risk considered in experiment 3 had to do with a competitor that was currently on the flower of interest and could potentially interfere with the focal bee, as well as reducing the amount of resources available.

It should be noted that the stimuli (dead bees) used were not naturalistic. Freeze-killed bees do not perfectly resemble live competitors and crush-killed bees do not perfectly resemble a bee that has been killed by a predator. In particular, the amount of damage caused by crushing a bee probably far exceeds that caused by an invertebrate predator. The crush-killed bees used here may be a supernormal stimulus and it is possible that the response to a predator-killed bee is less extreme. Similarly, the olfactory cue used in experiment 2 was likely stronger than what would be present after a predation event. The stimulus bees in experiment 2 were cut along the medial axis before being rubbed on the flower. This likely released a variety of body fluids including hemolymph and chemicals from the glands that exist in the head, thorax, and abdomen of bumblebees. As far as I know, no research has considered what body fluids are released during a predation event, so it is not, as of yet, clear how closely the olfactory stimuli used in experiment 2 corresponds to what would be present on a flower after a natural predation event. It does seem, however, that even predators that cause minimal damage to the exoskeleton of their prey (e.g., crab spiders, ambush bugs) should cause the release of body fluids (particularly hemolymph) and related odours that could be used as an olfactory cue of predation risk.

These results are consistent with studies showing that a dead bee is perceived as a cue of predation risk (Dukas 2001a) and that the presence of a predator (and therefore the potential presence of cues of past predation events) affects visitation rates of pollinators at flowers (Elliott and Elliott 1994; Dukas and Morse 2003; Suttle 2003; Muñoz and Arroyo 2004; Robertson and Klemash Maguire 2005). These results may also explain why other studies (Morse 1986; Elliott and Elliott 1991; Wilkinson et al. 1991; Dukas et al. 2005) have found little or no effect of predators on visitation rates. It is possible that in these situations, foraging pollinators were unable to detect cues that indicated past predation events. This could be because the predation rate was so low that few of these past predation events had occurred or because some feature of the predator, or the flower, allowed evidence of past predation events to quickly decay (see below).

My results are also consistent with studies in other systems which show that individuals respond to evidence of the predation of conspecifics as a cue of predation risk. For example, it has been found that the spider mite *Tetranychus urticae* Koch, 1836 avoids patches containing artificially damaged conspecific eggs or adults (Grostal and Dicke 1999). Similarly, slimy sculpins (*Cottus cognatus* Richardson, 1836) respond to chemicals released by damaged conspecifics as if they were cues of predation risk (Bryer et al. 2001). Additionally, brook trout (*Salvelinus fontinalis* (Mitchill, 1814)) appear to use chemicals released by damaged conspecifics to learn about the odours of novel predators (Mirza and Chivers 2000).

If avoidance of flowers displaying evidence of past predation events is an adaptation for reducing predation risk, evidence of past predation events must accurately predict current predation risk. However, there are a number of situations where this may not be the case.

Firstly, if predators are very mobile, any cue of predation risk based on past events may be useless. Although avian and wasp predators may capture bees on flowers, they search for them while flying over large areas (Dukas 2001b, 2005). This means that a flower where a predation event involving an avian or wasp predator has occurred in the past may not be more risky than any other flower. It is likely that any avoidance based on cues of past predation events evolved in response to the risk imposed by ambush predators such as crab spiders or ambush bugs that attempt to catch many prey items on the same flower, umbel, or plant.

Secondly, the presence of cues of past predation events may actually signal the presence of a feeding or satiated predator and could possibly be a cue of reduced predation risk. This concern does not apply if predators have large appetites, in which case cues of recent predation events may not mean that the predator is no longer actively hunting. As well, if the cue of past predation events is persistent, then it might predict the presence of a predator that is no longer satiated. For example, if the corpses of past prey items remain on, or near, the area in which the predator is hunting, then bees may be able to respond to current predation risk. Similarly if, as suggested in experiment 2, a major component of the cue of past predation events is olfactory, then it is possible that bees could respond long after the corpses have been removed. Additionally, if predators are aggregated, then the presence of one feeding or satiated predator may predict the presence of other actively hunting predators. However, while many ambush bugs are found in pairs, with one male mate guarding one female, they appear to share captured prey so that one member of this pair will not be hunting while the other is feeding (Balduf 1939; Greco and Kevan 1995).

Lastly, if predators remove corpses from their hunting sites, if the architecture of the plant causes discarded corpses to fall off the plant, or if scavengers remove corpses from flowers (Elliott and Elliott 1991; Morse 2001), then evidence of past predation events may be a cue that is not available to potential prey individuals and would therefore be uninformative. As noted above, if the smells associated with a corpse are persistent, the actual presence of the corpse may not be necessary.

It is also possible that cues of past predation events pre-

dict current predation, harassment, or competition risk because these cues attract other animals. For example, if an animal that is both a predator and a scavenger is attracted to the scent of dead insects, then bees might avoid flowers with dead insects to avoid encounters with this animal rather than avoiding encounters with the predator that killed the insect. Visscher (1983) found that the German yellowjacket, *Vespula germanica* (Fabricius, 1793), foraged on honeybee corpses. Although these wasps may be too small to threaten bumblebees, it is plausible that other larger predator/scavengers will also seek out dead insects. Bees may also avoid flowers that attract small predator/scavengers to minimize the risk of harassment or competition, even if the risk of mortality is small.

## Acknowledgements

Reuven Dukas provided guidance on all aspects of this research. R. Dukas, Heather Poole, and four anonymous reviewers provided comments on previous drafts of the manuscript. Doug and Elsie Morse and the Darling Marine Center were very hospitable while working in Maine. Whitney Brim-DeForest, Taylor Jones, and D. Morse kindly helped with fieldwork. M. Daly, Margo Wilson, and Paul O'Hara provided information on the location of wild rose patches in the Hamilton area. Sigal Balshine, Martin Daly, and D. Morse provided helpful discussions. This research was supported by the Natural Sciences and Engineering Research Council of Canada, Canada Foundation for Innovation, and Ontario Innovation Trust grants to R. Dukas and Ontario Graduate Scholarships to K. Abbott.

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