Solitary floral specialists do not respond to cryptic flower-occupying predators

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**Abstract**

The impacts of predators on bee foraging behavior are varied, but have been suggested to depend on both the type of predator (namely their hunting strategy) and also risk assessment of the prey (i.e., ability to perceive predators and learn to avoid them). However, nearly all studies have explored these impacts using social bees, despite the fact that solitary bees are extremely diverse, often specialized in their floral interactions, and may exhibit different behaviors in response to flower occupying predators. In this study, we examined foraging behaviors of wild solitary long-horned bees (*Melissodes* spp.)in response to a cryptic predator, the ambush bug (*Phymata americana*) on their primary floral host, the prairie sunflower (*Helianthus petiolaris*). We found sex-specific differences in foraging behaviors of bees, but little evidence that ambush bugs affected either pre-landing or post-landing foraging behaviors. Male bees visited flowers three times more often than females but female bees were five times more likely to land than males. Ambush bugs did not reduce visitation in either sex. These results suggest that cryptic ambush bugs are either rarely detected by these solitary bees, or that foraging *Melissodes* do not alter their foraging behavior because of the perceived risk of predation. We discuss the implications of these findings and compare them to other studies of social bees.

**Key words:**

solitary bees, cryptic predator, foraging, risk, avoidance behavior

**Introduction**

Bees (Apoidea) and their responses to predators are of particular importance, given that foraging bees serve as pollinators in both agricultural and natural ecosystems ([Aizen et al. 2009](#_ENREF_1), [Davila et al. 2012](#_ENREF_5)) and interactions between bees and their predators can influence bee foraging behavior ([Dukas 2001](#_ENREF_7), [Jones 2010](#_ENREF_17), [Kacelnik and El Mouden 2013](#_ENREF_19)) and subsequently their impacts on plant reproduction ([Higginson et al. 2010](#_ENREF_12)). However, many of the cues bees use for optimizing foraging are also used by predators ([Greco and Kevan 1994](#_ENREF_9), [Heiling et al. 2004](#_ENREF_10)), and many predators occupy flowers as hunting platforms, potentially increasing predation risk to bees while foraging. A recent review found that the presence of predators on flowers reduced floral visitation by 36% and the duration of visits by 51% compared to flowers without predators (Romero et al. 2011). However, the responses to predators differed across bee taxa, suggesting that there could be differences in response by social and solitary Hymenoptera ([Romero et al. 2011](#_ENREF_32)). This highlights the need for more studies addressing the role of flower-occupying predators on different types of bees, especially since a better understanding of the impacts of predators on foraging bees is crucial to our understanding of the role of multi-trophic interactions in pollination systems.

The behavioral responses of foraging bees to predators likely depend on the bees’ ability to recognize predators and whether or not they can learn to avoid them. While bee taxa vary greatly in many biological and natural history characteristics that could impact foraging behavior and their interactions with flower-occupying predators, most behavioral studies have focused exclusively on eusocial bees in controlled laboratory settings (REFS), using artificial predators (REFS). Such studies have shown that social bees become more discriminating in their floral choices after experiencing repeated simulated predation attempts ([Ings and Chittka 2008](#_ENREF_14), [Ings et al. 2012](#_ENREF_16)). This discrimination can include modulating their exposure to predators by avoiding patches of flowers with high predator densities, scanning flowers before landing on them, and aborting foraging attempts on predator-occupied flowers ([Ings and Chittka 2008](#_ENREF_14), [2009](#_ENREF_15), [Ings et al. 2012](#_ENREF_16)). In contrast, the behaviors of solitary bees in response to flower-occupying predators have rarely been studied.

The response of solitary bees to flower-occupying predators should vary from that of social bees, given differences in the cost of predatory interactions. Fitness optimization models predict that solitary bees should be more risk averse than social bees ([Jones 2010](#_ENREF_17), [Rodriguez-Girones and Bosch 2012](#_ENREF_31)), given that individual female solitary bees are the sole provisioners of their offspring. Female mortality while foraging would therefore effectively eliminate that individual's reproductive effort, compared to social bees in which foragers contribute indirectly through shared fitness. However, solitary bee response to predators could still vary greatly depending on a number of other factors. On the one hand, if solitary bees are risk averse, they should display pre-landing avoidance behaviors to flower occupying predators similar to those of eusocial bees. On the other hand, the impacts of predators likely vary based on their predatory behavior. For example, visually cryptic predators should only induce avoidance behaviors in bees that have experienced predation attempts ([Ings et al. 2012](#_ENREF_16)), whereas obvious predators may reduce the likelihood of visiting a flower regardless of experience ([but see Dawson and Chittka 2014](#_ENREF_6)). Alternatively, if the consequences of not detecting a predator are rarely realized by foragers (i.e., an extremely low chance of attack), ignoring the predator and visiting as many flowers as quickly as possible would maximize a bee’s foraging efficiency ([Burns 2005](#_ENREF_3)). Moreover, while female solitary bees forage for nectar and pollen on flowers, males forage mainly for nectar, which takes less time, enabling males to visit flowers more frequently in search of mates and ultimately leading to differential effects on the pollination of the flowers they visit ([Ne'eman et al. 2006](#_ENREF_25)). Understanding how solitary bees respond to predators in more natural settings would provide important insights, not only into bee foraging strategies, but also the resulting intra-community interactions.

To test whether a cryptic predator would affect the foraging behaviors of solitary bees, we experimentally manipulated predators on flowers in an experimental common garden and observed freely foraging solitary bee behaviors. The ambush bug, *Phymata americana* Melin, (Reduviidae) is one of the most common predators found on sunflowers across the plains and attacks the most common sunflower visitors, solitary long-horned bees, *Melissodes* spp. Latreille (Apidae). To determine whether ambush bugs would affect the foraging behavior of long-horned bees we manipulated ambush bug presence on prairie sunflowers (*Helianthus petiolaris* (Nuttall), Asteraceae), and recorded the foraging behavior of bees while visiting predator occupied versus control flowers. Given that male and female bees exhibit sex-specific foraging behaviors, we also explored sex-specific responses of foraging bees to predators. We predicted that if solitary long-horned bees were risk averse, they would respond to predators by modifying their foraging behaviors on predator occupied flowers. Specifically, we predicted that solitary bees would respond to flowers with predators by 1) visiting those flowers less frequently, 2) spending less time per visit, and 3) being less likely to collect pollen and nectar when visiting. In addition, if the cost of male predatory encounters differed from that of females, we predicted 4) males would be more risk-averse and exhibit greater behavioral responses to predators than females.

**Materials and Methods**

**Study system**Sunflowers (*Helianthus* spp., Asteraceae) are a dominant flower across the plains of North America and the primary food resource for at least 31 species of bee (Hurd et al. 1980), including many long-horned bees, members of the solitary bee genus *Melissodes*, which often specialize on sunflowers and have specialized morphology and behaviors for collecting asteraceous pollen ([Parker et al. 1981](#_ENREF_27), [Cane 2017](#_ENREF_4)). The prairie sunflower, *Helianthus petiolaris,* is especially abundant in sandy disturbed soils found throughout urban and rural environments ([Heiser 1947](#_ENREF_11), [Hurd et al. 1980](#_ENREF_13)) and along roadsides on the plains of Colorado, where densities of plants can be as high as four plants per meter (Ntransects = 32, mean ± SE = 22 ± 8.96 plants/ 50 m, Schwantes, *unpub. data*). Each plant has multiple flowers borne on a highly branched stem. The flowers are used primarily by foraging bees and other insects that consume floral nectar or pollen. In Colorado, *Melissodes* are the most frequent visitor, and in the height of summer, females can be found collecting both nectar and pollen to provision offspring while males forage for nectar and occur at even higher densities while patrolling for potential mates (A. Carper personal observation).

In addition to bees, the flowers of *H. petiolaris* in CO are also frequently occupied by the jagged ambush bug, *Phymata americana*, which can be easily observed on the discs of flowers (Figure 1). Ambush bugs are common, occurring on roughly 40% of flowering plants in August and September, with an average density of 0.08 ± 0.03 ambush bugs per flower head (Ntransects = 32). They are cryptic predators, preferentially occupying yellow flowers ([Greco and Kevan 1994](#_ENREF_9)), which match their bright yellow color; are capable of capturing prey many times their own size; and have been reported preying on at least 18 different species of bees, including *Melissodes* ([Balduf 1943](#_ENREF_2), [Mason 1977](#_ENREF_22), [Elliott and Elliott 1994, Supplementary Videos 1 and 2](#_ENREF_8)). Moreover, ambush bugs also consume nectar from the flowers on which they hunt, allowing them to survive longer periods of time without prey ([Yong 2003](#_ENREF_35)), and enabling them to be very effective sit-and-wait predators.

**Common Garden**We conducted this experiment and all observations in a common garden of *Helianthus petiolaris* at the University of Colorado’s 30th Street greenhouse (Boulder, Colorado, USA). Plants were grown from seeds collected from wild plants growing in 32 sites across eastern Colorado during September of 2013. Seeds from all sites were mixed before storage to reduce any impacts of local phenotypes. In March of 2014, seeds were germinated in petri dishes and then planted in groups of five seedlings into 10cm x 10cm pots in the greenhouse. In May, individual sunflowers were transplanted into outdoor flowerbeds, spaced 60 cm apart to mimic natural plant densities, and watered regularly throughout the summer. Plants bloomed for two weeks prior to experimental trials to insure they were attractive to local bees and continued to bloom several weeks after the trials ended. Before the experiments took place, no predators were observed on any experimental plants.

**Experimental design** To determine how foraging bees responded to ambush bugs, we manipulated their presence on individual sunflower inflorescences. We implemented a matched-pair design with paired observations of occupied and unoccupied flowers on three consecutive days. We used two DSLR cameras to record paired observations (see below). Pairing enabled us to control for phenology of flowers, display size, and daily visitor activity. We assigned identification numbers to 40 undamaged, recently opened inflorescences (hereafter flowers) that were accessible for filming, and randomly assigned each to one of two treatments: occupied or control. This resulted in 20 flowers receiving ambush bugs and 20 left as unoccupied controls (Supplementary Figure 2). Individual flowers received the same treatment throughout the three day experiment but we randomly paired treatment flowers with control flowers on each day, so that pairings were not constant over the three day period to reduce bias due to observation time or position in the garden.

We conducted all experimental observations from August 15th to 17th 2014. We collected 75 individual ambush bugs from patches of sunflowers growing on roadside edges in agricultural areas near Boulder, Colorado. Each ambush bug was stored in an individual container inside of a growth chamber (Percival LLVL) maintained at 25˚C during the day and 20˚C at night with a 14-hour day length. At the start of each observation day, any arthropods greater than 1mm were removed from experimental flowers and each flower was inspected for damage; if a flower was damaged or senescing, we used another flower on the same plant. After the inspection, ambush bugs were placed on treated flowers and recording began. If an ambush bug left the flower, it was replaced and the trial was continued. If it left undetected, any data collected after it left were not included in analyses. At the end of the observation period, all ambush bugs were re-collected from flowers and replaced in the growth chamber over-night for possible use the next day. All experimental flowers were observed in the order of their random draw positions for 10 minutes (Figure 2). Observations were recorded using high definition digital single lens reflex cameras (Canon EOS 10D and Nikon D5200), placed 40 cm from blooms and recording at 30 frames per second with a resolution of 1920×1080 pixels. Using digital recordings allowed for frame-by-frame analysis of visits with a temporal resolution of 0.03 seconds. Observations began at 07:40 and finished when all pairs in both blocks had been observed (approximately four hours).

**Bee foraging behavior assessment** To assess bee foraging behaviors, we reviewed all videos of flowers and recorded a number of behaviors which could represent different components of foraging behavior and potentially different risk avoidance behavior (or lack thereof). For instance, if ambush bugs are truly cryptic predators, foraging bees may be unable to perceive them from a distance and may not be able to distinguish between control and occupied flowers until after visiting them. If so, avoidance behaviors may not be expected for visitation *per se*, but may be more likely after initial inspection of the flower. For each experimental flower, we recorded total visitation as it likely reflects detection of ambush bugs from a distance. We then calculated the proportion of visiting bees that actually landed on flowers to determine if ambush bugs deterred visitors once close enough to a flower to detect them. Once bees landed, ambush bugs are presumably detectable by visiting bees, and foraging may then be contingent upon perceived risk while foraging for nectar or pollen. Subsequently, for each individual bee recorded, we calculated the duration of each landing visit (measured as the number of seconds making contact with the flower), and also scored individual foragers for both nectar and pollen collection. If a bee inspected a flower but did not land, we included it in visitation analyses but not duration. Bees were scored as collecting nectar if they placed their head into a disk flower or if their proboscis was visibly extended into a disk flower. Similarly, bees were scored as collecting pollen when they passed over anthers and moved pollen to their scopal hairs. Because our study involved focal animals in the field, we were unable to implement blinding methods when recording and analyzing data. To reduce observer bias, C. Schwantes therefore scored all visitation behaviors to help standardize observations. All bee visitors were sexed and identified to genus from video with the help of V. Scott at the University of Colorado Museum of Natural History Entomology Collection.

**Statistical Analyses** All statistical analyses were run in R version 3.1.3. We compared visitation (pre-landing) behavior to ambush bug-occupied versus control flowers using linear modeling, with the sex of the visiting bee, the presence of ambush bugs, and their interaction as fixed effects. We summed visits to each experimental flower over the three-day period and assessed the effects of ambush bug presence on the total number of bee visits, the number of bees that landed on flowers, the proportion of visits that landed, and the proportion of landing bees that collected nectar and pollen. Given that only female bees collected pollen, we excluded males from the pollen collection analysis and only had the main effect of ambush bug presence as a fixed factor. To meet the assumptions of normality, we log10 transformed the total number of visits to flowers, log10(+1) transformed the total number of bees that landed on flowers, and logit-transformed the proportion of visits that landed on flowers, collected nectar, or collected pollen ([Warton and Hui 2011](#_ENREF_33)). We compared the duration of landing visits with a linear mixed effect model (lme4 package) and log10-transformed the seconds spent per flower. We included the sex of bee, treatment, and their interaction as fixed effects and included a unique flower ID to account for multiple measures of bee visit duration on the same plant. A significant effect of ambush bug presence on visitation would suggest that bees can perceive them from a distance, while an interaction between sex and ambush bug presence would suggest that either male and female bees perceive ambush bugs differently, or that the perceived risk of visiting flowers is different for male and female bees.

**Results**

Video footage revealed that ambush bugs tended to remain stationary on the periphery of the floral disk, staying in place for 8:52.2 (­SE + 28.7 seconds) minutes on average. Overall, we observed 704 individual bees from 14 genera visiting sunflowers during recording bouts. As expected, long-horned bees were by far the most frequent visitors, making up 87% of all recorded visits (Table 1). Of the other genera that visited the patches, only three, *Bombus*, *Apis*, and *Halictus* (entirely *Halictus ligatus)*, included species are known to be eusocial. Those eusocial bees accounted for just 5 % of all recorded visits. Of the 704 total recorded visits to ambush bug occupied flowers, only one predation event was recorded, representing just 0.15% of visits to occupied flowers. The ambush bug successfully captured and fed on a foraging honeybee. The honeybee landed on top of the ambush bug with its head and abdomen oriented in the same direction as the predator. As the bee moved towards the center of the flower, the ambush bug grasped it with its forelegs and inserted its beak in the membrane between the head and thorax. The bee beat its wings and attempted to sting the bug but was unable free itself. After 25 seconds the bee stopped struggling. Over the course of 9 minutes the ambush bug repositions itself so the bee is hanging straight down from the flower. No attempted predation events were observed.

**Bee Visitation to Flowers**

Summed across all three days, we recorded 613 total visits from *Melissodes* to 17 control flowers and 18 occupied flowers. We found a significant effect of sex on visitation, with male *Melissodes* visiting experimental flowers three times more frequently than females (F1 = 25.49, P < 0.001), with females making up 24% of visits (147 compared to 466 male visits). We found no significant effect of ambush bug presence on total visitation (F1 = 0.01, P = 0.904), and while females bees visited ambush bug occupied flowers 26% less than controls compared to a 12% increase in male visitation to occupied flowers (Figure 3), the interaction between the sex of long-horned bee visitor and ambush bug presence was not significant (F1 = 2.94, P = 0.091).

Of the 613 total visits from *Melissodes* recorded during the experiment, 222 landed on flowers. We found no effect of ambush bug presence on landing bees (F1 = 0.34, P = 0.560) and no interaction between ambush bug presence and bee sex on XXX (F1 = 0.01, P = 0.711). However, while male bees visited more frequently, twice as many female bees landed on experimental flowers (F1 = 10.64, P = 0.002). Moreover, female bees were more than 5 times more likely to land when visiting a flower than male bees (92% vs 17% respectively, F1 = 111.39, P < 0.001, Figure 4). While the presence of ambush bugs increased the proportion of females landing on a particular flower by 13%, it decreased the proportion of males landing by over 30%, although the interaction between ambush bug presence and sex again was not significant (F1 = 3.38, P = 0.071) and there was no overall main effect of ambush bug presence(F1 = 0.42, P = 0.518).

**Bee Visitation at Flowers**

In general, bees that did not land spent very little time at flowers, likely just inspecting them in search of mates. Only 14 female bees inspected flowers without landing compared to 377 males, making statistical comparison difficult. Qualitatively, males tended to briefly visit flowers (mean ± SE = 1.75 seconds ± 0.64) and regularly visited flowers occupied by other bees. On average, male bees spent 45% more time inspecting flowers before deciding to leave than female bees (.36 vs .20 seconds, respectively). Of those non-landing male bee visits, the presence of ambush bugs reduced the duration of inspection times by roughly 45%, though this was primarily driven by two outliers of 11 and 33 seconds, respectively. Summed over the three days of observation, 133 female and 89 male *Melissodes* landed on flowers. The amount of time bees spent on flowers averaged 6.4 seconds, though some bees that landed spent an exceptionally long time on flowers (up to 46 seconds, apparently simply resting and not foraging). We therefore identified 12 extreme outliers that were above the 95th percentile and excluded them from analyses. Once landed, female bees spent 2.5 times longer on flowers than male bees (F1 = 29.34, P < 0.001). While ambush bug presence tended to reduce the duration of visits by some 30% (13.4 % in females vs 57.6% in males) the effect was not significant (F1 = 3.20, P = 0.073) and there was no significant interaction of ambush bug presence with sex (F1 = 0.05, P = 0.765). The proportions of females nectaring once landed was 37% higher than males (F1,52 = 13.75, P < 0.001) but there was no effect of ambush bug presence on nectaring (F1,52 = 2.47 P = 0.122), no interaction with sex (F1,52 = 1.75, P = 0.191), and no effect of ambush bug presence on the proportion of females collecting pollen during visits (F1,29 = 0.95, P = 0.339).

**Discussion**

Overall, our results suggests that cryptic predatory ambush bugs in this study had little impacts on the foraging behaviors of long-horned bees and may not be a significant factor driving *Melissodes* foraging decisions. Bees visiting ambush bug occupied flowers spent similar amounts of time on those flowers compared to those visiting unoccupied blooms and there was little effect of the presence of ambush bugs on other bee foraging behaviors. However, we did detect sex-specific differences in bee foraging behaviors which suggest that male and female bees vary in exposure to flower-occupying predators. These finding are novel, given the paucity of studies evaluating solitary bee foraging behavior in response to predators, and suggest that much of what we know about predator risk assessment and avoidance in social bees may not necessarily apply to solitary bees, given differences in both their ecology and natural history.

Our findings contrast what others have found studying social bee response to flower-occupying predators. For example, honeybees foraging on *Solidago odora* Ait. (Asteraceae)spent significantly less time foraging on flowers with *Phymata americana* present, although total visitation did not vary between occupied and unoccupied flowers ([Elliott and Elliott 1994](#_ENREF_8)). However, most studies have used non-cryptic predators such as XXX, and often see effects of predators after repeated exposure. In experiments where eusocial honeybees and bumble bees learn to recognize predators, they only become wary of predator-occupied flowers after repeatedly experiencing simulated attacks ([Dukas 2001](#_ENREF_7), [Ings et al. 2012](#_ENREF_16)). In our experiments 1 in XXX visits to occupied flowers resulted in ambush bugs attacking bees and the attack was successful, meaning we observed no opportunities for bees to learn to recognized predators. Solitary bees may therefore have less information about the risk posed by ambush bugs, given the low, but successful, attack rate.

Most other research on solitary bees has focused on crab spiders. In one of the few other studies using solitary bees, Reader *et al* (Year) found no effect of non-cryptic crab spider presence on visitation by the solitary bee *Eucera notata* (family) to flowers of *Cistus ladanifer* L. (family)*,* even though honeybees avoided both inspecting and landing on flowers when crab spiders were present ([Reader et al. 2006](#_ENREF_30)). In contrast, models of non-cryptic spiders altered behavior of both males and females of the solitary bee *Ptilothrix fructifera* (Holmber) (family), altering male territorial perching behavior, and reducing female visitation and foraging time ([Oliveira et al. 2016](#_ENREF_26)). However, these studies used non-cryptic predators, and differences between these and our study suggest that some unique mechanisms may be driving solitary bee response to predators. For example, we found that males tended to land and collect nectar less often during visits to ambush bug occupied flowers, while females showed no response to predators, although our sample sizes were fairly low and the interaction was not significant. One possible explanation could be differences in exposure to predators between sexes. While both male and female *Melissodes* are typically most active in the early morning, females rest in burrows in the afternoons and overnight while males often gather in sleeping aggregations on sunflower heads with between 2 and 20 bees sheltering under ray flowers until morning ([Parker et al. 1981](#_ENREF_27)). This could to lead to males having greater risk exposure, and therefore add to their potential assessment of risk when visiting predator occupied flowers. More studies are needed to verify if there are indeed sex-specific differences in risk-assessment in solitary bees.

Interestingly, some studies suggest that the lack of effects may not necessarily indicate the lack of avoidance behaviors, depending on the scale of measurement. Indeed, the capacity for social bees, such as *Bombus*, to learn has been shown to create effects spillover, where predator presence on flowers can indirectly lead to reduced visitation across whole types of plants ([Ings and Chittka 2009](#_ENREF_15)). That is, bees weary of predators may exhibit reduced foraging behaviors to all flowers in a patch. One study exploring speed-accuracy trade-offs in foraging bumbles in response to cryptically colored robotic crabspiders, found that foraging bees spent longer inspecting flowers before landing, and had more false alarms after experiencing cryptic predators, even on flowers that were predator free ([Ings and Chittka 2008](#_ENREF_14)). This suggests social bees have the capacity to learn about predator presence but also that their spatial knowledge of flowering patches during the pre-landing phase of foraging may be intricate to their ability to mitigate predation risk. Our experimental garden was relatively small (~25m2) and the effects of predators may have been diffuse over the entire flowering patch. Alternatively, strong impacts of ambush bugs on sunflowers could be buffered by their cryptic coloration and behavior ([Romero et al. 2011](#_ENREF_32)). That we did not find strong impacts of cryptic ambush bugs in our results could suggests that solitary bees likely have less potential to learn, or are simply constrained in the foraging behavior.

Decisions to return to flowers following experienced predation risk may also depend on floral rewards ([Jones and Dornhaus 2011](#_ENREF_18)). Experiments with honeybees foraging in patches with manipulated resource abundance and predator occupancy showed that they visited predator occupied flowers with abundant floral resources at the same rate as they visited unoccupied flowers with scarce floral resources ([Llandres et al. 2012](#_ENREF_21)). The depletion of floral resources on unoccupied flowers could be overwhelming the effect of ambush bugs on bee foraging behaviors. That is, if bees preferentially forage on unoccupied flowers, by the end of each day and the end of the trials, the resources available at occupied flowers would be substantially elevated relative to the unoccupied flowers. Bee activity at sunflowers is also correlated with nectar and pollen resources ([Minckley et al. 1994](#_ENREF_24)) which may decline over the course of the day as they are consumed, and initial observations indicated that visits tended to decline over the course of the observation period. Explicitly disentangling the roles of floral resources and predation was outside the scope of this project, but warrant further study, especially with solitary bees.

An alternative explanation for the lack of effects of predators in this study could be driven by the ecology of the system. Unlike most social bees such as honey bees and bumble bees which are generalists and have the capacity to change floral hosts depending on predator presence, *Melissodes* are sunflower specialists and may be constrained to one or only a few pollen host species during their life at any given location. Thus maximizing foraging, at least for pollen by females, may be the best strategy to mitigate combined risk of predation and resource competition. Therefore, ignoring other floral occupants altogether, both before and after landing, may be the best foraging strategy for the bee, as they gain access to more floral resources ([Burns 2005](#_ENREF_3)) without losing time required to discriminate other occupants. This could also make intuitive sense, given that sunflowers are very large, and are more often than not occupied by several insects at any given time, including other bees, beetles, butterflies, and predators. The relative importance of competitive vs predatory interactions at flowers is nearly unstudied but could play an important role in foraging decisions, especially for specialist solitary bees.

In summary, these results show that there appear to be few consequences for bees failing to respond to ambush bugs. Even though the result of an ambush bug attack is fatal, attacks may not be sufficiently frequent to have an impact on foraging patterns in the field. The best foraging strategy of female solitary bees may thus be to largely ignore floral occupants when assessing floral characteristics and respond to floral occupants as necessary after landing.

**Cuts:**

Predatory interactions can have either direct or indirect effects on interacting species ([Wootton 1994](#_ENREF_34)) and can cause shifts in traits that influence foraging behaviors and the distribution of organisms in space and time ([Peacor and Werner 2001](#_ENREF_28)). Such changes in behaviors can subsequently impact other species interactions, community dynamics, and even ecosystem services ([Menge 1995](#_ENREF_23), [Leibold 1996](#_ENREF_20), [Peckarsky et al. 2008](#_ENREF_29)).

Maybe not enough time to find predation, or lack of acclimation time, though in lab experiments ambush bugs only took between 15-18 minutes to choose a hunting substrate ([Greco and Kevan 1994](#_ENREF_9)), suggesting plenty of time

**Table 1**. Bee visitation and behavior by genus during the ambush bug experiment. “Visits” is the total number of occurrences of each genus during the experiment. “Pollen” and “Nectar” are the number of pollen and nectar collection events recorded for each genus. “Male” and “Female” refers to the number of visits by each sex. “Ambush” and “Control” are the numbers of visits to flowers with or without ambush bugs, respectively.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Genus** | **Sociality** | **Visits** | **Pollen** | **Nectar** | **Male** | **Female** | **Ambush** | **Control** |
| *Agapostemon* | Solitary | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Andrena* | Solitary | 18 | 3 | 5 | 14 | 4 | 8 | 10 |
| *Anthidium* | Solitary | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Apis* | Eusocial | 6 | 0 | 2 | 0 | 6 | 3 | 3 |
| *Bombus* | Eusocial | 8 | 2 | 5 | 1 | 7 | 6 | 2 |
| *Colletes* | Solitary | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Diadasia* | Solitary | 5 | 1 | 3 | 2 | 3 | 3 | 2 |
| *Eucera* | Solitary | 2 | 1 | 1 | 0 | 2 | 0 | 2 |
| *Halictus* | Eusocial | 22 | 2 | 4 | 8 | 14 | 11 | 11 |
| *Lasioglossum* | Social | 5 | 1 | 1 | 1 | 4 | 3 | 2 |
| *Lithurgus* | Solitary | 19 | 5 | 9 | 4 | 15 | 11 | 8 |
| *Megachile* | Solitary | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Melissodes* | Solitary | 613 | 45 | 148 | 466 | 147 | 313 | 300 |
| *Perdita* | Solitary | 2 | 0 | 0 | 0 | 2 | 2 | 0 |

**Table 2.** Summary of *Melissodes* foraging behavior during the experiment. “Treatment” refers to whether or not there was an ambush bug present. “Inspection” refers to the average amount of time in seconds non-landing bees spent before leaving. “Landings” refers to the number of bees that landed. “Duration” refers to the average length of landing visits in seconds. “Pollen” and “Nectar”” refer to the number of events in which pollen or nectar was collected.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Treatment** | **Visits** | **Landings** | **Inspection (s)** | **Duration (s)** | **Nectar** | **Pollen** |
| control | 300 | 112 | 0.46 | 6.89 | 84 | 24 |
| female | 80 | 72 | 0.18 | 8.18 | 59 | 23 |
| male | 220 | 40 | 0.47 | 4.58 | 25 | 1 |
| ambush | 313 | 110 | 0.26 | 5.94 | 64 | 21 |
| female | 67 | 61 | 0.22 | 7.87 | 44 | 20 |
| male | 246 | 49 | 0.26 | 3.54 | 20 | 1 |
| **Total** | **613** | **222** | **0.35** | **6.42** | **148** | **45** |

Figure Legends

**Fig. 1** *Phymata americana* on *Helianthus petiolaris* inflorescence.

**Fig. 2** Ambush bug presence had no effect on a) the total number of *Melissodes* visits per flower, b) the number of landing visits per flower, or c) the proportion of visiting bees that landed on flowers, although there were sex-specific visitation behaviors, with male bees visiting flowers more frequently than female bees which landed a higher proportion of visits than males.

**Fig. 3** Ambush bugs also had no effect on a) non-landing and b) landing visit durations, though females spent longer on flowers than males.

Figure 1.



Figure 2.

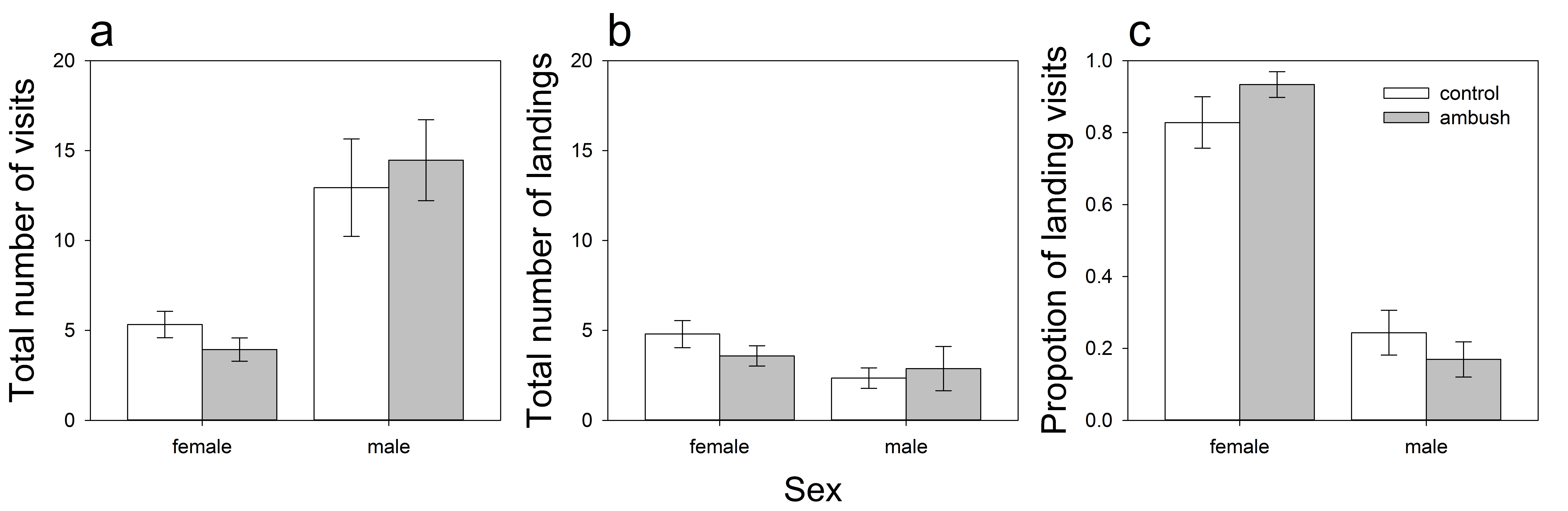
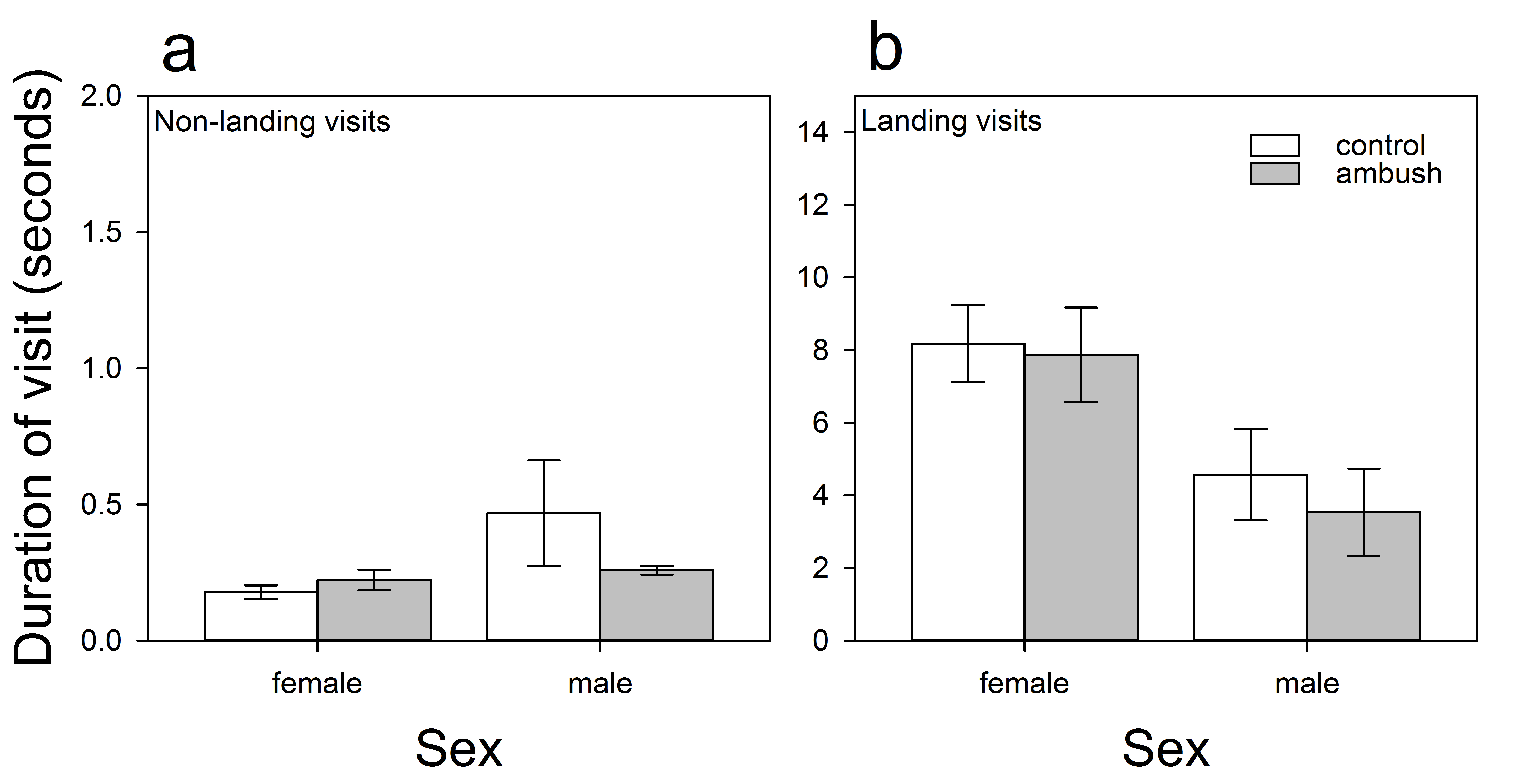


Figure 3.



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