DO FLOWER-OCCUPYING INSECTS MEDIATE

FORAGING BEHAVIOR IN SOLITARY BEES?

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Acknowledgments. We thank Travis Bildahl, Tom Lemeuix, Janice Harvey, and Silas Tittes for help with the experiments and the Animal Behavior Reading Group at the University of Colorado Boulder, the Plant Insect Group of Washington D.C., the Bowers laboratory at the University of Colorado for comments on previous versions of this manuscript. This research was supported by a grant from the Department of Ecology and Evolutionary Biology at the University of Colorado and a grant from the United States Department of Agriculture (NIFA # 2012-04195) to M. Jamieson, D. Bowers and A. Norton.

**Abstract**

Foraging behavior is often affected by interactions with other organisms that fall into two broad categories, competition and predation. Cues provided by competitors and predators may be important in determining both foraging behaviors and efficiency. In this study, we examined whether and how wild solitary bees adjust their foraging behaviors in response to an interference competitor, a pollen-feeding soldier beetle (*Chauliognathus basilis,* Cantharidae), and a cryptic ambush bug predator (*Phymata americana,* Reduviidae)while foraging on prairie sunflowers (*Helianthus petiolaris,* Asteraceae). We found that the interference competitor significantly reduced the amount of time bees spent on flowers, while the predator did not affect any of the recorded foraging behaviors. These results suggest that interference competitors may have a larger effect on bee foraging behaviors than predators. Such an effect may lead to increased dispersal of bees in the landscape, potentially increasing pollen transport and the likelihood of entering predator occupied space.

**Key words:**

solitary bees, foraging, risk, avoidance behavior

**Introduction**

Foraging behavior is affected by interactions with other organisms that often fall into one of two broad categories, competition and predation. Competitive and predatory interactions can have either direct or indirect effects on interacting species (Wooten 1994, ), and can cause shifts in traits that influence foraging behaviors and the distribution of organisms in space and time(Peacor and Werner 2001). Such changes in behaviors can subsequently impact other species interactions, community dynamics, and even ecosystem services (Menge 1995, Leibold 1995, Peckarsky et al 2008). For instance, bees (Apoidea) are of particular importance, given their importance as pollinators in both agricultural and natural ecosystems (Aizen et al 2009, Davila et al 2012), and their responses to competitors and predators may influence not only their behavior, but also their impact on plant reproduction (Higginson et al 2010) . . For example, the experimental removal of western yellow jackets (*Vespula pensylvanica*), a nectar competitor of bees in Hawaiian forests, increased bee visitation to *Metrosideros polymorpha* (Myrtaceae) blooms 3 to 16 fold (Hanna et al. 2014). Moreover, bees visiting flowers in sections of forest without yellow jackets displayed distinct foraging behaviors, collecting pollen and making contact with floral stigmas more frequently than bees in control plots(Hanna et al. 2014). While yellow jackets can also predate bees, whether such changes were driven by competitive or predatory interactions is still unknown. Studies exploring the impacts of both predatory and competitive interactions are needed to explore mechanisms driving bee foraging behavior.

While foraging, a bee considers a suite of floral characteristics to assess floral quality (Chittka and Raine 2006); however, the presence of predators or competitors adds another dimension to floral quality: the risk of physical harm via predation or interference competition (Dukas 2001a, Jones 2010, Rogers et al. 2013, Kacelnik and El Mouden 2013). Predation and interference competition both involve physical interactions between a bee and a floral occupant, but interference competition is rarely deadly. While the risk of encountering a predator on any given flower may be small, a lifetime of foraging significantly increases its probability.

Therefore, the behavioral responses of foraging bees to predators and competitors likely depend on the bees’ ability to recognize those putative antagonists. While bees vary greatly in many biological and natural history characteristics which could impact foraging behavior, most behavioral studies have focused on eusocial bees. Studies have shown that social bees become more discriminating in their floral choices after experiencing repeated simulated predation attempts (Ings et al. 2012, Llandres et al. 2012). This 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, Ings et al. 2012). However, the behaviors of solitary bees in response to flower-occupying predators or competitors are less understood.

Fitness optimization models predict that solitary bees should be more risk averse than social bees (Jones 2010, Rodríguez-Gironés and Bosch 2012), given that individual female solitary bees are the sole caretakers of their offspring. Female mortality while foraging would therefore effectively eliminate their reproductive effort. However, bee response to predators or competitors could vary greatly depending on a number of factors. On the one hand, if solitary bees are more risk averse, they may display pre-landing avoidance behaviors to flower occupying predators and competitors that are similar to those of social bees. On the other hand, many of the cues bees use for optimizing foraging are also used by predators and competitors (Greco and Kevan 1994, Heiling et al. 2004), potentially increasing predation risk and competition. In addition, visually cryptic predators should induce these avoidance behaviors in experienced bees (Ings et al. 2012), whereas obvious competitors may reduce the likelihood of visiting a flower regardless of experience (but see Dawson and Chittka 2014). Alternatively, if the consequences of not detecting a predator or competitor are rarely realized by foragers, ignoring the floral occupant and visiting as many flowers as quickly as possible would maximize a bee’s foraging efficiency (Burns 2005). Understanding how solitary bees respond to floral occupants in non-laboratory settings would provide important insights into bee foraging strategies and the resulting intra-community interactions.

Here we examine the behavior of solitary bees visiting prairie sunflowers (*Helianthus petiolaris*, Asteraceae) in response to the presence of predators and competitors. We observed solitary bee foraging behaviors using freely foraging bees in an experimental garden and compared bee foraging activities in response to a competitive beetle and a cryptic predatory hemipteran.. We predicted that if solitary bees were more risk averse, they would respond to non-threatening floral occupants (competitors) in the same way they responded to ambush predators. If however, solitary bees could learn to disregard floral occupants that pose no threat, we hypothesized that they would respond to floral occupants differently by modifying their foraging behaviors to better assess floral characteristics and avoid encounters. Specifically, we predicted that solitary bees would: 1) be less likely to collect pollen and nectar from occupied flowers, 2) visit occupied flowers less frequently, and 3) spend less time per visit on occupied flowers.

**Materials and Methods**

**Study system**Sunflowers (*Helianthus* spp, Asteraceae) are a dominant floral resource across the plains of North America and the primary food resource for at least 31 species of bee (Hurd et al. 1980). The prairie sunflower, *Helianthus petiolaris* (Nuttall)*,* is especially abundant in sandy disturbed soils found throughout urban and rural environments (Heiser Jr. 1947, Hurd et al. 1980) and along roadsides on the plains of Colorado, densities 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 addition to bees, the flowers of *H. petiolaris* in CO are also frequently occupied by the Colorado soldier beetle, *Chauliognathus basalis* LeConte, (Cantharidae) and the jagged ambush bug, *Phymata americana* Laporte (Phymatidae), both of which can be easily observed on the discs of flowers (Figure 1a-b). Ambush bugs are common, occurring at roughly XX% 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) to match their bright yellow color, where they are capable of capturing prey many times their own size, including bees (as in Balduf 1943, Mason 1977, Elliott and Elliott 1994, see Supplementary Video 1). Colorado soldier beetles co-occur with ambush bugs and in even higher densities, with nearly half of all flowers having at least one beetle (0.45 ± 0.06 beetles/flower, Appendix I). Male soldier beetles occupy floral territories for extended periods of time and physically harass both conspecific- and heterospecific floral visitors with their legs and mandibles (Rausher and Fowler 1979, Hurd et al. 1980, see Supplementary Video 2). In contrast to the cryptic ambush bugs, they are bright orange and black and their constant motion on flower heads makes them quite apparent. Based on field observations of sunflowers, the most common bee visitors likely to interact with these species are bees the genera *Melissodes*, *Andrena*, and *Megachile* and each of these three genera of solitary bee has at least one abundant species of sunflower specialist that could occur at our experimental site (Hurd et al. 1980, Scott et al. 2011).

**Common Garden**We conducted the experiment and all observations in a common garden of *Helianthus petiolaris* plants 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 the sites were thoroughly 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 two different sized outdoor flowerbeds: one received 25 plants and the other received 35 plants. Within flowerbeds, sunflowers were planted 60 cm apart to mimic natural plant densities and watered regularly throughout the summer. Plants were in bloom for two weeks before the trials were conducted and continued to bloom several weeks after the trials ended. Before the experiments took place, neither the competitor nor the predator was observed in either patch.

**Experimental design** To determine how foraging bees responded to floral occupants, we manipulated predator (ambush bug) and competitor (soldier beetle) presence in the two blocks of sunflowers. We implemented a blocked, matched-pair design with paired observations of occupied and unoccupied flowers on three consecutive days. Pairing enabled us to control for phenology of flowers, display size, and daily visitor activity, while blocking enabled us to account for variation between the two flowerbeds. Starting in the northeastern corner of each block, we assigned identification numbers to 20 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 10 flowers in each block receiving occupants and 10 left as unoccupied controls (Figure 2). Individual pairs of occupied and control flowers were the same throughout the three day experiment, unless flowers were damaged in some way.

Different rounds of experimental observations were conducted for competitors and predators to reduce potential confounding effects between predatory and competitive interactions. The first round for ambush bug occupied flowers (predator present) was conducted from August 15th to 17th and the second for soldier beetle occupied flowers (competitor present) was conducted from September 5th to 7th. We collected 75 individual ambush bugs and 60 individual soldier beetles from patches of sunflowers growing on roadside edges in agricultural areas near Boulder, Colorado. Each insect 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 flowers and flowers were inspected for damage; if a flower was damaged or senescing, we used another flower on the same plant. After the inspection, floral occupants (either a single ambush bug or soldier beetle) were placed on flowers and recording began. If an occupant left the flower, it was replaced and the trial was continued. If an occupant left undetected, any data collected after the occupant left were not included in analyses. At the end of the observation period, all occupants 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 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 (about four hours). This means that flower occupants that did not leave were in place for a minimum of four hours per day.

**Bee foraging behavior assessment** To assess bee foraging behaviors, we reviewed all videos of flowers and recorded a number of behaviors: visit duration, nectar or pollen collection, predation attempts, or exclusionary behavior. Visit duration measured how long a bee spent on a flower or investigating it. To quantify visit duration for visits where the bee landed, we used the duration from the initial time it made contact with the flower to the moment it was no longer contacting the flower. If a bee inspected a flower but did not land, we subtracted the initial time it oriented its body towards the flower from the time that it oriented away from the flower. We further separated inspections from bees passing through the frame of view by excluding flights less than 0.1 seconds (Ings et al. 2012). 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. All bee visitors were identified to genus from video with the help of V. Scott at the University of Colorado Museum of Natural History Entomology Collection. .The behavior of the flower occupants was also recorded as predation attempts for ambush bugs and exclusionary behavior for soldier beetles. Predation attempts were recorded if an ambush bug caught or tried to catch a bee using its forelimbs. Exclusionary behaviors occurred when soldier beetles oriented their heads towards bees and used their feet or mouthparts to move or contact a bee. We scored occupants as exhibiting these behaviors when they initiated contact with bees or reacted to contact by a bee in a way that caused the bee to leave the flower or, in the case of the ambush bug, become prey.

**Statistical Analyses** To test the effect of floral occupant type on landing, nectar collection, and pollen collection, we used chi-square contingency tests. These tested whether landing, nectar collection or pollen collection were happening more frequently than expected on occupied compared to unoccupied flowers. Changes in visitation rate could indicate that bees are learning to avoid flowers, although visitation rate also depends on the number of bees visiting the plot. Bee activity at sunflowers is correlated with nectar and pollen resources (Minckley et al 1994) 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 (see results). Therefore, to test the effect of floral occupancy on visitation rate, we used a generalized linear model with the number of visits as the response (Poisson distribution and logit link, lme4 package) floral occupant (predator, competitor, or control) as a fixed factor, and day, block, and flower pair as random effects. By including these elements as random effects, it was possible to control for their contribution to variance in the dataset, allowing for a more accurate assessment of the effect of occupancy.

To test the effect of floral occupancy on visit duration, we used linear mixed effects models with log-transformed data to meet the assumptions of normality. Randomized elements were included in the full model as fixed effects if they appeared to influence the structure of the residuals. To compare models, we used AIC scores and model selection methods, sequentially eliminating non-significant components of the model. Linear mixed effect models were run using the lmer package (Bates et al. 2014). All statistical analyses were run in R version 3.1.3.

**Results**

**Bee visitation: who were the visitors?** Solitary bees were the most frequent visitors to the patches during both experiments (Table 1 and Table 2). Of the 14 genera that visited the patches, only three genera, *Bombus*, *Apis*, and *Halictus* (entirely *Halictus ligatus)*, included species that are eusocial. Those eusocial bees accounted for 36 of the 704 visits during ambush bug trials and 12 of the 113 visits during beetle trials. Members of the solitary bee genus *Melissodes* (species cannot be distinguished on the wing) were the most frequent visitors in both experiments, with 613/704 visits during the ambush bug experiment and 60/113 visits during the soldier beetle experiment. Male and female bees visited flowers during both trials. Male *Melissodes* accounted for 466 of the 613 *Melissodes* visits. Males tended to briefly visit flowers (mean ± SE = 1.75 seconds ± 0.64) and regularly visited flowers occupied by other bees. Female solitary bees from 11 genera accounted for 173 of the visits to flowers during the ambush trials and 51 visits during the beetle trials. Because of their abundance during both trials and essential role in brood-care, all analyses were conducted using data from solitary female bee visits.

**Ambush bug and soldier beetle behavior**Video footage revealed that ambush bugs and soldier beetles occupied flowers in different ways. Ambush bugs tended to remain stationary on the periphery of the floral disk while soldier beetles moved around almost constantly while on a bloom. Foraging soldier beetles made steady circles around the disk as they collected nectar. Both occupants remained on the flower for a majority of the 10-minute observation period. On average, ambush bugs stayed for 8:52.2 (SE + 28.7 seconds) minutes and soldier beetles stayed for 8:33.4 (SE +34.2 seconds) minutes.

**Bee visitation: effects of predators and competitors**A chi-square contingency test showed that solitary female bees were not more or less likely to land, collect pollen, or collect nectar on a flower if it was occupied (Table 3 and Table 4). Ambush bugs had no detectable effect on any foraging behavior (landing: X2 = 0.02, df = 1, *p* = 0.88; collecting nectar: X2 = 0.92, df = 1, *p* = 0.34; collect pollen: X2 = 0.00, df = 1, *p* = 1). Soldier beetles also had no detectable effect on what foraging bees did on flowers (landing: X2 = 0.03, df = 1, *p* = 0.87; collecting nectar: X2 = 0.17, df = 1, *p*-value = 0.68; collecting pollen: X2 = 0.00, df = 1, *p* = 1).

The number of visits per observation period was not significantly affected by the presence of ambush bugs (Figure 3a). The full GLMM included treatment as a fixed effect and block, day, and pair as random effects. “Pair” refers to which pair of sunflowers was being observed. Our experimental design allowed us to use pair as an approximation for time of observation. The estimated effect size of ambush bug occupation, -0.86 visits per observation (log likelihood = -140.0, *z* = -0.96, *p* *=* 0.34, *n* *=* 74), was not particularly strong. The random effect “Pair” explained nearly one third of the total variance in visitation rate (varpair =0.15, vartotal = 0.46). The effect of “Pair” on visitation rate is clear in Figure 3c as the number of visits per pair drops steadily.

The presence of soldier beetles did not significantly impact the visitation rate of solitary female bees *(p* *=* 0.90, Figure 3b). The estimated effect size of soldier beetle occupation was -0.03 visits per observation (log likelihood = -52.2, *z* = -0.9128, *p* *=* 0.90, *n* *=* 40). During the beetle trials, no random effect (including ‘Pair’) explained an appreciable amount of the variance in the dataset (Figure 3d).

When ambush bugs occupied flowers, there was no statistically significant decrease in visit duration (estimate of mean decrease = -0.64 seconds, *F*1,189.94= 2.96, *p* = 0.09) (Figure 4a). When the random effects that do not contribute to the variance are dropped from the model, only “Pair” is left. Nearly one fifth of the variance in the data can be explained by the random effect “Pair” (varpair =0.55, vartotal = 3.23) (Figure 4c). Using AIC scores to compare model fits between the concise model and the null model, there is a negligible difference between the null and concise models (AICconcise = 803.05, AICnull = 803.98).

Visit duration did decline when soldier beetles occupied flowers (Figure 4b). “Pair” is the only random effect that contributes marginally to the variance term (varpair =0.06, vartotal = 1.76) (Figure 4d). After proceeding through the same model selection process as described in the preceding paragraph, all random effects terms were dropped. The most concise model only included the fixed effect of treatment. A comparison of AIC values between the most concise model and a null model shows that the most concise model is a better fit (AICconcise = 206.33, AICnull = 208.41). The presence of soldier beetles significantly reduced bee visit duration (estimate of mean decrease = -1.68 seconds, *F*1,57= 4.04, *p* = 0.048).

**Discussion**

In this study, soldier beetles, competitors for floral resources, influenced female solitary bee foraging behavior more than predatory ambush bugs. Bees visiting beetle occupied flowers spent significantly less time on blooms compared to those visiting unoccupied blooms; however there was no effect of the presence of ambush bugs on bee foraging. Other bee behaviors were not affected by the presence of either the beetles or the ambush bugs.

The behavior of bees in this common garden experiment provides insight into how bees perceive risk while foraging in patches of resources. In experiments where eusocial honeybees and bumble bees learn to recognize predators, they only became wary of predator occupied flowers after repeatedly experiencing simulated attacks and honeybees only became weary of predators after repeatedly experiencing harassment (Dukas 2001b, Ings et al. 2012). In our experiments, of the 704 recorded visits to ambush bug occupied flowers, only two predation events were recorded (0.3% of visits to occupied flowers) and both were successful, leaving little opportunity for bees to learn. In contrast, of the 109 recorded visits to beetle occupied flowers, there were two recorded events of physical exclusion (1.8% of visits to beetle occupied flowers). Importantly, bees may have less information about the risk posed by ambush bugs, given the low, but successful, attack rate. In contrast, relatively frequent and non-lethal harassment by beetles may mean that bees have more information about the risk they pose.

Visitation rates give insight into bees’ responses to occupants and their spatial knowledge of the patch during the pre-landing phase of foraging. Although not statistically significant, there were slightly reduced mean visitation rates to both ambush bug and beetle occupied flowers compared to unoccupied flowers (Figure 3). 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). The depletion of floral resources on unoccupied flowers could be overwhelming the effect of floral occupants on bee foraging behaviors. 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.

Interestingly, landing, collecting pollen, and collecting nectar were equally likely to occur on occupied and unoccupied flowers, even during the shorter visits to beetle occupied flowers. Beetles on flowers, in contrast to ambush bugs, moved nearly constantly, a behavior that should make beetles visually obvious to bees given their sensitivity to moving stimuli (Dafni et al. 1997, Chittka and Raine 2006). That bees landed, collected pollen, and collected nectar at the same rates on flowers occupied or unoccupied by beetles or ambush bugs indicates that bees largely ignored floral occupants during visits. Ignoring the occupant before and after landing may be the best foraging strategy for the bee, as they gain access to more floral resources (Burns 2005). Because bees did not discriminate between occupied and unoccupied flowers and spent less time on lower risk competitor occupied flowers (average visit duration to unoccupied flowers = 7.93 ± 2.94 seconds, visit duration to beetle occupied flowers = 1.35 ± 0.3 seconds), they may be pushed from relatively safe competitor occupied flowers to higher risk flowers occupied by predators.

In summary, these results show that there appear to be few consequences for the bee for failing to identify an ambush bug or a beetle on a flower before landing. 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. In patches with abundant floral resources and few predators, the reduced amount of time bees spend on beetle occupied flowers may actually increase foraging efficiency, as bees leave flowers that have been depleted by beetles for other flowers. The 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. In the broader biological context, these results suggest that interference competitors have a larger effect on bee foraging behaviors than predators. Such an effect may lead to increased dispersal of bees in the landscape, potentially increasing pollen transport.

References

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., & Klein, A.M. (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*.

Davila, Y.C., Elle, E., Vamosi, J.C., Hermanutz, L., Kerr, J.T., Lortie, C.J., Westwood, A.R., Woodcock, T.S., & Worley, A.C. (2012) Ecosystem services of pollinator diversity: a review of the relationship with pollen limitation of plant reproduction. *Botany-Botanique*, **90**, 535-543.

Higginson, A.D., Ruxton, G.D., & Skelhorn, J. (2010) The impact of flower-dwelling predators on host plant reproductive success. *Oecologia*, **164**, 411-421.

Balduf, W. V. 1943. Third annotated list of *Phymata* prey records. The Ohio Journal of Science 43:74–78.

Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2014. {lme4}: Linear mixed-effects models using Eigen and S4.

Burns, J. G. 2005. Impulsive bees forage better: The advantage of quick, sometimes inaccurate foraging decisions. Animal Behaviour 70:1–5.

Chittka, L., and N. E. Raine. 2006. Recognition of flowers by pollinators. Current Opinion in Plant Biology 9:428–435.

Dafni, a., M. Lehrer, and P. G. Kevan. 1997. Spatial flower parameters and insect spatial vision. Biological Reviews of the Cambridge Philosophical Society 72:239–282.

Dawson, E. H., and L. Chittka. 2014. Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments. Proceedings of the Royal Society B: Biological Sciences b-biological sciences 281:20133174.

Dukas, R. 2001a. Effects of perceived danger on flower choice by bees. Ecology letters 4:327–333.

Dukas, R. 2001b. Effects of perceived danger on flower choice by bees. Ecology Letters 4:327–333.

Elliott, N., and W. Elliott. 1994. Recognition and avoidance of the predator *Phymata americana* Melin on *Solidago odora* Ait . by late season floral visitors. American Midland Naturalist 131:378–380.

Greco, C. F., and P. G. Kevan. 1994. Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decisions by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata americana*). Canadian Journal of Zoology 72:1583–1588.

Hanna, C., D. Foote, and C. Kremen. 2014. Competitive impacts of an invasive nectar thief on plant-pollinator mutualisms. Ecology 95:1622–1632.

Heiling, A. M., K. Cheng, and M. E. Herberstein. 2004. Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). Behavioral Ecology 15:321–326.

Heiser Jr., C. B. 1947. Hybridization between the sunflower species *Helianthus annuus* and *H. petiolaris*. Evolution 1:249–262.

Hurd, P. D., W. E. Laberge, and E. G. Linsley. 1980. Prinicipal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera: Apoidea). Smithsonian Contributions to Zoology 310:1 - 158.

Ings, T. C., and L. Chittka. 2008. Speed-accuracy tradeoffs and false alarms in bee responses to cryptic predators. Current Biology 18:1520–1524.

Ings, T. C., M. Y. Wang, and L. Chittka. 2012. Colour-independent shape recognition of cryptic predators by bumblebees. Behavioral Ecology and Sociobiology 66:487–496.

Jones, E. I. 2010. Optimal foraging when predation risk increases with patch resources: an analysis of pollinators and ambush predators. Oikos 119:835–840.

Kacelnik, A., and C. El Mouden. 2013. Triumphs and trials of the risk paradigm. Animal Behaviour 86:1117–1129.

Llandres, A. L., E. De Mas, and M. A. Rodríguez-Gironés. 2012. Response of pollinators to the tradeoff between resource acquisition and predator avoidance. Oikos 121:687–696.

Mason, L. G. 1977. Prey preferences and ecological sexual dimorphism in *Phymata americana* Melin. American Midland Naturalist 97:293-299.

Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences of the United States of America 98:3904–3908.

Rausher, M. D., and N. L. Fowler. 1979. Intersexual aggression and nectar defense in *Chauliognathus distinguendus* (Coleoptera: Cantharidae). Biotropica 11:96-100.

Rodríguez-Gironés, M. a., and J. Bosch. 2012. Effects of body size and sociality on the anti-predator behaviour of foraging bees. Oikos 121:1473–1482.

Rogers, S. R., P. Cajamarca, D. R. Tarpy, and H. J. Burrack. 2013. Honey bees and bumble bees respond differently to inter- and intra-specific encounters. Apidologie 44:621–629.

Scott, V., J. Ascher, T. Griswold, and C. Nufio. 2011. The bees of Colorado. University of Colorado Museum of Natural History, Boulder, Co.

Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology And Systematics*, **25**, 443-466.

Leibold, M.A. (1996) A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist*, **147**, 784-812.

Menge, B.A. (1995) INDIRECT EFFECTS IN MARINE ROCKY INTERTIDAL INTERACTION WEBS - PATTERNS AND IMPORTANCE. *Ecological Monographs*, **65**, 21-74.

Minckley, R.L., Wcislo, W.T., Yanega, D., & Buchmann, S.L. (1994) BEHAVIOR AND PHENOLOGY OF A SPECIALIST BEE (DIEUNOMIA) AND SUNFLOWER (HELIANTHUS) POLLEN AVAILABILITY. *Ecology*, **75**, 1406-1419.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., Orrock, J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J., & Trussell, G.C. (2008) Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, **89**, 2416-2425.

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| Genus | Sociality | Total Visits | Duration (s) | S.E. | Pollen | Nectar | Attack | Male | Female | Present | Absent |
| *Agapostemon* | Solitary | 1 | 0.33 | - | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Andrena* | Solitary | 18 | 2.55 | 1.52 | 3 | 5 | 0 | 14 | 4 | 8 | 10 |
| *Anthidium* | Solitary | 1 | 0.20 | - | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Apis* | Eusocial | 6 | 38.77 | 18.51 | 0 | 2 | 1 | 0 | 6 | 3 | 3 |
| *Bombus* | Eusocial | 8 | 7.94 | 3.47 | 2 | 5 | 0 | 1 | 7 | 6 | 2 |
| *Colletes* | Solitary | 1 | 3.57 | - | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Diadasia* | Solitary | 5 | 6.48 | 3.92 | 1 | 3 | 0 | 2 | 3 | 3 | 2 |
| *Eucera* | Solitary | 2 | 11.13 | 7.33 | 1 | 1 | 0 | 0 | 2 | 0 | 2 |
| *Halictus* | Eusocial | 22 | 2.57 | 1.27 | 2 | 4 | 0 | 8 | 14 | 11 | 11 |
| *Lasioglossum* | Social | 5 | 8.24 | 3.67 | 1 | 1 | 0 | 1 | 4 | 3 | 2 |
| *Lithurgus* | Solitary | 19 | 5.87 | 2.74 | 5 | 9 | 0 | 4 | 15 | 11 | 8 |
| *Megachile* | Solitary | 1 | 2.47 | - | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Melissodes* | Solitary | 613 | 2.55 | 0.26 | 45 | 148 | 1 | 466 | 147 | 313 | 300 |
| *Perdita* | Solitary | 2 | 0.53 | 0.10 | 0 | 0 | 0 | 0 | 2 | 2 | 0 |

Table 1 Bee visitation and behavior by genus during the ambush bug experiment. The sociality of each genus is noted. “Visits” is the total number of occurrences of each genus during the soldier beetle experiment. “Duration” is the mean visit duration in seconds and S.E. is 1 standard error of the mean. “Pollen” and “nectar” are the number of pollen and nectar collection events is recorded for each genus. “Exclusion” is the number exclusionary behaviors performed by the soldier beetle (see text). “Male” and “female” refers to the number of visits by each. “Present” and “Absent” refer to the occupancy status of the flower and numbers in those columns are the numbers of visits to flowers with or without occupants.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Genus | Sociality | Total Visits | Duration (s) | S.E. | Pollen | Nectar | Exclusion | Male | Female | Present | Absent |
| *Andrena* | Solitary | 30 | 4.42 | 1.94 | 10 | 12 | 1 | 3 | 27 | 9 | 21 |
| *Apis* | Eusocial | 5 | 1.15 | 0.28 | 0 | 2 | 1 | 0 | 5 | 5 | 0 |
| *Bombus* | Eusocial | 7 | 7.83 | 6.22 | 0 | 3 | 0 | 0 | 7 | 4 | 3 |
| *Lithurgus* | Solitary | 11 | 1.77 | 0.91 | 1 | 3 | 0 | 0 | 11 | 10 | 1 |
| *Melissodes* | Solitary | 60 | 1.71 | 0.47 | 4 | 17 | 0 | 37 | 23 | 21 | 39 |

Table 2 Bee visitation and behavior data by genus during the soldier beetle experiment. The sociality of each genus is noted. “Visits” is the total number of occurrences of each genus during the soldier beetle experiment. “Duration” is the mean visit duration in seconds and S.E. is 1 standard error of the mean. “Pollen” and “nectar” are the number of pollen and nectar collection events is recorded for each genus. “Exclusion” is the number exclusionary behaviors performed by the soldier beetle (see text). “Male” and “female” refers to the number of visits by each. “Present” and “Absent” refer to the occupancy status of the flower and numbers in thos columns are the numbers of visits to flowers with or without occupants.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Treatment | Land | Total Visits | Duration (s) |  | S.E. | Pollen | Nectar | Attack |
| Absent | No | 20 | 0.39 |  | 0.17 | 0 | 0 | 0 |
| Absent | Yes | 82 | 8.84 |  | 1.12 | 30 | 66 | 0 |
| Present | No | 20 | 0.26 |  | 0.03 | 0 | 0 | 0 |
| Present | Yes | 73 | 7.82 |  | 1.12 | 27 | 53 | 0 |

Table 3 Summary of female solitary bee visits during ambush bug treatment. “Treatment” refers to whether or not there was an ambush bug present. “Land” refers to whether or not the bee landed. “Duration” refers to the length of the visit in seconds and “S.E.” is the standard error of that mean. “Pollen” and “nectar”” refer to the number of events in which pollen or nectar were collected. “Attack” refers to the number of predation attempts by the ambush bug; there were no attempted attacks on female solitary bees.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Treatment | Land | Visits | Mean Duration(s) |  | S.E. | Pollen | Nectar | Exclusion |
| Absent | No | 12 | 0.43 |  | 0.04 | 0 | 0 | 0 |
| Absent | Yes | 19 | 7.93 |  | 2.94 | 8 | 14 | 0 |
| Present | No | 10 | 0.46 |  | 0.07 | 0 | 0 | 0 |
| Present | Yes | 20 | 1.35 |  | 0.30 | 7 | 11 | 1 |

Table 4 Summary of female solitary bee visits during soldier beetle treatment. “Treatment” refers to whether or not there was a soldier beetle present. “Land” refers to whether or not the bee landed. “Duration” refers to the length of the visit in seconds and “S.E.” is the standard error of that mean. “Pollen” and “nectar”” refer to the number of events in which pollen or nectar were collected. “Exclusion” refers to the number of exclusion attempts by the soldier beetle.

Figure Legends

**Fig. 1** *Phymata americana* (left) and *Chauliognathus basilis* (right) on *Helianthus petiolaris* inflorescences.

**Fig. 2** Diagram of the sampling design for one block in the experimental garden. Each cell represents one flower. Matching numbers in a cell indicate flower pairs and the order of observations. The shading represents the treatment of the flower. Flowers received the same treatment throughout the experiment. The order they were observed in and the flower they were paired with was randomly assigned each day

**Fig. 3** Ambush bug presence had no effect on the total number of solitary bee visits per flower (a), although there was a significant random effect of Pair (synonymous with Observation time) suggesting the visits declined over the day when predators were present (b). Soldier beetles had no overall effect on the number of solitary bee visits (c) which were uniformly low across the observation period (d).

**Fig. 4** Duration (in seconds) of bee visits to flowers with and without occupants (Mean ± SE). (a) Mean visit duration of female solitary bees to ambush bug occupied and unoccupied flowers. (b) Mean visit duration of female solitary bees to beetle occupied and unoccupied flowers. (c) Effect of observation pair on solitary bee visit duration during the ambush bug trials. (d) Effect of observation pair on solitary bee visit duration during beetle trials