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DO FLOWER-OCCUPYING INSECTS MEDIATE FORAGING BEHAVIOR IN SOLITARY BEES?

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Abstract:	<p>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 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 (<i>Chauliognathus basilis</i> Cantheridae), and a cryptic ambush bug predator (<i>Phymata Americana</i> Reduviidae), while foraging in an experimental garden planted with sunflowers (<i>Helianthus petiolaris</i>, Asteraceae). We found that interference competitors significantly reduced amount of time bees spent on flowers, while predators did not affect any of the recorded foraging behaviors. 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 the likelihood of entering predator occupied space.</p>	
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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 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* Cantheridae), and a cryptic ambush bug predator (*Phymata Americana* Reduviidae), while foraging in an experimental garden planted with sunflowers (*Helianthus petiolaris*, Asteraceae). Of the 704 recorded visits to predator occupied flowers, there were two predation events (0.3% of visits). Of the 109 recorded visits to competitor occupied flowers, there were two recorded events of physical exclusion (1.8% of visits). We found that interference competitors significantly reduced amount of time bees spent on flowers, while predators did not affect any of the recorded foraging behaviors. 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 and the likelihood of entering predator occupied space.

Key words

Solitary Bees, foraging, risk, avoidance behavior

Significance Statement

An animal's foraging behavior may change based on the species it encounters while foraging. We studied how wild bee foraging behavior changes in the presence of a common predator and

competitor under realistic conditions. Given the potentially deadly outcome of encountering a predator, bees should modify their foraging behavior to avoid flowers with predators. We found that predator presence had no detectable effect on bee foraging behavior; however, the presence of a competitor significantly reduced the amount of time a bee spent foraging on a flower. There were more competitor-bee interactions and competitors and those interactions were non-lethal. Our results show foraging bees changed their behavior based the species present but only after landing. This suggests female solitary largely ignore floral occupants when foraging and respond to floral occupants as necessary after landing, potentially resulting in visits to more flowers and increasing the chance of encountering a predator.

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Introduction

Foraging behavior is affected by interactions with other organisms that fall into two broad categories, competition and predation. Those interactions, either direct or indirect, may cause shifts in traits that influence foraging behavior and the distribution of organisms in space (Peacor and Werner 2001). For example, the experimental removal of western yellow jackets (*Vespula pensylvanica*), a predator and nectar competitor for bees, from sections of Hawaiian forest increases bee visitation to *Metrosideros polymorpha* blooms 3 to 16 fold (Hanna et al. 2014). Additionally, bees visiting flowers in sections of forest without yellow jackets display distinct foraging behaviors, collecting pollen and making contact with floral stigmas more frequently than bees in control plots with yellow jackets (Hanna et al. 2014). Understanding how bees respond to interactions with predators and competitors while foraging is especially important because of their crucial role in flowering plant reproduction.

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: 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 increases its probability significantly. Here we examine the behavior of solitary bees visiting sunflowers (*Helianthus petiolaris*, Asteraceae) that are unoccupied, have an ambush bug predator, or a beetle competitor present.

What, if any, behavioral responses foraging bees have to predators and competitors depend on their ability to recognize those putative antagonists. Social bees become more

discriminating in their floral choices after experiencing repeated simulated predation attempts (Ings et al. 2012, Llandres et al. 2012). They modulate 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). 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). This is because solitary bees are the sole caretakers of their offspring: if they die while foraging, their reproductive effort is wasted. If solitary bees are more risk averse, they may display similar pre-landing avoidance behaviors to flower occupying predators and competitors. Relatively few studies, however, have examined the effects of antagonists on the foraging behavior of solitary bees.

Bees adept at finding high quality flowers will likely have higher fitness; however, many of the cues bees use for optimizing foraging are also used by predators and competitors (Greco and Kevan 1994, Heiling et al. 2004). This could put bees that are adept foragers at higher risk of predation and competition, so they need to adopt strategies for predator or competitor avoidance. 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 bees, especially solitary bees, respond to floral occupants in non-laboratory settings provides important insights into bee foraging strategies and the resulting intra-community interactions. We examined solitary bee foraging behaviors using freely foraging bees in an experimental garden planted with the prairie sunflower, *Helianthus petiolaris* Nuttall (Asteraceae) as a food resource. We used the presence or absence of two flower occupants, the Colorado soldier beetle, *Chauliognathus basalis* LeConte, (Cantharidae) (Figure 1) and an ambush bug, *Phymata americana* Laporte (Phymatidae) (Figure 1), as the competitor and predator respectively. If solitary bees are more risk averse, they may initially respond to non-threatening floral occupants in the same way as they respond to ambush predators. However, bees may also learn to disregard floral occupants that pose no threat. We hypothesized that solitary bees would respond to both floral occupants by modifying their foraging behaviors to better assess floral characteristics and avoid encounters with occupants. Specifically, we predicted that 1) solitary bees will be less likely to collect pollen and nectar from occupied flowers, 2) solitary bees will visit occupied flowers less frequently and 3) solitary bees will spend less time per visit on occupied flowers.

Materials and Methods

Study system - Sunflowers are a dominant floral resource for bees 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*, is especially abundant in sandy disturbed soils found throughout urban and rural environments (Heiser Jr. 1947, Hurd et al. 1980). Along roadsides on the plains of Colorado, densities can be as high as four plants per meter ($N_{\text{transects}} = 32$, mean \pm 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 by foraging bees and other floral nectar and pollen consumers, and provide hunting platforms for ambush predators.

The predatory ambush bug, *Phymata americana*, and the nectarivorous soldier beetle, *Chauliognathus basilis*, occupy sunflowers at high densities in August and September respectively ($N_{\text{transects}} = 32$, mean \pm SE = 0.08 ± 0.03 ambush bugs/flower, mean \pm SE = 0.45 ± 0.06 beetles/flower; Schwantes, unpub. data). Ambush bugs are common, easily manipulated, cryptic predators capable of capturing prey many times their size, including bees (Balduf 1943, Mason 1977, Elliott and Elliott 1994). Hunting ambush bugs preferentially occupy yellow flowers (Greco and Kevan 1994). Colorado soldier beetles occupy floral territories for extended periods of time and physically harass both con- and heterospecific floral visitors with their legs and mandibles to maintain their territories (Rausher and Fowler 1979, Hurd et al. 1980). These beetles are brightly colored black and red to the human eye and their constant motion on flower heads makes them quite apparent (Figure 1). Based on field observations of these sunflowers, the most common bee visitors would likely be from three genera: *Melissodes*, *Andrena*, and *Megachile*. 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 - Helianthus petiolaris plants were grown from seeds collected from 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, then planted into pots (10cm x 10cm) in groups of five seedlings and moved into a greenhouse. In May, sunflowers were transplanted into two outdoor flowerbeds at the University of Colorado's 30th street greenhouse (Boulder, Colorado, USA). Flowerbed one received 25 plants and flowerbed two received 35 plants. Sunflowers were planted 60 cm apart

and watered regularly throughout the summer. The flowers 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 respond to floral occupants, predator and competitor presence were manipulated in the two blocks of sunflowers and observations of paired occupied and unoccupied flowers recorded simultaneously. We implemented a blocked, matched-pair design with paired observations of occupied and unoccupied flowers on three consecutive days. Starting in the northeastern corner of each block, we assigned identification numbers to 20 undamaged, recently opened blooms that were accessible for filming. We then randomly assigned treatments to these flowers such that 10 flowers in each block received occupants, and 10 were controls with no occupants (Figure 2). Treated and control flowers were the same throughout the three day experiment, unless flowers were damaged in some way. Each day, occupied and unoccupied flowers were randomly paired for observation. Pairs 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. This means that flower occupants that did not leave were in place for a minimum of four hours per day. Bee visitors were identified to genus from the recordings.

Two different experiments were run; the first was from August 15th to 17th for ambush bug occupied flowers and the second from September 5th to the 7th for soldier beetle occupied

flowers. At the start of each day, any arthropods greater than 1mm were removed from flowers and flowers were inspected for damage; if a flower were damaged or senescing, we used another flower on the same plant. After the inspection, floral occupants 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.

To evaluate bee foraging responses to cryptic predators, we placed ambush bugs on designated blooms. We collected 75 individual ambush bugs from patches of sunflowers growing on roadside edges in agricultural areas near Boulder, Colorado, before the experimental trials began. After collection, each ambush bug was stored in an individual container at 20°C inside of a growth chamber (Percival LLVL) maintained at 25°C during the day and 20°C at night with a 14-hour daylength. Ambush bugs were re-collected from flowers at the end of each day of trials and placed in the growth chamber over-night for possible use the next day.

To evaluate bee foraging responses to obvious competitors, we placed soldier beetles on blooms. We collected 60 individuals from patches of sunflowers growing on roadside edges in agricultural areas near Boulder, Colorado, before the experimental trials began. After collection, each soldier beetle was stored in an individual container at 20°C inside a growth chamber under the same conditions described above. Soldier beetles were re-collected from flowers at the end of each day of trials and placed in the growth chamber over-night for possible use the next day.

Bee foraging behavior assessment -To assess bee foraging behaviors, we viewed all videos of flowers and noted the following information: visit duration, nectar or pollen collection, predation attempts, or exclusionary behavior. Visit duration measures how long bees spend on a flower or investigating it. To quantify visit duration, for visits where the bee landed, we used the duration from the initial time a bee made contact with the flower to the moment it was no longer

196 contacting the flower. If a bee inspected a flower but did not land, we subtracted the initial time
197 it oriented its body towards the flower from the time that it oriented away from the flower. We
198 further separated inspections from bees passing through the frame of view by excluding flights
199 less than 0.1 seconds (Ings et al. 2012). Bees were scored as collecting nectar if they placed their
200 head into a disk flower or if their proboscis was visibly extended into a disk flower. Similarly,
201 bees were scored as collecting pollen when they passed over anthers and moved pollen to their
202 scopal hairs. Because our study involved focal animals in the field, we were unable to implement
203 blinding methods when recording and analyzing data.

204 The behavior of the flower occupants was also assessed as predation attempt for ambush
205 bugs and exclusionary behavior for beetles. Predation attempts were recorded if an ambush bug
206 caught or tried to catch a bee using its forelimbs. Exclusionary behaviors occurred when beetles
207 oriented their heads towards bees and used their feet or mouthparts to move or contact a bee. We
208 scored occupants as exhibiting these behaviors when they initiated contact with bees or reacted
209 to contact by a bee in a way that caused the bee to leave the flower or, in the case of the ambush
210 bug, become prey.

211 *Statistical Analyses* - To test the effect of floral occupancy on landing, nectar collection,
212 and pollen collection, we used chi-square contingency tests. These tested whether landing, nectar
213 collection or pollen collection were happening more frequently than expected on occupied
214 compared to unoccupied flowers.

215 Changes in visitation rate could indicate that bees are learning to avoid flowers; however,
216 bee visitation rate will also depend on the number of bees visiting the plot and the data showed
217 that visits tended to decline over the course of the day (see results). To test the effect of floral
218 occupancy on visitation rate, we used a generalized linear model with a Poisson distribution (link

= logit). Generalized linear models are capable of using non-normally distributed data and including categorical fixed and random effects. In this study, visitation rate, the number of visits over the time of an observation, had a non-normal distribution and the presence or absence of an occupant is categorical. Because the experimental design is randomized, day, block, and pair can be used 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 ordinary least squares regression 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 models with random effects 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*), include species that are eusocial. Those eusocial bees account 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 \pm SE = 1.75 seconds \pm 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 \pm 28.7 seconds) minutes and soldier beetles stayed for 8:33.4 (SE \pm 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 whether or not any of these foraging behaviors would occur (Land: $X^2 = 0.02$, df = 1, $p = 0.88$; Collect Nectar: $X^2 = 0.92$, df = 1, $p = 0.34$; Collect Pollen: $X^2 = 0.00$, df = 1, $p = 1$). Soldier beetles also had no detectable effect on what foraging bees did on flowers (Land: $X^2 = 0.03$, df = 1, $p = 0.87$; Collect Nectar: $X^2 = 0.17$, df = 1, p -value = 0.68; Collect Pollen: $X^2 = 0.00$, 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 generalized linear mixed model includes

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 allows 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 ($\text{var}_{\text{pair}} = 0.15$, $\text{var}_{\text{total}} = 0.46$). The effect of “Pair” on visitation rate is clear in Figure 3C as the number of visits per pair drops steadily.

The presence of a soldier beetle does not significantly impact the visitation rate of solitary female bees ($p = 0.90$) (Figure 3B). The estimated effect size of soldier beetle occupation is -0.03 visits per observation (log likelihood = -52.2, $z = -0.9128$, $p = 0.90$, $n = 40$). During the beetle trials, no random effect 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” ($\text{var}_{\text{pair}} = 0.55$, $\text{var}_{\text{total}} = 3.23$) (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 ($\text{AIC}_{\text{concise}} = 803.05$, $\text{AIC}_{\text{null}} = 803.98$).

Visit duration declines when soldier beetles occupy flowers (Figure 4B). “Pair” is the only random effect that contributes marginally to the variance term ($\text{var}_{\text{pair}} = 0.06$, $\text{var}_{\text{total}} = 1.76$) (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 ($AIC_{\text{concise}} = 206.33$, $AIC_{\text{null}} = 208.41$). 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. The behavior of bees in this common garden experiment provides insight into how bees perceive risk while foraging in patches of resources such as those found in human-modified landscapes. 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 (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

are 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 soldier beetles occupying flowers influence post-landing behaviors in solitary female bees. 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 imply 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 and the likelihood of entering predator occupied space.

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

Table 1 Bee visitation and behavior data 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

421 the occupancy status of the flower and numbers in those columns are the numbers of visits to flowers with or without
 422 occupants.

423

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

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

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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

435

436 Table 3 Summary of female solitary bee visits during ambush bug treatment. “Treatment” refers to whether or not there was an
437 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.”
438 is the standard error of that mean. “Pollen” and “nectar” refer to the number of events in which pollen or nectar were collected.
439 “Attack” refers to the number of predation attempts by the ambush bug; there were no attempted attacks on female solitary bees.

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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

444

445 Table 4 Summary of female solitary bee visits during soldier beetle treatment. “Treatment” refers to whether or not there was a soldier
 446 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
 447 standard error of that mean. “Pollen” and “nectar” refer to the number of events in which pollen or nectar were collected.
 448 “Exclusion” refers to the number of exclusion attempts by the soldier beetle.

449 Figure Legends

450 Figure 1 *Phymata americana* (left) and *Chauliognathus basilis* (right) on *Helianthus petiolaris*
451 blooms

452

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

458 Figure 3 Number of visits (mean \pm SE) per observation for female solitary bees. (A) Mean
459 visitation rate of female solitary bees to ambush bug occupied and unoccupied flowers. (B)
460 Visitation rate of female solitary bees to beetle occupied and unoccupied flowers. (C) Effect of
461 observation pair (an analog of time, as pair 1 was observed first and pair 10 was observed last on
462 each day) on solitary bee visitation rates during the ambush bug trials. (D) Effect of observation
463 pair on solitary bee visitation rates during beetle trials

464 Figure 4 Duration (in seconds) of bee visits to flowers with and without occupants (Mean \pm SE).
465 (A) Mean visit duration of female solitary bees to ambush bug occupied and unoccupied flowers.
466 (B) Mean visit duration of female solitary bees to beetle occupied and unoccupied flowers. (C)
467 Effect of observation pair on solitary bee visit duration during the ambush bug trials. (D) Effect
468 of observation pair on solitary bee visit duration during beetle trials

469

Figure1

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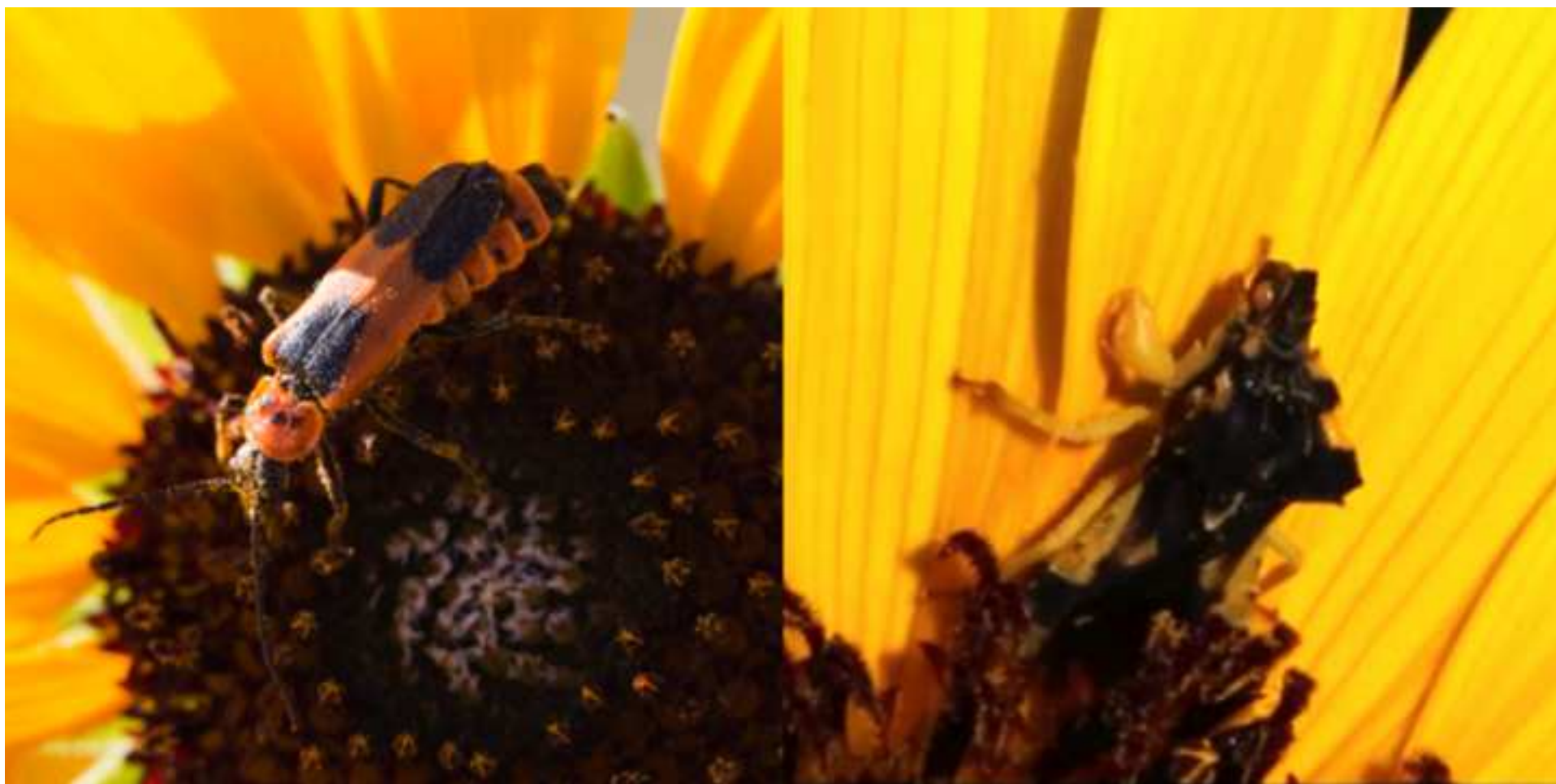


Figure2

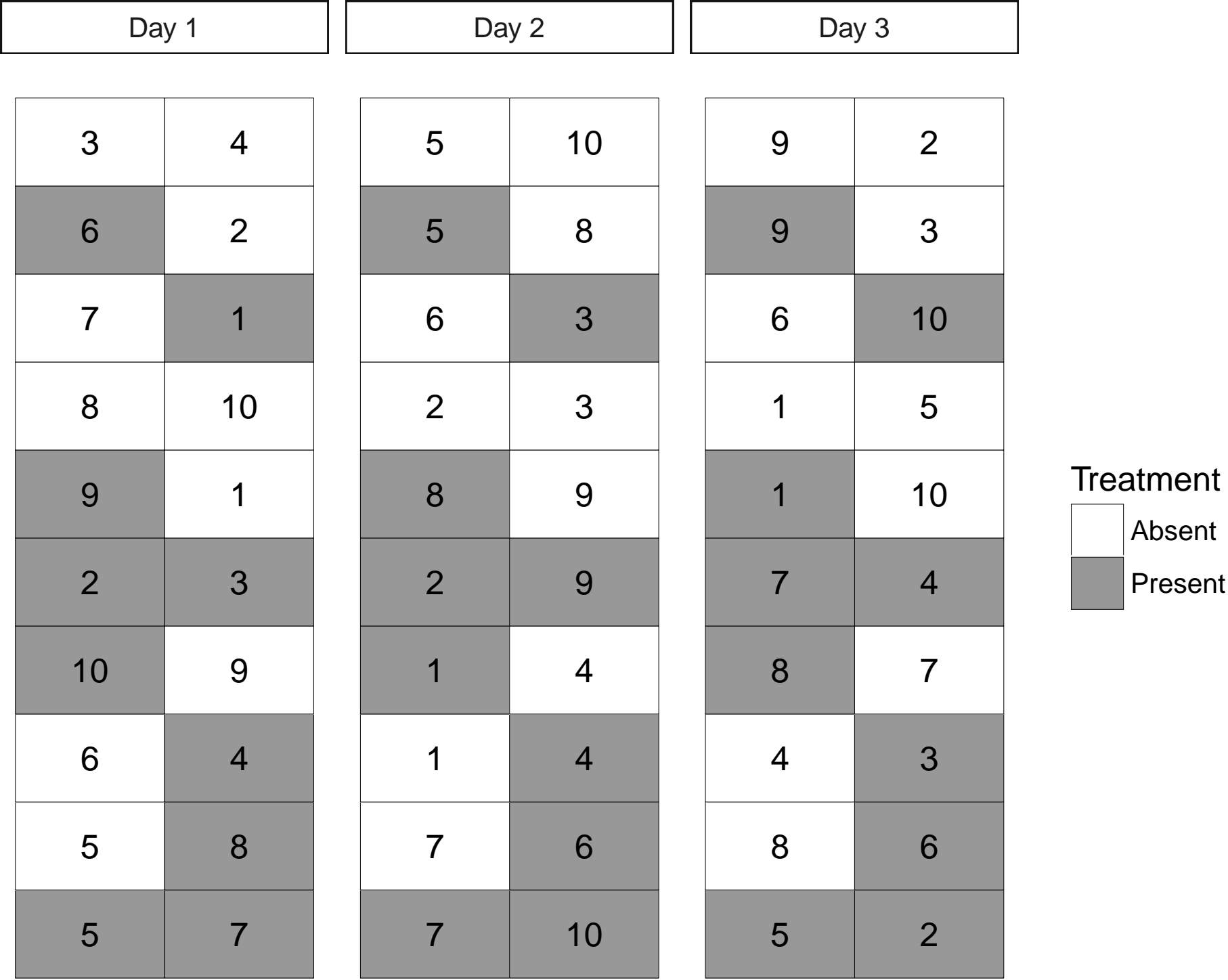


Figure3

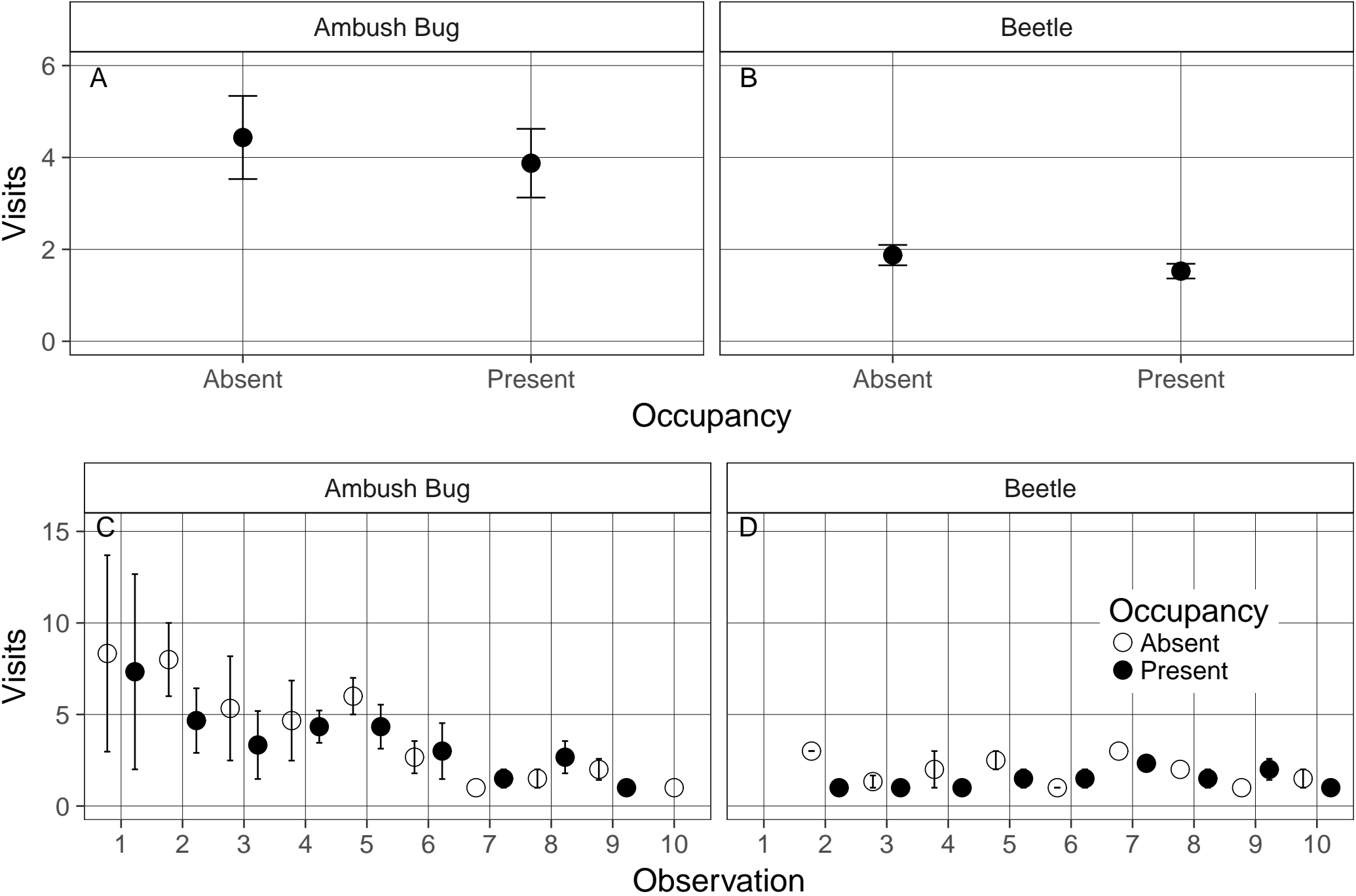
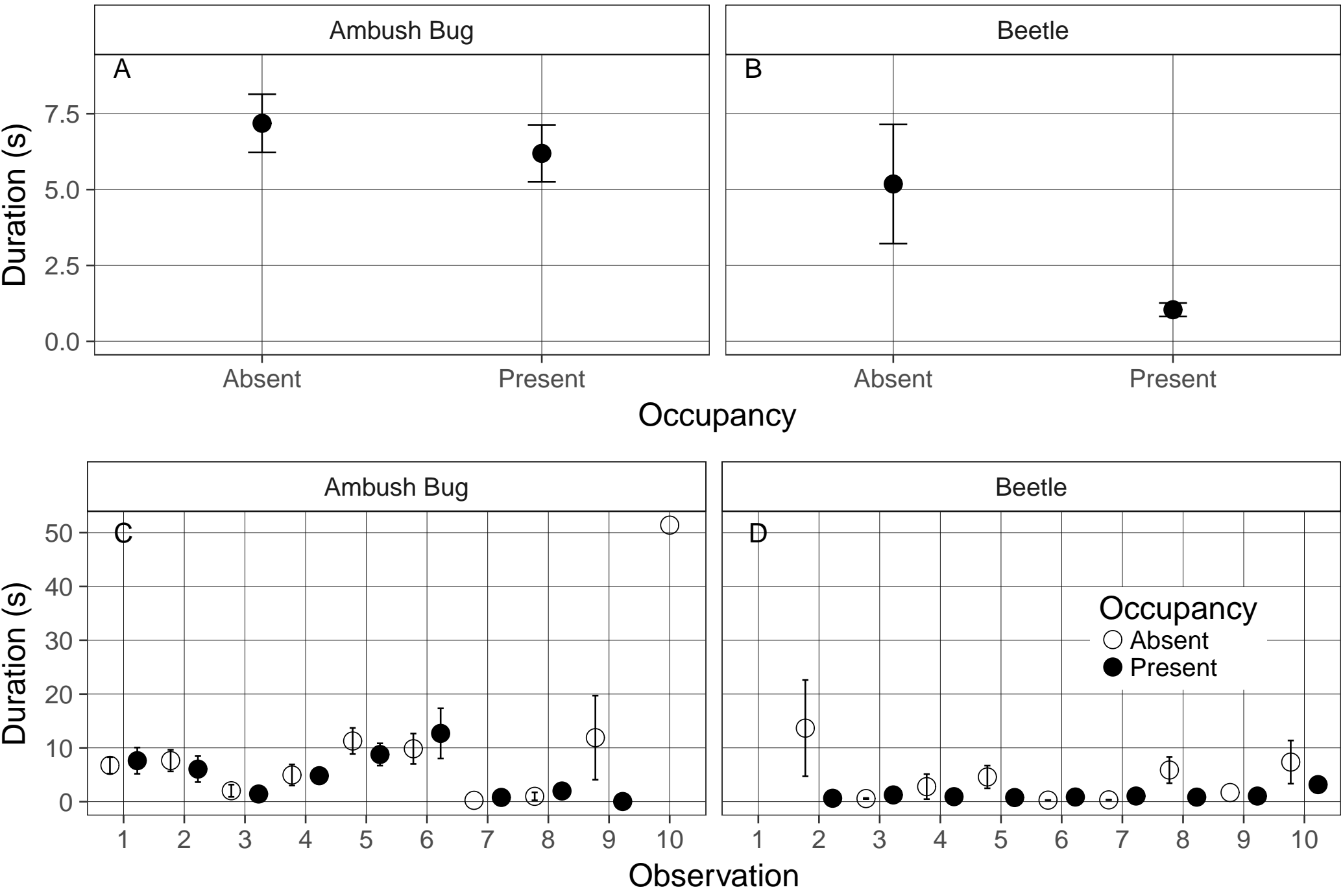


Figure4





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