Title: Impact of tillage on the crop pollinating, ground nesting bee, *Peponapis pruinosa* in California.

Authors:

Katharina S. Ullmann^{a,*}, Matthew H. Meisner^a, Neal M. Williams^a

^aDepartment of Entomology and Nematology, University of California, Davis, One Shields Ave, Davis, California 95616 USA; Tel: 530-752-0492; Fax:530-752-1537

*Corresponding author: kullmann@ucdavis.edu

Abstract:

Wild bees, especially ground nesting species, are important for crop pollination. However, the extent to which regular disturbance, such as tillage, impacts ground nesting bees is poorly known. We conducted a two-year tillage experiment on the squash bee, *Peponapis pruinosa* (Say), to quantify how tillage impacted offspring survival, offspring sex ratio, and timing of emergence. We established *P. pruinosa* nests in twenty 3 meter by 3 meter cages and then randomly assigned a tillage treatment to half of those cages. The following summer we trapped emerging offspring. We used a Bayesian framework to analyse the data. Offspring emergence varied greatly, but there was modest evidence that tillage reduced offspring emergence in treatment cages. There was limited evidence that tillage reduced the proportion of male bees emerging into cages, suggesting that tillage did not impact sex ratio. There was strong evidence that tillage delayed emergence of surviving offspring. 1 Tillage practices should be considered when manging fields for this ground nesting bee. However, even disturbed squash fields may contribute to this species' persistence in agricultural landscapes.

Key Words:

Cucurbita; squash; agriculture; disturbance; sex ratio

1. Introduction

Wild native pollinators, including ground-nesting bees, are important for global crop pollination (Garibaldi *et al.*, 2013; Klein *et al.*, 2007). They directly increase crop yields and can also interact synergistically with honey bees to increase the pollination effectiveness of honey bees (Brittain, Kremen, & Klein, 2013; Garibaldi *et al.*, 2013; Greenleaf & Kremen, 2006). Although wild pollinator diversity benefits crop yield (Brittain, Williams, Kremen, & Klein, 2013; Garibaldi *et al.*, 2013; Hoehn, Tschardtke, Tylianakis, & Steffan-Dewenter, 2008; Winfree & Kremen, 2009), agriculture is a leading driver of land use change and biodiversity loss (Tilman *et al.* 2001; Foley *et al.* 2005). In addition, agricultural intensification increases management practices that negatively impact native bee abundance and diversity (Tschardtke *et al.* 2005; Winfree *et al.* 2009; Williams *et al.* 2010).

Agricultural landscapes are often mosaics of disturbed and undisturbed ground. Within these landscapes ground nesting bees nest in natural and semi-natural areas including hedgerows (H. Sardiñas unpublished data), flower strips (N. Williams unpublished data), forest fragments (J. H. Cane, 1994), grasslands and chaparral (Sardiñas & Kremen, 2014; Straka & Rozen, 2012). They also nest in fallow and active crop fields, which experience regular disturbance in the form of tillage (Minckley *et al.* 1994; Kim, Williams & Kremen 2006; Julier & Roulston 2009; Xie, Qiu & Chen 2013; Sardiñas *et al.* 2015). Intensified agricultural landscapes are dominated by ground that is frequently disturbed, which may reduce the population persistence of, and pollination by, wild pollinators (Tschardtke *et al.*, 2005).

Tillage is used to incorporate soil amendments, manage crop residues, control weeds, and reduce soil compaction as part of normal farm management to improve crop yield (Köller, 2002). These practices can negatively affect ground-nesting bees, but ground-nesting bee population persistence in agricultural landscapes may depend on whether some, all, or no bees survive tillage (Williams et al., 2010). Many ground-nesting bees nest at a depth that is within the tillage zone (e.g. < 30cm from the soil surface (J. Cane & Neff, 2011). Thus tillage may directly kill developing offspring or alter emergence cues such as soil moisture and temperature (Wuellner 1999). If male and female offspring are placed at different depths within the nest, as is the case for *Calliopsis persimilis* (Danforth 1990), then tillage may alter the population's sex ratio. Tillage may also have positive effects on soil properties for ground-nesting bees such as creating open bare ground, loosening compacted soils, or changing the predator community (Roger-Estrade, Anger, Bertrand, & Richard, 2010).

The few studies investigating the impact of tillage on bees in agricultural fields provide conflicting results. Anecdotal evidence suggests that tillage can directly impact bee survival and delay emergence time (Mathewson, 1968; Wuellner, 1999). Observational studies on squash and pumpkin (*Cucurbita* spp.) farms in the United States found that the abundance of a ground nesting bee (*Peponapis pruinosa*) was negatively correlated with tillage in the previous season (Shuler, Roulston, & Farris, 2005). However, a follow up study on pumpkin (*Cucurbita pepo*) found no such effect (Julier & Roulston, 2009). Neither study directly measured the impact of tillage on ground nesting bees.

We conducted a two-year, tillage experiment on the squash bee, *Peponapis pruinosa*. We were specifically interested in parameters that might influence the population dynamics of this species and asked the following questions: (1) Do fewer offspring emerge in tilled plots? (2) Does tillage alter the sex ratio of emerging offspring? (3) Do offspring emerge later in tilled plots compared to control plots?

2. Materials and Methods

2.1 Study site

The experiment was carried out at an agricultural field station in Yolo County located in the Central Valley of California (-121.69648, 38.518914). This region has a Mediterranean climate, and the study site's soils are primarily made up of Yolo Loam (<http://websoilsurvey.sc.egov.usda.gov/>). Yolo Loam is a well-draining, silty loam (soil family: fine-silty, mixed, superactive, thermic Fluventic Haploxerepts; https://soilseries.sc.egov.usda.gov/OSD_Docs/Y/YOLO.html). Vertical soil properties associated with the Yolo Series are fairly similar, all horizons from 0 cm-152 cm are made up of a silty loam except for the horizon at 41-58 cm which is made up of a silt clay loam. *Peponapis pruinosa* is a univoltine, specialist, ground nesting bee that nests preferentially under plants of the genus *Cucurbita*, its host plant (Hurd, Linsley, & Michelbacher, 1974; Julier & Roulston, 2009; Mathewson, 1968). Previous nest excavations in the northern Central Valley of California suggested that nest cells can range from 8.9 cm deep to 68.6 cm deep, with most falling between 12.7 cm and 30.4 cm (Hurd et al 1974).

2.2 *Establishing artificial nesting sites:* On August 15, 2012 we set up twenty 3 m × 3 m x 1.8 m sealed flight cages over plantings of three varieties of squash planted earlier in the season. This included 14 cages over: *C. pepo* cv. “Reward”, 2 cages over *C. pepo* cv. “Magician”, and 4 cages over *C. maxima* cv. “Redondo de Trunco” (see Fig. 1). Cages were made of fine mesh Lumite screen (Lumite Inc, Alto, Georgia, USA). Cloth landscape fabric (30 cm wide) was staked down on the internal perimeter of each cage to prevent bees from nesting near the cage edge. Plants were drip irrigated, and fruit were harvested regularly to extend bloom following usual agricultural practices.

Previous studies suggested that female *P. pruinosa* bee populations peak in mid-August (Tepedino 1981). On August 20, 2012 we established artificial *P. pruinosa* nesting sites within each flight cage. In the early morning we collected 40 female and 40 male *P. pruinosa* from a single farm located 42 km from our study site. Females were only collected if they were not carrying pollen. We assumed that these individuals had not yet established nests. Bees were placed in individual plastic vials and transported in coolers to the study site. Later that morning we marked each bee for individual recognition with paint (Testors Enamel paint, Testors, Vernon Hills, Illinois, USA) on the thorax and then released two females and two males into each 3 m × 3 m x 1.8 m cage. *Peponapis pruinosa* is a gregarious ground nesting bee where nesting densities can range from an average of 1.7 nests to 5.3 nests per 0.09 square meters (Hurd *et al.* 1974.) However, when walking through squash fields, isolated nests are also observed (K. Ullmann, pers. observation.) To confirm that bees were nesting, we surveyed each cage daily for nest entrances. We also observed bee activity for 10 minutes each morning and noted the presence of males and females, whether females were collecting or carrying pollen and if females entering

the nest carried pollen and left without pollen. We stopped monitoring a cage when females in that cage were not seen for thirty days. Monitoring of the last cage ended on October 1, 2012.

2.3 Tillage treatment and monitoring offspring emergence: In late fall 2012 we marked the cage perimeters with gypsum powder, dismantled the cages, and removed the landscape fabric and drip tape. We then randomly selected ten former cage locations to receive the tillage treatments, seven were from the “Reward” variety, one from the “Magician” variety, and two from the “Redondo de Trunco” variety. The tillage treatment included disking to 15.2 cm, ripping to 40.6 cm with a three-shank sub-soiler set at 0.76 m between shanks, and then disking again at 15.2 cm. Shallow tilling occurs regularly in row crop fields irrigated with buried drip lines. This deep tillage regime is typically implemented every three years in Yolo County (J. Mitchell, University of California Cooperative Extension cropping systems specialist, personal communication). Control plots were driven over, but received no tillage.

In early spring 2013 we set up drip irrigation and erected the cages in their previous locations. We irrigated cages twice per week for two hours and weeded cages four times over the course of the summer. Within each cage we set up blue vane traps (Springstar Inc, Woodinville, Washington, USA) filled with soapy water (one tablespoon dish soap (“Dawn”) per gallon water) to trap emerging bees (Stephen & Rao, 2005). We removed and recorded the sex of all trapped bees every three or four days between May 26 and September 26, 2013.

2.4 Statistical analysis: We used a Bayesian statistical modelling framework for fitting generalized linear mixed models to quantify the relationship between tillage and the number of

offspring emerging, offspring sex ratio and offspring emergence date. The Bayesian approach allowed us to quantify our uncertainty in these estimated relationships. Models were fitted using Hamilton Monte Carlo sampling, a type of Markov Chain Monte Carlo, using the rstan package (v2.3.0) in R (v3.03). We used uninformative, flat priors for all models. We ran three chains for 40,000 samples. The first 5,000 samples for each chain were discarded as burn-in. We used the potential scale reduction statistic $\hat{R}$ to confirm that chains had converged, i.e. we confirmed that $\hat{R}$ was equal to one. We considered tillage to have a strong effect on the response variable if the 95% highest posterior density (HPD) interval, a Bayesian analogue of a confidence interval, for the tillage parameter did not overlap zero (Severini, 1991). Alternatively, if the HPD interval partially overlapped zero, we used additional information about the posterior distribution to quantify the evidence for an effect of tillage on the response variable.

We fitted an overdispersed Poisson mixed model with a log link function to quantify the effect of tillage on the number of emerging *P. pruinosa* offspring trapped per cage. Treatment (1 if tilled; 0 if not tilled), number of nests per cage, and *Cucurbita* variety were included as fixed effects. Cage ID (1, 2, ..., n, where n is the total number of cages) was included as a subject level random effect to account for overdispersion (Gelman & Hill, 2009).

We fit a logistic model with a logit link function to explore the effect of tillage on offspring sex ratio by quantifying the change in log odds of being male between tilled and control cages. The response variable was either 1 (for male) or 0 (for female). Treatment and *Cucurbita* variety were included as fixed effects. Cage ID was included as a random effect to account for cage effects. To determine whether control cages were male biased we calculated, for each variety, the

HPD interval for the probability of being male, and asked whether or not that interval included 0.5.

We fit a linear (e.g. Gaussian) mixed model with an identity link function to determine if tillage had an effect on emergence date, using emergence Julian date as the response variable. The response variable was log transformed to better satisfy assumptions of normality. We analysed two separate models, one for males and one for females to determine if treatment affected males and females differently because males emerge before females (Tepedino, 1981). Treatment, number of nests per cage and *Cucurbita* variety were included as fixed effects. Cage ID was included as a random effect to account for cage effects. We could have used one model and included gender as a fixed effect. However, we decided against including the term in our model because offspring gender may be an intermediate outcome of the treatment that could in turn alter the response (Gelman & Hill, 2009). For example, it is plausible that treatment day might affect sex ratio, and sex ratio in turn affects emergence date. If we were to include gender in the model, then the treatment term in the model would quantify the difference in sex ratio between bees which did receive the treatment and those that did not, among bees with the same gender. However, bees that had the same gender, but received different treatments, may have been inherently different before receiving the treatment. Thus, we would be comparing units that differ in their underlying characteristics and potentially not accurately measuring the treatment effect. As a result, we chose to start with models that did not include intermediate outcomes as fixed effects and instead modelled males and females separately.

3. Results

We found a total of 40 nests (average per cage = 1.9 ± 0.3 (SE)). At twenty-nine of those nests we observed a female bee enter the nest with pollen and leave without pollen, with one such record for 19 of the 20 cages. This suggests that we were successful in establishing artificial nesting sites.

3.1 Offspring emergence: There was some evidence that tillage was associated with decreased offspring emergence (Figs 2a and 2b). The mean number of bees emerging into control cages $\pm$ one standard error was 11 ± 1.05 and in tilled cages was 7.5 ± 0.87 . After accounting for covariates, the posterior mean change in bee emergence between tilled and control cages was -0.66. We exponentiated (e.g. back transformed) this number in order to determine the multiplicative effect on number of bees emerging in tilled cages relative to control cages; there were 0.51 times fewer bees emerging in tilled cages compared to control cages. There was an 89% posterior probability that emergence was lower in tilled cages than in control cages. The parameter's 95% HPD interval was -1.87, 0.49, overlapping zero.

3.2 Effects of tillage on sex ratio: There was partial evidence that tillage was associated with a decrease in the proportion of male offspring (Figs 3a and 3b). There was a 78% posterior probability that the log-odds of being male in tilled cages was lower than the log odds of being female; the 95% HPDI included zero (-1.21, 0.56). There was strong evidence that offspring emerging into control cages planted with cv. "Reward" were female biased. Within these cages, the mean posterior log-odds of being male was -1.19 (HDP interval was -1.85, -0.55). There was some evidence that control cages planted with cv. "Redondo de Trunco" were female biased (mean posterior log-odds of being male was -0.72, HPD interval was -1.63, 0.13) and no

evidence that control cages planted with cv. “Magician” were female biased (mean posterior log-odds of being male was 0.18, HPD interval was -1.00, 1.34).

3.3 Effects of tillage on emergence date: Male bees in tilled cages were associated with later emergence dates than bees in control cages (Figs 4a and 4b); the posterior probability of male bees emerging later in tilled cages was 99%. The posterior mean change in male bee emergence date between tilled and control cages was 0.92 days (95% HPD interval: 0.16, 1.68). Female bees responded more weakly to the treatment; there was a 95% posterior probability that female bees emerged later in tilled cages (Figs 4c and 4d). The posterior mean change in female bee emergence date between tilled and control cages was 0.55 days (95% HPD interval: -0.15, 1.23).

4. Discussion

Tillage impacted *P. pruinosa* offspring in a variety of ways, some with potentially negative consequences for population growth. There was some evidence that tillage reduced offspring emergence, on average by about 50% compared to no-till plots. These results are consistent with previous studies conducted on other soil-dwelling organisms. Tillage has a negative effect on some soil-dwelling species. Larger organisms (e.g., earthworms) appear to be more sensitive to tillage than smaller organisms (e.g., fly larvae; Kladivko 2001). Two studies directly measured insect emergence and activity post tillage. The first, from the United Kingdom, found that 50% more sawflies emerged in fields left untilled than in fields that had been ploughed to a depth of 25 cm (A. M. Barker, Brown, & Reynolds, 1999). Sawflies can overwinter at depths of 20 cm (A. Barker & Reynolds, 2004). Similarly, in Maine, beetle (*Harpalus rufipes*) activity was more than 50% higher in untilled fields compared to tilled fields and fields that had been chiselled 20

cm deep than in fields that had been mouldboard ploughed 25 cm deep or rotary tilled 15 cm deep (Shearin, Reberg-Horton, & Gallandt, 2007). This suggests that some tillage implements (e.g. chisel ploughs) are less destructive than other implements (e.g. mouldboard plough). A previous study found that *H. rufipes* creates burrows up to roughly 17 cm deep, but depth depends on larval instar stage (Luff 1980).

Although tillage appeared to affect offspring emergence negatively, roughly half of the bees survived this disturbance compared to those in control plots. Populations of this species may, therefore, be able to persist despite this form of disturbance. In our experiment the greatest disturbance occurred at the depth of disking (<15cm) and no disturbance occurred below 40 cm (e.g. depth of chisel). The majority of *P. pruinosa* cells are found at depths of 10 - 45cm (Hurd, Linsley & Michelbacher 1974, Ullmann unpublished data), suggesting that some individuals nested outside of the range of the most intensely disturbed tillage zone, i.e. they nested below 15 cm from the soil surface or were not directly hit by the three shank sub-soiler at deeper depths. *Peponapis pruinosa*'s ability to survive disturbance may contribute to this species' ability to persist in agricultural landscapes throughout Central and North America.

The effect of tillage on sex ratio of emerging offspring is less certain. There was limited evidence that tillage reduced the log-odds of male bees emerging into cages. In general, the sex ratio of solitary bees tend to be male biased (Frohlich & Tepedino, 1986; Helms 1994). However, there is some evidence that a 1:1 ratio can exist (Danforth 1990) and that sex ratio can vary over the course of the season; Torchio and Tepedino (1980) found that, for a trap nesting *Osmia* species, sex ratios were female biased at the start of the season and male biased at the end

of the season. Potential differences between tilled and control plots could be explained if male offspring were placed at shallower depths than female offspring. Non-random placement of male and female offspring has been observed in other bee species. For example, *Megachile* spp. and other cavity nesters tend to place males towards the front of nests (Scott, Kelley, & Strickler, 2000), and males of the ground nesting species *Calliopsis persmimiles* are placed at more shallow depths than females (Danforth 1990). Although we have evidence that treatment affects emergence day, there was little evidence that treatment affects sex ratio directly. In addition, there was no strong indication that treatment affects sex ratio as mediated by changes in emergence day.

There was strong evidence that male bees in tilled cages emerged later than those in control cages and some evidence that tilling delayed female bee emergence. We originally hypothesized that, if tilling destroyed more male than female offspring, then emergence day would be delayed in tilled cages. Previous research on *Peponapis pruinosa* found that males emerge before females over the course of the summer (Tepedino 1981). However, there was little evidence that tilling affected the sex ratio. This suggests that there must be an alternative reason why bees in tilled cages emerged later than those in control cages.

It is unclear whether delayed emergence in tilled plots was due to differences in emergence cues between tilled and control plots or differences in ability to reach the soil surface. Temperature is considered an important external cues that terminate diapause (Danforth, 1999; Forrest & Thomson, 2011; Kostál, 2006). A previous study found that when a dirt road was ploughed and planted with soy, bees emerged roughly four days later than those emerging into the untilled dirt

road (Wuellner, 1999). Wuellner (1999) suggested that the delay in emergence was result of cooler soil temperatures associated with increased vegetation in tilled areas. Within our study system it seems unlikely the soil temperature differed between tilled and control plots because both had similar vegetation cover (K. Ullmann, pers. observation). Tillage can change soil structure, making it more difficult for the bees to dig their way out (Hamza & Anderson, 2005). Finally, if offspring are emerging from deeper cells because shallower cells were destroyed due to tillage, then it may take longer for bees to reach the soil surface.

Offspring could be impacted in two ways by delayed emergence. Firstly, previous studies have shown that bees that emerge later have lower carbohydrate and lipid stores (Dmochowska, Giejdasz, Fliszkiewicz, & Zóltowska, 2013). Lipid stores in insects are thought to be important for flight, immune response, starvation avoidance, and oocyte maturation (Arrese & Soulages, 2010). We did not determine if bees emerging from control and tilled plots differed in body weight or nutrient stores. However, if *P. pruinosa* offspring emerging into tilled cages had lower nutrient stores, this could have left them at a disadvantage by potentially changing their fecundity and longevity. Secondly, a phenological mismatch between crop and foraging pollinators could limit resources available for offspring provisioning. However, this seems unlikely to affect *P. pruinosa* in central California, given that the delay in emergence was fairly short and that fresh market production of summer and winter squash provides successional plantings (and bloom) across the season. However, bees that rely on isolated fields that do not have successional plantings and bees that emerge at the end of the season may have limited access to pollen.

Delayed emergence in tilled areas is unlikely to change crop yields if other pollinators, such as bumble bees or honey bees, are present in the field. However, if these pollinators are absent and pollination depends completely on *P. pruinosa*, then fruit set could be delayed for early crop plantings. However, this reduction could be offset by high densities of *P. pruinosa* in the crop field.

5. Conclusion

Research over the last decade has largely focused on the contribution of natural and semi-natural habitat to wild native bees, but ours and other recent studies suggest that crop fields may provide important resources as well. Mass flowering crops can increase the abundance of both social and solitary bee species (Holzschuh, Dormann, Tschardtke, & Steffan-Dewenter, 2013; Riedinger, Renner, Rundlöf, Steffan-Dewenter, & Holzschuh, 2014). In addition, floral resources provided by mass flowering crops increased colony growth of a *Bombus* sp. and offspring production of an *Osmia* sp. (Jauker, Peter, Wolters, & Diekötter, 2012; Westphal, Steffan-Dewenter, & Tschardtke, 2009). Crop fields also provide nesting resources for ground-nesting bees (Julier & Roulston, 2009; Kim et al., 2006; Minckley et al., 1994; Wuellner, 1999). However, tilling could limit the number of bees able to persist in crop fields. Our research shows that at least for *P. pruinosa*, as many as 50% of individuals do not survive a typical deep tillage regime. Population viability analysis would reveal how sensitive population persistence may be to such a reduction in survival at this life stage. More research should be carried out to explore how tillage regimes might impact different bee species (e.g. social and solitary, small and large, those with different phenology, and those that nest at shallower and deeper depths), in different soil types, and using different tillage implements (e.g. type and depth of implement used) at different times of the

year. In addition, tillage frequency, which can vary depending on crop, soil type, or region, should be considered. Frequent tilling may negatively impact population persistence of ground nesting bees. Even though tilling had a negative effect on *P. pruinosa* offspring emergence compared to areas that were not tilled, roughly half of the bees survived. This suggests that even disturbed crop fields should not be overlooked in their contribution to this species persistence, especially given that these same fields provide essential floral resources.

Acknowledgements

We would like to thank Jessica Forrest, Rei Scampavia, Dena Grossenbacher, Kitty Bolte, Meslissa Cruz, Shengpei Wang, Julia Aaronson, Nicole Aha, Arun Durvasula, Felicia Dyer, Prema Krishnan, Rosie Murphy-Deak, Kao Saelee, Mary Watson, Samantha Yu, Isabelle Ka Lui, Karen Whitestone, Jochen Freund, Jillian Sturgess, Billy Synk, Miles DaPrato and Nina Suzuki for their assistance in the field. Jason Cavatorta shared field equipment. HM-Clause Inc. allowed us to conduct our study on their property. Jay Rosenheim, Sebastian Schreiber, and Kimiora Ward provided feedback that greatly improved the manuscript. K. Ullmann was supported by National Science Foundation Graduate Research Fellowship Program under Grant No. 1148897, the Western Sustainable Agriculture Research and Education Graduate Student Grant (GW13-018), and Department of Entomology at the University of California, Davis.

References

- Arrese, E. L., & Soulages, J. L. (2010). Insect fat body: energy, metabolism, and regulation. *Annual Review of Entomology*, 55, 207–25. doi:10.1146/annurev-ento-112408-085356
- Barker, A. M., Brown, N. J., & Reynolds, C. J. M. (1999). Do host-plant requirements and mortality from soil cultivation determine the distribution of graminivorous sawflies on farmland? *Journal of Applied Ecology*, 36(2), 271–282. doi:10.1046/j.1365-

2664.1999.00394.x

- Barker, A., & Reynolds, C. (2004). Do host-plant interactions and susceptibility to soil cultivation determine the abundance of graminivorous sawflies on British farmland? *Journal of Agricultural and Urban Entomology*, 21(4), 257–269.
- Brittain, C., Kremen, C., & Klein, A.-M. (2013). Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology*, 19(2), 540–7. doi:10.1111/gcb.12043
- Brittain, C., Williams, N., Kremen, C., & Klein, A.-M. (2013). Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings. Biological Sciences / The Royal Society*, 280(1754), 20122767. doi:10.1098/rspb.2012.2767
- Cane, J. H. (1991). Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *J.Kansas Entomol.Soc.*, 64, 406 – 413.
- Cane, J. H. (1994). Nesting biology and mating behavior of the Southern Blueberry Bee, *Habropoda laboriosa* (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society*, 67(3), 236–241.
- Cane, J., & Neff, J. (2011). Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation*, 2631 – 2636.
- Danforth, B. (1990). Provisioning behavior and the estimation of investment ratios in a solitary bee, *Calliopsis* - (*Hypomacrotera*)-*persimilis* (Cockerll) (Hymenoptera, Andrenidae). *Behavioral Ecology and Sociobiology*, 27(3), 159–168. 1
- Danforth, B. (1999). Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings. Biological Sciences / The Royal Society*, 266, 1985–1994. doi:10.1098/rspb.1999.0876
- Dmochowska, K., Giejdasz, K., Fliszkiewicz, M., & Zółtowska, K. (2013). Prolonged postdiapause: influence on some indicators of carbohydrate and lipid metabolism of the red mason bee, *Osmia rufa*. *Journal of Insect Science (Online)*, 13, 77. doi:10.1673/031.013.7701
- Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... Snyder, P. K. (2005). Global consequences of land use. *Science (New York, N.Y.)*, 309(5734), 570–4. doi:10.1126/science.1111772
- Forrest, J. R. K., & Thomson, J. D. (2011). An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs*, 81(3), 469–491. doi:10.1890/10-1885.1
- Frohlich, D. . R. . & Tepedino, V. . J. . (1986). Sex Ratio , Parental Investment , and Interparent Variability in Nesting Success in a Solitary. *Evolution*, 40(1), 142–151.
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., ... Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science (New York, N.Y.)*, 339(6127), 1608–11. doi:10.1126/science.1230200
- Gelman, A., & Hill, J. (2009). *Data analysis using regression and multilevel/hierarchical models*. Cambridge: Cambridge University Press.

- Greenleaf, S. S., & Kremen, C. (2006). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences of the United States of America*, 103(37), 13890–5. doi:10.1073/pnas.0600929103
- Hamza, M. A., & Anderson, W. K. (2005). Soil compaction in cropping systems. *Soil and Tillage Research*, 82(2), 121–145. doi:10.1016/j.still.2004.08.009
- Hoehn, P., Tschardtke, T., Tylianakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings. Biological Sciences / The Royal Society*, 275(1648), 2283–91. doi:10.1098/rspb.2008.0405
- Holzschuh, A., Dormann, C. F., Tschardtke, T., & Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia*, 172(2), 477–484.
- Hurd, P. D., Linsley, E. G., & Michelbacher, A. E. (1974). Ecology of the Squash and Gourd Bee, *Peponapis pruinosa*, on Cultivated Cucurbits in California (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology*, (168), 1–28.
- Jauker, F., Peter, F., Wolters, V., & Diekötter, T. (2012). Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic and Applied Ecology*, 13(3), 268–276.
- Julier, H. E., & Roulston, T. (2009). Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behaviour and landscape effects. *Journal of Economic Entomology*, 102, 563 – 573.
- Kim, J., Williams, N., & Kremen, C. (2006). Effects of Cultivation and Proximity to Natural Habitat on Ground-nesting Native Bees in California Sunflower Fields. *Journal of the Kansas Entomological Society*, 79(4), 309–320. doi:10.2317/0507.11.1
- Kladivko, E. J. (2001). Tillage systems and soil ecology. *Soil and Tillage Research*, 61(1-2), 61–76. doi:10.1016/S0167-1987(01)00179-9
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschardtke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings. Biological Sciences / The Royal Society*, 274(1608), 303–13. doi:10.1098/rspb.2006.3721
- Köller, K. (2002). Techniques of Soil Tillage. In A. El Titi (Ed.), *Soil Tillage in Agroecosystems* (pp. 1–25). CRC Press.
- Kostál, V. (2006). Eco-physiological phases of insect diapause. *Journal of Insect Physiology*, 52(2), 113–27. doi:10.1016/j.jinsphys.2005.09.008
- LUFF, M. L. (1980). The biology of the ground beetle *Harpalus rufipes* in a strawberry field in Northumberland. *Annals of Applied Biology*, 94(2), 153–164. doi:10.1111/j.1744-7348.1980.tb03907.x
- Mathewson, J. A. (1968). Nest Construction and Life History of the Eastern Cucurbit Bee, *Peponapis pruinosa* (Apoidea: Hymenoptera). *Journal of the Kansas Entomological Society*, 41(2), 255–261.
- Minckley, R. L., Weislo, W. T., Yanega, D., & Buchmann, S. L. (1994). Behavior and Phenology of a Specialist Bee (*Dieunomia*) and Sunflower (*Helianthus*) Pollen Availability. *Ecology*, 75(5), 1406. doi:10.2307/1937464

- 431 Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., & Holzschuh, A. (2014). Early
432 mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape*
433 *Ecology*, 29(3), 425–435.
- 434 Roger-Estrade, J., Anger, C., Bertrand, M., & Richard, G. (2010). Tillage and soil ecology:
435 Partners for sustainable agriculture. *Soil and Tillage Research*, 111(1), 33–40.
436 doi:10.1016/j.still.2010.08.010
- 437 Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee
438 populations. *Annual Review of Entomology*, 56, 293–312. doi:10.1146/annurev-ento-
439 120709-144802
- 440 Sardiñas, H. S., & Kremen, C. (2014). Evaluating nesting microhabitat for ground-nesting bees
441 using emergence traps. *Basic and Applied Ecology*, 15(2), 161–168.
442 doi:10.1016/j.baae.2014.02.004
- 443 Scott, V. L., Kelley, S. T., & Strickler, K. (2000). Reproductive Biology of Two
444 <I>Coelioxys</I> Cleptoparasites in Relation to Their <I>Megachile</I> Hosts
445 (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, 93(4), 941–
446 948. doi:10.1603/0013-8746(2000)093[0941:RBOTCC]2.0.CO;2
- 447 Severini, T. A. (1991). On the Relationship Between Bayesian and Non-Bayesian Interval
448 Estimates. *Journal of the Royal Statistical Society . Series B (Methodological)*, 53(3), 611–
449 618.
- 450 Shearin, A. F., Reberg-Horton, S. C., & Gallandt, E. R. (2007). Direct Effects of Tillage on the
451 Activity Density of Ground Beetle (Coleoptera: Carabidae) Weed Seed Predators.
452 *Environmental Entomology*, 36(5), 1140–1146. doi:10.1603/0046-
453 225X(2007)36[1140:DEOTOT]2.0.CO;2
- 454 Shuler, R. E., Roulston, T. H., & Farris, G. E. (2005). Farming practices influence wild
455 pollinator populations on squash and pumpkin. *Journal of Economic Entomology*, 98(3),
456 790–5.
- 457 Stephen, W. P., & Rao, S. (2005). Unscented Color Traps for Non-Apis Bees (Hymenoptera:
458 Apiformes). *Journal of the Kansas Entomological Society*, 78(4), 373–380.
459 doi:10.2317/0410.03.1
- 460 Straka, J., & Rozen, J. G. 1928-. (2012). First observations on nesting and immatures of the bee
461 genus *Ancyla* (Apoidea, Apidae, Apinae, Ancylaini). (American Museum novitates, no.
462 3749).
- 463 Tepedino, V. (1981). The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the
464 honey bee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). *Journal of the Kansas*
465 *Entomological Society*, 54(2), 359–377.
- 466 Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Swackhamer, D.
467 (2001). Forecasting agriculturally driven global environmental change. *Science (New York,*
468 *N.Y.)*, 292(5515), 281–4. doi:10.1126/science.1057544
- 469 Torchio, P. . F., & Tepedino, V. . J. (1980). Sex Ratio , Body Size and Seasonality in a Solitary
470 Bee , *Osmia lignaria propinqua* Cresson (Hymenoptera : Megachilidae). *Evolution*, 34(5),
471 993–1003. Retrieved from <http://www.jstor.org/stable/2408004>
- 472 Tschardtke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape

- perspectives on agricultural intensification and biodiversity ecosystem service management. *Ecology Letters*, 8(8), 857–874. doi:10.1111/j.1461-0248.2005.00782.x
- Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46(1), 187–193.
- Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143(10), 2280–2291. doi:10.1016/j.biocon.2010.03.024
- Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90(8), 2068–2076. doi:10.1890/08-1245.1
- Winfree, R., & Kremen, C. (2009). Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings. Biological Sciences / The Royal Society*, 276(1655), 229–37. doi:10.1098/rspb.2008.0709
- Wuellner, C. T. (1999). Nest site preference and success in a gregarious, ground-nesting bee *Dieunomia triangulifera*. *Ecological Entomology*, 24(4), 471–479. doi:10.1046/j.1365-2311.1999.00215.x
- Xie, Z., Qiu, J., & Chen, X. (2013). Decline of nest site availability and nest density of underground bees along a distance gradient from human settlements. *Entomological Science*, 16(2), 170–178. doi:10.1111/ens.12009

Figure captions

Figure 1. Cages set up over *Cucurbita* spp. Two female and two male *P. pruinosa* were released into each cage to establish nests.

Figure 2. Figure showing the mean number of bees emerging per cage and $\pm$ one standard error bar for tilled and control cages, based on the raw data (2a). Figure showing the posterior distribution of change in offspring survival between tilled and control cages (2b).

Figure 3 Figure showing the mean proportion of males and $\pm$ one standard error bar for tilled and control cages, based on the raw data (3a). Figure showing the posterior distribution of change in log odds of being male between tilled and control cages (3b).

Figure 4 Figure showing the mean emergence day of male bees and $\pm$ one standard error bar for tilled and control cages, based on the raw data (4a). On average male bees emerged later in tilled cages than in control cages. Figure showing the posterior distribution of change in male bee emergence day between tilled and control cages (4b).

Figure showing the mean emergence day of female bees and standard error bars for tilled and control cages, based on the raw data (4c). Figure showing the posterior distribution of change in female bee emergence day between tilled and control cages (4d).

518

519

520

2a

521

522

2b

523

524

525

526

527

3a

528

529

3b

530

531

532

4a

533
534
535

536

4b

537
538
539

540

4c

541

542

543

544

4d

545

546

547