Within-day Variation in Pollinator Activity on *Frasera speciosa* in a Mast Year

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Abstract

As temperature, wind, resource availability, and competition fluctuate, pollinators are unlikely to exhibit identical foraging behaviors or remain active at the same hours. Despite intuition and first principles, not much is known about within-day pollinator activity. Fine-scale (within-day) temporal sampling provides a thorough investigation into how pollination and pollinators respond to changing environmental conditions. In 2026, a mast flowering event of *Frasera speciosa* occurred in early June, providing abundant floral resources. This study used *F. speciosa* as a system to collect empirical evidence of within-day variation in pollinator activity. Specifically, I am interested in two questions: 1) How does pollinator activity on *Frasera* vary across the day? And 2) How do different pollinators forage on *Frasera*? I hypothesize that visitation rates will be the greatest in the early morning, as the temperature is cooler. I predict that visitation by all pollinators will generally decrease throughout the day, attributed to higher temperatures in the afternoon. I further predict that *Bombus* will prioritize collecting nectar, whereas *Megachile* will prioritize collecting pollen. From June to July, pollinator activity was recorded on plots of individual *Frasera speciosa* plants that included taxonomic identity of pollinators, number of visits on individual flowers, and foraging behaviors. A total of 789 pollinator observations were recorded across eight full days. Within-day community-level pollinator activity on *Frasera* had moderately higher activity in the morning, while foraging behavior differed strongly between *Bombus* and *Megachile*.

Introduction

It is highly unlikely organisms are spending an entire day foraging in the exact same manner. Pollinator activity should vary throughout the day, owing to variation in temperature, wind, resource availability, or biotic competition. Plant-pollinator interactions are necessary for a plant's reproductive success and mediating floral trait evolution (Bronstein et al., 2006). As many flowering plants rely on pollination, daily shifts in activity are crucial to an individual's reproductive output. In addition, insects that pollinate require floral resources to sustain metabolic rates, egg provisioning and overwintering preparations (Kevan & Baker, 1983). Yet, most of our understanding of species interactions, especially plant-pollinators, are seasonal or interannual (CaraDonna et al., 2021). It is not well-understood how pollinators may behave in response to real-time changes in the environment; only average conditions of the season are captured. Interactions within specific hours of the day are often excluded or obscured. Thus, examining within-day variation is crucial to understanding how variable abiotic factors may influence foraging behavior across pollinator groups.

Certain species may provide a resource pulse by masting. Masting events are widely proposed as predator-avoidance strategies for plants, by overproducing exceptional volumes of seeds or fruits (Soler et al., 2017). *Frasera speciosa,* (monument plant, elkweed, green gentian, deer's ears by Ute) is a monocarpic perennial that undergoes synchronous, sporadic flowering at high density across 2-4 year intervals (Inouye, 1986; Taylor & Inouye, 1985). The temporal and spatial inconsistency of synchronous flowering by *Frasera* results in an obligate dependence on insects for pollination (Beattie et al., 1973). The drought at the Rocky Mountain Biological Laboratory (RMBL) in 2026 coincided with an extensive mast event of *Frasera*. The abundance of *Frasera* may have created a "watering hole" effect, where early season pollinators may rely on it as an overabundant resource. Previous research suggests *Frasera* attracts a diverse pollinator community when in bloom, such as *Bombus spp.* and *Megachile spp.* (Beattie et al., 1973). During preliminary observation at RMBL, pollinators appeared concentrated on *Frasera* as one of the few overabundant floral resources in June.

Within-day variation was studied in the context of a floral resource pulse in a drought year. The questions we are interested in are: 1) How does pollinator activity on Frasera vary during the day? And 2) How do different pollinators forage on *Frasera*? We hypothesize that visitation rates will be the greatest in the early morning, as the temperature is cooler. As temperatures increase throughout the day, pollinators run the risk of overheating, thus lower visitation in the afternoon. Alternatively, if temperature conditions do not induce heat stress, then activity will remain the same. Secondly, as pollinators have been shown to partition floral rewards on *Frasera* (Beattie et al., 1973), we hypothesize that different

taxa will forage differently. Based on preliminary observations and previous work (Benkendorf et al. 2025), we predict that *Bombus* will spend a greater proportion of visits gathering nectar, whereas solitary bees (e.g., *Megachile*) will spend a greater proportion of visits collecting pollen. Finally, because *F. speciosa* provided an abundant floral display, we expected its concentrated floral resources to support a diverse pollinator community.

Methods

Study site. Observations were conducted across two macrosites, the Gothic townsite and research meadow near Copper Creek. Three microsites were created for each macrosite. Within each microsite, five plots of three *Frasera* were flagged for observation. Patches of flowering *Frasera* were abundantly located in clusters surrounding Treasury, Calder, and Enders cabins. Other flowering species located in both macrosites included *Delphinium barbeyi*, *Hymenoxys hoopesii*, *Ligusticum porteri*, *Osmorhiza occidentalis*, *Pseudocymopterus montanus* and *Veratrum californicum*. The research meadow contained hundreds of *Frasera* plants, therefore the three microsites were denoted as left of aspen (LA), right of aspen (RA), and back of aspen (BA) in reference to a protruding population of aspen trees. Both macrosites experience dramatic temperature fluctuations, with a range from 0° C to 30° C daily (Prather et al., 2023) . The absence of invasive species, such as *Apis mellifera* (European honeybee) diminishes potential competition that may confound data on the native species of pollinators.

Data collection. Observations began in mid-June until early July. *F. speciosa* bloomed in early June, providing a time-window of three weeks. Microsites were recorded for roughly an hour at a time, resulting in three replicates for each. Plots are the true experimental unit (n=30). This minimizes confounding factors with species turnover and changes in composition (Arrowsmith et al., 2025). Observation took place in the morning (9:00 - 12:00) and in the afternoon (13:00 - 16:00). Temperature (C°) and wind speed (m/s) were taken before each observation. Individuals seen actively engaging with the nectar pads or anthers were counted. Data was not collected on days where wind exceeded 3.5 m/s or when it rained.

Taxonomic classification. As there was no insect collection, individuals were simply marked by ability to identify based on quick observation. Bumblebees (*Bombus spp.)* were identified by species level. The bumblebee species included in observation were *B. flavifrons*, *B. bifarius*, *B. appositius*, *B. occidentalis*, *B. nevadensis*, and *B. centralis*. Solitary bees were denoted as *Halticus*, *Hoplitis*, or *Megachile*. Hoverflies were classified as syphrids as it is difficult to discern between individual species. Other pollinators were identified to the finest taxonomic level possible or by common name. When pollinators were unable to be identified in the field, iNaturalist was used to gather greater input on classification using photographs.

Nectar availability. Individual flowers were plucked from plants within the plots to check for resource availability. This was conducted in the late season, after pollinator observations were completed. 0.25 µL capillary tubes (MicroCaps®, Drummond Scientific Company) were used on each nectar pad on a flower, then measured by a handheld ruler (cm). The tube was held perpendicular to the nectar pad to diminish the risk of false-zeroes. Individual petals were pulled from the base of the flower to ensure only nectaries were targeted.

Statistical analysis. Data analysis was conducted in R 4.6.1 (R Core Team, 2026) after field collection.

I. Effect of time of day on average pollinator visitation.

A generalized linear mixed model (GLMM) was used using the *glmmTMB* package (Brooks et al., 2017). The predictor variable was temperature and response variable was pollinator counts per observation window. The model also distinguished “morning” from “afternoon” by sorting into timebins in order to be considered as a fixed effect. Sampling data, microsite, and patch ID were considered random intercepts. A negative binomial distribution was used to account for

overdispersion. The main effects were evaluated using a type II ANOVA test, subsequently with calculating the estimated marginal means using the *emmeans* package (Lenth, 2026).

II. Effect of temperature on average pollinator visitation.

A linear mixed effects model was used to ensure temperature varied significantly within a day, using the *lme* package (Bates, 2015). Date and microsite were random effects. A GLMM was used to understand how temperature throughout time may have an effect on pollinator visitation counts. Date and microsite remained as random effects, and a negative binomial distribution was used to account for overdispersion. Main and interaction effects were further tested using a type II ANOVA test. Instead of computing the estimated marginal means, the marginal trends of temperature for the morning and afternoon sessions were calculated using *emtrends* (Lenth, 2026).

III. Foraging preferences of pollinator taxa

A contingency table was utilized to identify the proportions of behaviors across two distinct taxa, *Bombus spp.* and *Megachile spp. Bombus* were quantified as "BOMB" and *Megachile* individuals as "MEGA". Observations with no presence of either grouping were negated. Foraging interactions were defined as "pollen", "nectar" or "both". As the predictor (taxa), and response (foraging interactions), are categorical, a pair-wise fisher's test was used.

To test how overall pollinator behavior varied over time, visitors were further grouped into five guilds: bees, beetles, flies, *Lepiotodera*, and other (ants and wasps). A generalized linear mixed effects model tested the count of visits in response to time of day, with behavior as an interaction. Date and microsite were random effects. Next, the estimated marginal means was calculated to understand whether the rate of pollinator visits changes depending on the specific foraging behavior (both, nectar, or pollen) they are performing.

IV. Effect of nectar availability on pollinator visitation

Nectar availability measurements occurred at the end of the observational window, after observations of pollinators concluded. At this point in time, these measurements prove to be representative of the end of season availability, with most measurements concluding dry nectaries on individual plants. No statistical tests were run to further investigate how pollinator activity varies in a single day.

Results

I. Sampling Information

A total of 789 individual pollinator observations were collected across eight days of sample collections. The most abundant pollinator class was *Bombus*, (n= 423 visits), and the least abundant class was butterfly (n= 7). The most common visitor to *Frasera* was *B. bifariu*s (n = 298 visits), followed by *B. flavifrons* (n = 253 visits). Visits were combined to represent the total amount per observation session (n=182 observation sessions). There were a total of 12 unique pollinator identities. These 12 identities were further sorted into five guilds: bees, flies, *Lepiotodera*, beetles and other (ants and wasps). The average sum of visits by a single visitor was three per observation. The minimum temperature was 14.3 C and maximum was 29.4 C. The average wind speed was 0.67 m/s.

II. How does pollinator activity vary within a single day?

There was a significant difference between temperatures in the morning versus afternoon ($t = -6.1$, $df = 128$, $p < 0.001$) . Visitation was slightly higher during morning observations than afternoon observations. The mean morning temperature was 22.18 °C, and the mean afternoon temperature was 24.09 °C. Morning temperatures were 1.91°C lower

than afternoon temperatures. There was a slight significant effect of time on pollinator visits on *Frasera* (chi^2 = 4.11, df = 1, p = 0.042). The estimated marginal means indicated that there were 2.8 visits per observation in the morning (SE = 0.356) and 3.4 visits per observation in the afternoon (SE = 0.439). A quadratic temperature curve was considered alongside a linear relationship to account for potential non-linear changes in activity. The effects of temperature's interaction with time on activity were not significant (Type II ANOVA, chi^2 = 0.32, df = 1, p = 0.56). The quadratic model estimated a peak in visitation near 20.9 °C. The estimated marginal trend did not reveal a significant trend of temperature in the morning (-0.816, SE = 0.787, p = 0.29), or in the afternoon (-0.0326, SE = 0.378, p = 0.38). Temperature did not significantly explain the deviance in total visit counts, either as a linear predictor (chi^2 = 2.21, df = 1, p = 0.137) or as a quadratic predictor (chi^2 = 2.52, df = 1, p = 0.112).

III. How do pollinators forage on *Frasera*?

There was a strong, significant difference in how *Bombus* and *Megachille* foraged on the plant during observations (pairwise fisher's test, $p < 0.001$) . There were 423 *Bombus* and 79 *Megachile* visits. Across both taxa, there were 437 instances of nectar foraging, 50 of pollen foraging, and 15 of both behaviors by the same individual. *Bombus* visits were overwhelmingly associated with nectar collection (97%), whereas *Megachile* visits were more frequently associated with pollen collection (60%) (Table 1.1).

The overall rate of pollinator visits was not influenced by foraging behavior across the five guilds (chi^2 = 8.75, df = 2, p = 0.12). There was no significant effect of time of day on pollinator foraging behaviors (ANOVA type II, chi^2 = 0.71, df = 1, p = 0.40). Morning visitations in comparison to afternoon visits were unable to be distinguished from each other. There was a strong, significant correlation between behavior and pollinator (GLME, $chi^2 = 9.47$, df = 2, p = 0.008). A Tukey-adjusted post-hoc pairwise test revealed visitors that forage for both nectar and pollen were more frequent than pollen collection (df = 1, z = 2.81, p = 0.004). There was no significant trend on nectar and pollen foraging.

Discussion

The masting of *F. speciosa* in 2026 coincided with steady pollinator activity during its flowering period. The community of visitors to *Frasera* over the three-week study period comprised a relatively diverse portfolio of pollinators, indicating that *F. speciosa* is a largely generalist resource attractive to many pollinators . Examining pollinator behavior at a within-day scale provides a finer-scale perspective on plant-pollinator interactions than comparisons across seasons or years. Pollinator activity can change over the course of the day as temperature, humidity and resource availability fluctuate. Pollinator visitation and foraging behaviors on *F. speciosa* remained consistent between the morning and afternoon, with slightly more activity in the early hours, but the effect size was modest (Fig 1). In contrast, *Bombus* and *Megachile* differed strongly in their use of floral resources, with *Bombus* predominantly collecting nectar and Megachile more frequently collecting pollen. These findings suggest that community-level measures of pollinator activity may obscure important differences among taxa and highlight the value of examining plant–pollinator interactions at fine temporal and taxonomic scales.

I. The observed temperature range did not significantly explain variation in pollinator activity.

While temperature did fluctuate significantly at the finer scale, the range of temperatures observed may not have been extreme enough to deter visitors from foraging. Both sites did not document afternoons cooler than 20 °C , a missing weather condition that detects responses to cooler temperatures. Particularly, *Bombus* and *Megachile* individuals possess physiological adaptations that allow activity across broad thermal ranges. Members of *Bombus* have been documented to withstand variable abiotic conditions in their environments (Heinrich & Esch, 1994). Specifically, *B. bifarius* and *B. flavifrons* have been observed at temperatures above 40 °C in experimental studies (Dotson, 2024). Theories concentrated

on bumble bee's thermal range is attributed to heterothermy, or the ability to self-regulate based on environmental conditions and energy levels (Maia-Silva et al., 2021). Members of *Megachile* are also capable of enduring higher temperatures, exceeding 45 °C (Barthell et al., 2012).

The lack of a significant effect of temperature on overall pollinator visitation may obscure taxon-specific responses among smaller ectothermic visitors. In comparison, syrphid flies are sensitive to warmer and drier conditions (Høye & Forchhammer, 2008). The observed decrease in activity for syphrid flies during warmer afternoons may suggest examining variation at the community level may mask individual activity levels. Previous research at RMBL observes syphrid fly pollination declining rapidly in warmer and drier years (Iler et al., 2013). However, the lack of significant effect of temperature on pollinator activity is not sufficient to explain the behavior of smaller ectothermic visitors on *Frasera*.

As temperature had no effect on pollinator visitation at the finer-scale, the context of the *F. speciosa* masting event should be considered. In early June, populations of *Frasera* bloomed, prior to other highly pollinator-dependent species in these areas. This included *Delphinium barbeyi*, to which *Frasera* shared the same visiting *Bombus* species this season (Elliot & Irwin, 2009). Perhaps the masting event of *Frasera* created a "watering hole" effect, maintaining pollinator visitation despite fluctuating temperatures. Pollinators may have continued visiting *Frasera* as there were not many alternative floral resources during the early portion of the season.

II. Foraging behaviors differed dramatically between *Bombus spp.* & *Megachile spp.*

The strong difference in floral resource use between *Bombus spp*. and *Megachile spp.* is consistent with resource partitioning on *F. speciosa*. *Bombus* are eusocial insects that invest in brood care for an entire colony, (Michener, 1974). At the start of the summer, *Bombus* populations are rapidly growing and nest establishment is critical for the colony's existence (Iserbyrt & Rasmont, 2012). Workers and queens are mainly driven by the need for nectar, as the greatest threat at this stage of colony establishment is starvation (Iserbyrt & Rasmont, 2012). For *Megachile*, males emerge first and subsequently mate with females who then lay one egg per nest (Michener, 1953). The integrity of the nest is built upon proteins from pollen loads and nectar, creating "bee loaves" for larvae to feed on (Michener, 1953). The timing of the *Frasera* flowering event may have increased its importance as a resource for *Megachile*. This could explain why *Megachile* individuals were utilizing *Frasera* as a pollen provision, as the plant was one of the few active resources in the early season.

There were many instances of attempted nectar-robbing noted during observation by *Bombus* individuals. Visitors would attempt to push open individual petals from the front or back of flowers. Instances of nectar-robbing suggest that some visits may have contributed less directly to pollination than visits involving contact with the flower's reproductive structures. Nectar robbing can reduce reproductive success when nectar is removed without facilitating pollen transfer, although its effects vary depending on the plant and pollinator involved (Irwin et al. 2010). *Megachile* may have had more direct contact with the reproductive structures of *F. speciosa* while pollen foraging. These personal observations suggest that between the two pollinator groups, potential contributions to plant fitness may have also differed. Future studies measuring pollen deposition, seed set, or fruit production could directly evaluate whether pollinator effectiveness differs between *Bombus* and *Megachile*.

III. Foraging choices for all pollinators appeared to be independent of time of day.

Pollinator visitation showed a moderate but statistically significant effect of time of day, whereas temperature itself did not significantly explain variation in visitation. Foraging selection also remained consistent between morning and afternoon. This consistency suggests that pollinators may have sustained foraging preferences despite within-day environmental variation. This consistently across time may have occurred due to *Frasera* serving as a resource pulse in the time of drought. At the start of the season, *Frasera* provided resources not yet made available by other flowering species. In conjunction with earlier emergence times, pollinators had little room for floral choice to take place. Previous research on

the masting tree *Sorbus aucuparia* similarly suggests that pollinator communities can maintain consistent interactions as floral abundance increases (Szymkowiak, 2026). With that, it is entirely plausible that foraging choices remain consistent in the wake of overabundance. Future research directions when studying fine-scale pollinator activity should consider how insect life histories shift in response to masting events.

IV. Fine-scale pollinator studies should incorporate taxon-specific interactions and floral resource availability.

Previous studies have demonstrated that weather variation can influence pollinator activity and plant-pollinator interactions (Bartomeus et al., 2013; Barbeta et al., 2015; Koenig et al., 2015). At RMBL, previous insight on floral resource attractiveness may be relatively dependent on temperature changes (Arrowsmith et al., 2025). For pollinator activity on *Frasera* to appear unaffected by temperature and marginally affected by time of day, other abiotic or biotic factors may offer greater explanations. One important limitation is that floral resource availability was not measured throughout the flowering period. In the context of the drought year, nectar production may have been reduced as a consequence of low water availability and heat-induced stress on *Frasera* individuals. Drought-stressed plants produce less nectar per flower and lower sucrose concentration (Rering et al., 2020). Bumble bees appear to evaluate nectar temperature against sucrose concentration when foraging (Whitney et al., 2008). As nectar availability was measured at the tail-end of the season, it is difficult to discern resource allocation as a factor on foraging levels on *Frasera*. The unusual timing and abundance of Frasera flowering may have created a temporary resource pulse that reduced the importance of within-day environmental variation, although additional measurements of floral resources and weather conditions are needed to test this explanation. Other abiotic factors, such as precipitation, cloud cover, and nectar availability as components may clarify the missing line of reasoning for within-day variation of pollinator activity.

Studying within-day variation in pollinator activity revealed interesting findings in foraging behaviors across the summer season. Using *F. speciosa* permitted access to a variety of plant visitors across the morning and the afternoon. While weather variation has been attributed to influence pollinator activity in previous work, considering a multiplicity of abiotic factors is crucial when examining fine-scale trends. Pollinators are ectothermic, therefore environmental conditions beyond temperature may be impacting visitation rates and foraging behaviors. Studying within-day variation in activity proves to be beneficial in examining species-specific interactions with resource allocation, as demonstrated with differences in *Bombus* and *Megachile* behavior. Pollinator visitation on *F. speciosa* showed relatively little community-level sensitivity to the moderate temperature variation observed during the study period. With a marginal effect of time of day on visitation rates. In contrast, floral resource use varied strongly when comparing two different taxa, with *Bombus* predominantly collecting nectar and *Megachile* more frequently collecting pollen. As the pollinators collected can vary from each other in terms of body size and thermoregulatory abilities, its possible individual-specific activity may be masked at the community level. Reducing the number of pollinator classes, or studying a particular pollinator taxon may prove beneficial to avoid inadvertently generalizing trends.

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	Both	Nectar	Pollen
BOMB	0.260	0.969	0
MEGA	0.050	0.341	0.607

Table 1.Contingency table of *Bombus* & *Megachile*

	ratio	SE	p-value
Both / Nectar	0.207	1.865	0.1489
Both / Pollen	0.281	2.826	0.0131*
Nectar / Pollen	1.22	0.107	0.0610

Table 2. estimated marginal means comparison of foraging patterns across pollinator guilds

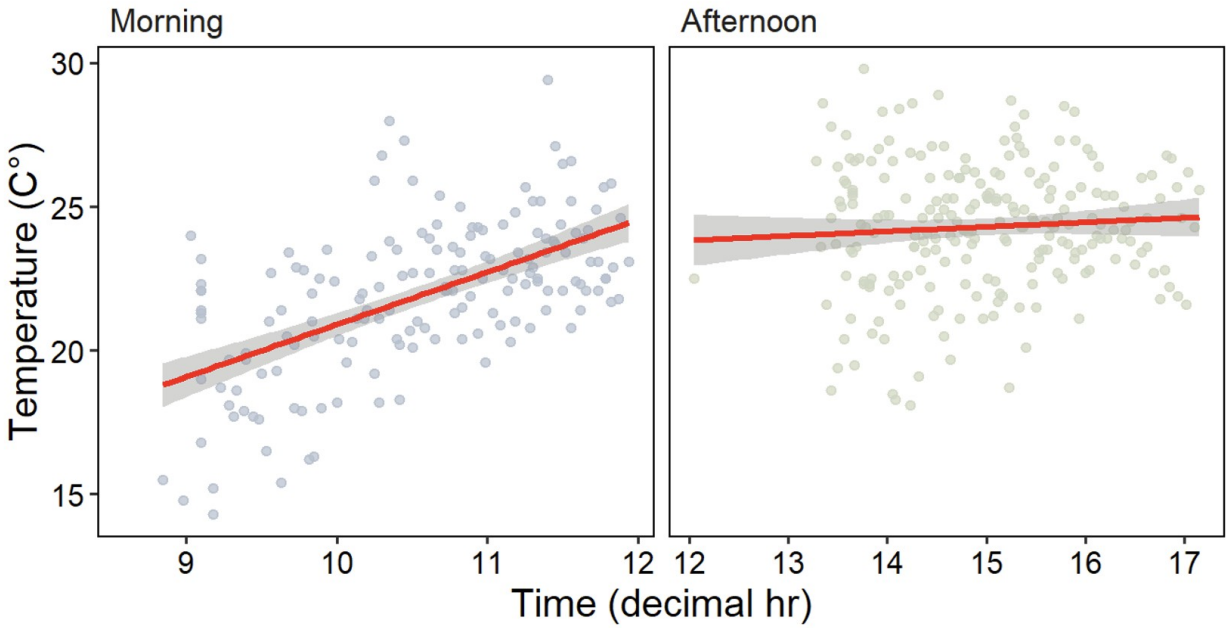

Figure 1. Temperatures across morning and afternoon time-blocks.

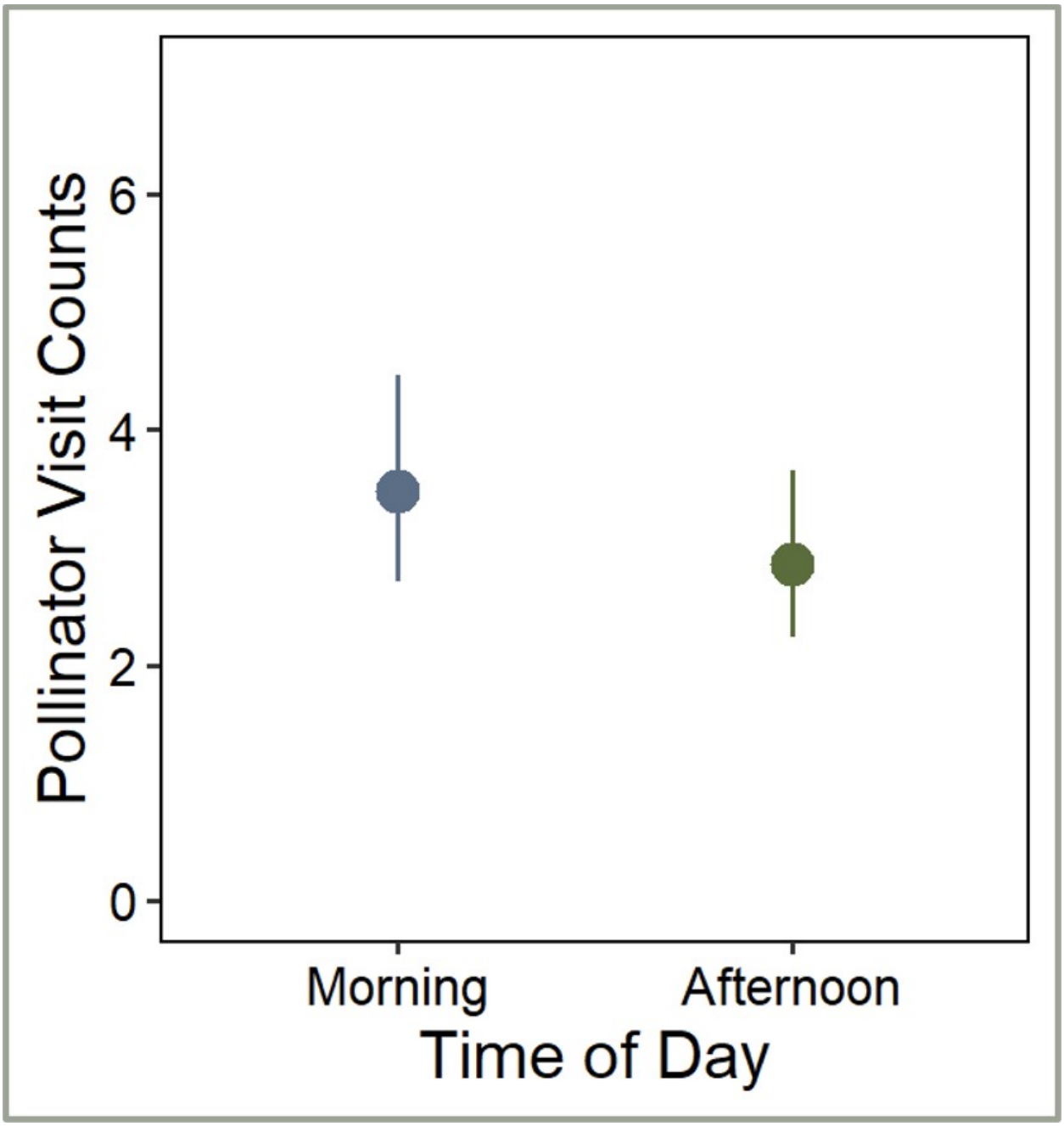

Figure 2. Morning and Afternoon observations comparing pollinator visit counts.

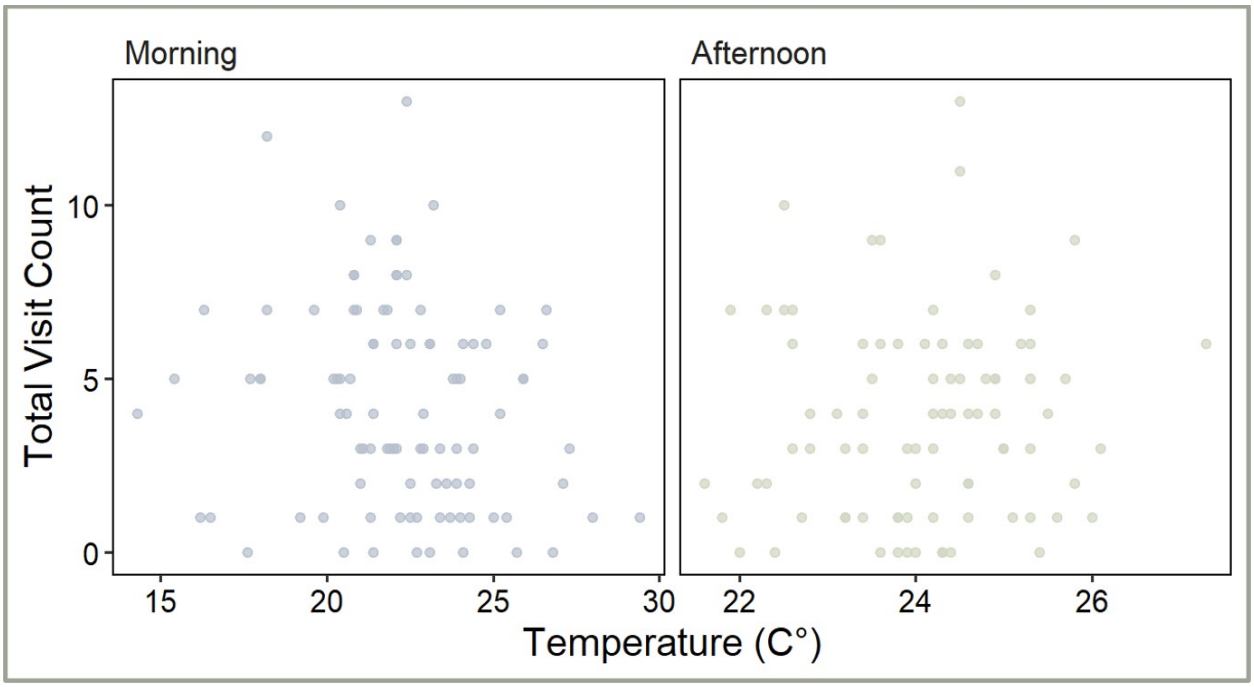

Figure 3. No effect of temperature on total visit count in the morning or afternoon.

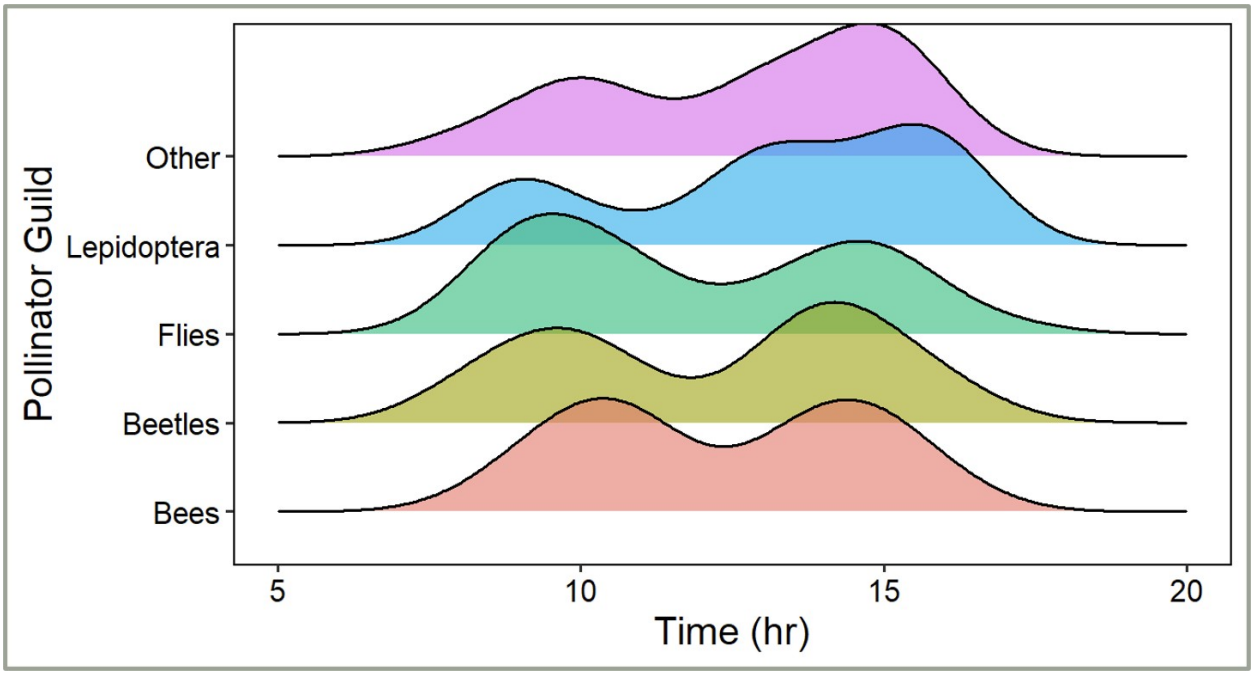

Figure 4. Activity density plot across the five pollinator guilds.

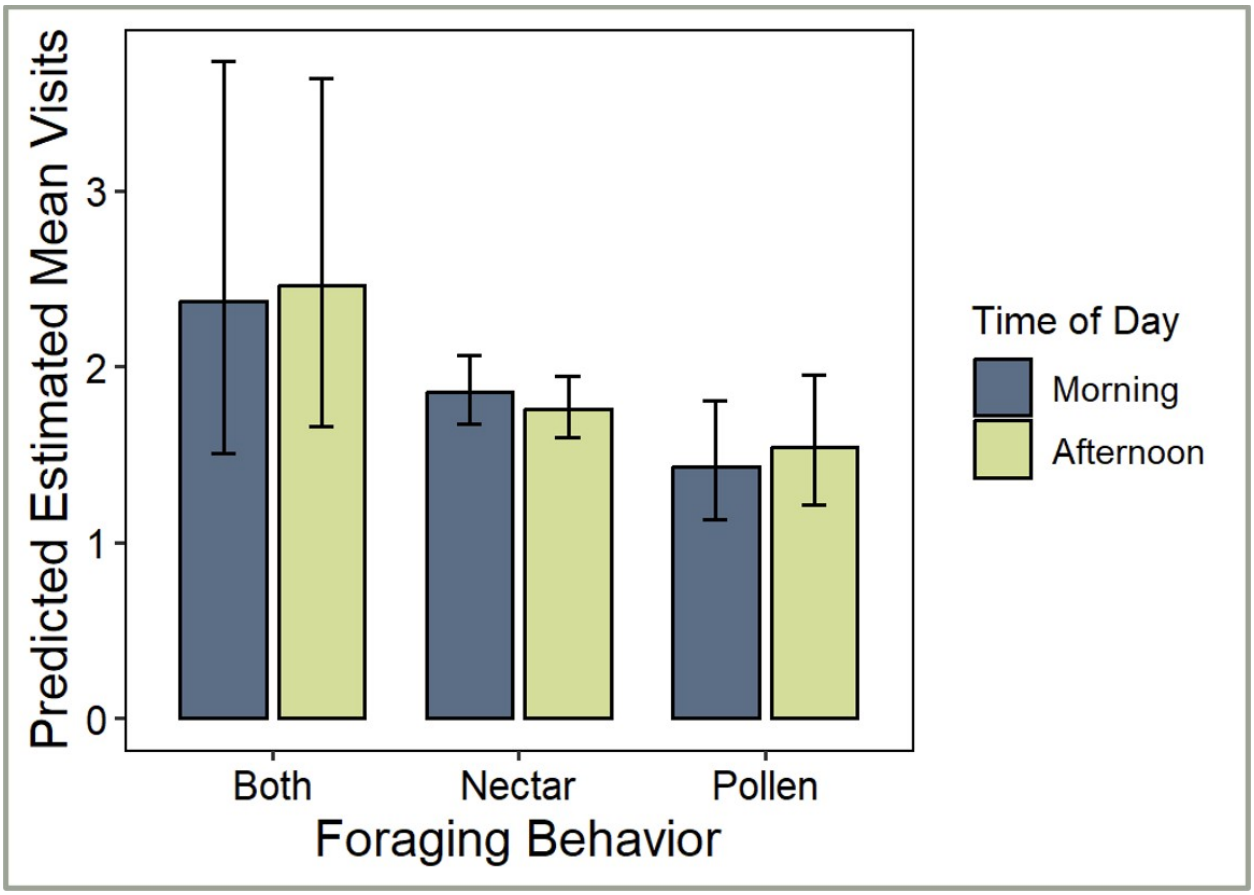

Figure 5. Time of day had no effect on foraging behavior patterns.

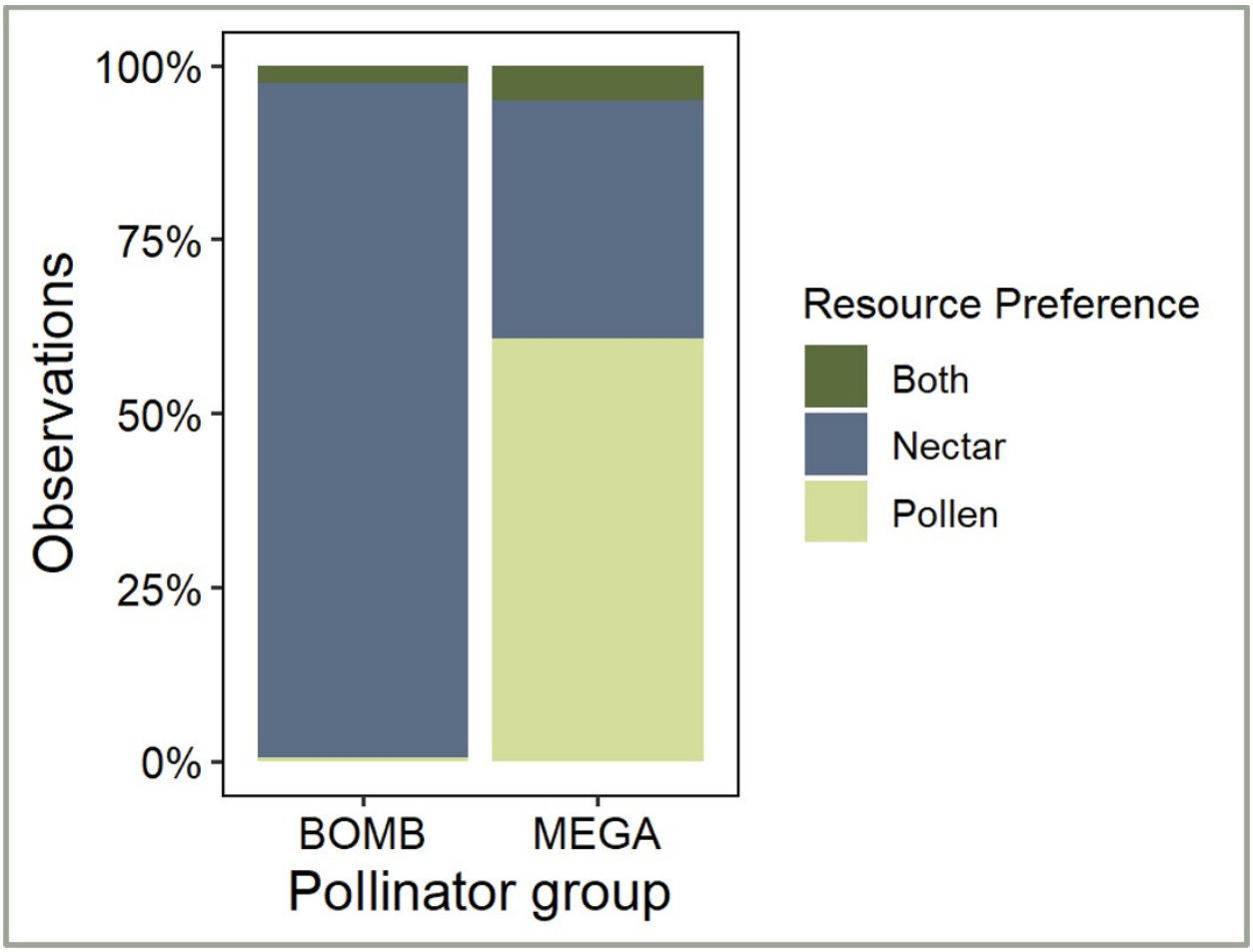

Figure 6. *Bombus* and *Megachile* foraged significantly different from each other on *Frasera* .

References

Arrowsmith, K. C., Strait, M. D., Chandar, M., Schiffer, A., & Brosi, B. J. (2025). Temperature influences pollinators' choice of floral partners independently of community composition. *Journal of Animal Ecology, 94*(12), 2390–2402. https://doi.org/10.1111/1365-2656.70158

Barbeta, A., Mejía-Chang, M., Ogaya, R., Voltas, J., Dawson, T. E., & Peñuelas, J. (2015). The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. *Global Change Biology, 21*, 1213–1225.

Barthell, J. F., Hranitz, J., Thorp, R. W., & Shue, M. K. (2002). High temperature responses in two exotic leafcutting bee species: *Megachile apicalis* and *M. rotundata* (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist, 78*, 235–246.

Bartomeus, I., Park, M. G., Gibbs, J., Danforth, B. N., Lakso, A. N., & Winfree, R. (2013). Biodiversity ensures plant–pollinator phenological synchrony against climate change. *Ecology Letters, 16*, 1331–1338.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beattie, A. J., Breedlove, D. E., & Ehrlich, P. R. (1973). The ecology of the pollinators and predators of *Frasera speciosa*. *Ecology, 54*(1), 81–91. https://doi.org/10.2307/1934376

Benkendorf, R. C., Woodworth, E. J., CaraDonna, P. J., Ogilvie, J. E., Taddeo, S., & Fant, J. B. (2025). Improving plant DNA metabarcoding accuracy with ecological filters and Angiosperms353: Field and pollen microscopy validation. *Applications in Plant Sciences, 13*(5), e70026. https://doi.org/10.1002/aps3.70026

Bronstein, J. L., Alarcón, R., & Geber, M. (2006). The evolution of plant–insect mutualisms. *New Phytologist, 172*, 412–428. https://doi.org/10.1111/j.1469-8137.2006.01864.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal, 9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

CaraDonna, P. J., Burkle, L. A., Schwarz, B., Resasco, J., Knight, T. M., Benadi, G., Blüthgen, N., Dormann, C. F., Fang, Q., Fründ, J., Gauzens, B., Kaiser-Bunbury, C. N., Winfree, R., & Vázquez, D. P. (2021). Seeing through the static: The temporal dimension of plant–animal mutualistic interactions. *Ecology Letters, 24*(1), 149–161. https://doi.org/10.1111/ele.13623

Dotson, A. (2024). *Seasonal variation in abundance and thermal tolerance of bumble bees (Bombus) in Grand Teton National Park* [Doctoral dissertation, University of Wyoming].

Elliott, S. E., & Irwin, R. E. (2009). Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi*. *American Journal of Botany, 96*, 912–919. https://doi.org/10.3732/ajb.0800260

Heinrich, B., & Esch, H. (1994). Thermoregulation in bees. *American Scientist, 82*(2), 164–170.

Høye, T. T., & Forchhammer, M. C. (2008). Phenology of high-arctic arthropods: Effects of climate on spatial, seasonal, and inter-annual variation. *Advances in Ecological Research, 40*, 299–324.

Iler, A. M., Inouye, D. W., Høye, T. T., Miller-Rushing, A. J., Burkle, L. A., & Johnston, E. B. (2013). Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Global Change Biology, 19*(8), 2348–2359.

Inouye, D. W. (1986). Long-term preformation of leaves and inflorescences by a long-lived perennial monocarp, *Frasera speciosa* (Gentianaceae). *American Journal of Botany, 73*(11), 1535–1540. https://doi.org/10.2307/2443919

Irwin, R. E., Bronstein, J. L., Manson, J. S., & Richardson, L. (2010). Nectar robbing: Ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution, and Systematics, 41*, 271–292. https://www.jstor.org/stable/27896224

Iserbyt, S., & Rasmont, P. (2012). The effect of climatic variation on abundance and diversity of bumblebees: A ten years survey in a mountain hotspot. *Annales de la Société Entomologique de France, 48*, 261–273.

Kevan, P. G., & Baker, H. G. (1983). Insects as flower visitors and pollinators. *Annual Review of Entomology, 28*, 407–453.

Koenig, W. D., Knops, J. M. H., Carmen, W. J., & Pearse, I. S. (2015). What drives masting? The phenological synchrony hypothesis. *Ecology, 96*(1), 184–192.

Lenth, R., & Piaskowski, J. (2026). *emmeans: Estimated marginal means, aka least-squares means* (R package version 2.0.4). Comprehensive R Archive Network. https://CRAN.R-project.org/package=emmeans

Maia-Silva, C., da Silva Pereira, J., Freitas, B. M., & Hrncir, M. (2021). Don't stay out too long! Thermal tolerance of the stingless bees *Melipona subnitida* decreases with increasing exposure time to elevated temperatures. *Apidologie, 52*, 218–229.

Michener, C. D. (1953). *The biology of a leafcutter bee (Megachile brevis) and its associates* (Mc. Paper 105).

Michener, C. D. (1974). *The social behavior of the bees: A comparative study*. Harvard University Press.

Morgan, K. R., & Heinrich, B. (1987). Temperature regulation in bee- and wasp-mimicking syrphid flies. *Journal of Experimental Biology, 133*(1), 59–71. https://doi.org/10.1242/jeb.133.1.59

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., De Cáceres, M., Durand, S., Evangelista, H., Hannigan, G., Hill, M., Lahti, L., Martino, C., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., & Weedon, J. (2026). *vegan: Community ecology package* (R package version 2.7-5). Comprehensive R Archive Network. https://CRAN.R-project.org/package=vegan

Prather, R. M., Underwood, N., Dalton, R. M., Barr, B., & Inouye, B. D. (2023). Climate data from the Rocky Mountain Biological Laboratory (1975–2022). *Ecology, 104*(11), e4153. https://doi.org/10.1002/ecy.4153

R Core Team. (2026). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rering, C. C., Franco, J. G., Yeater, K. M., & Mallinger, R. E. (2020). Drought stress alters floral volatiles and reduces floral rewards, pollinator activity, and seed set in a global plant. *Ecosphere, 11*(9), e03254. https://doi.org/10.1002/ecs2.3254

Soler, R., Espelta, J. M., Lencinas, M. V., Peri, P. L., & Martínez Pastur, G. (2017). Masting has different effects on seed predation by insects and birds in Antarctic beech forests with no influence of forest management. *Forest Ecology and Management, 400*, 173–180. https://doi.org/10.1016/j.foreco.2017.06.014

Szymkowiak, J., Bogdziewicz, M., Celary, W., Piechnik, Ł., Ledwoń, M., Szarek-Łukaszewska, G., Żywiec, M. (2026). Dynamic pollinator networks maintain pollination efficiency during mast flowering in an insect-pollinated tree. *Oikos, 2026*(2), e11682.

Taylor, O. R., & Inouye, D. W. (1985). Synchrony and periodicity of flowering in *Frasera speciosa* (Gentianaceae). *Ecology, 66*(2), 521–527. https://doi.org/10.2307/1940400

Whitney, H. M., Dyer, A., Chittka, L., Rands, S. A., & Glover, B. J. (2008). The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. *Naturwissenschaften, 95*(9), 845–850. https://doi.org/10.1007/s00114-008-0393-9

References

Arrowsmith, K. C., Strait, M. D., Chandar, M., Schiffer, A., & Brosi, B. J. (2025). Temperature influences pollinators' choice of floral partners independently of community composition. *Journal of Animal Ecology, 94*(12), 2390–2402. https://doi.org/10.1111/1365-2656.70158

Barbeta, A., Mejía-Chang, M., Ogaya, R., Voltas, J., Dawson, T. E., & Peñuelas, J. (2015). The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. *Global Change Biology, 21*, 1213–1225.

Barthell, J. F., Hranitz, J., Thorp, R. W., & Shue, M. K. (2002). High temperature responses in two exotic leafcutting bee species: *Megachile apicalis* and *M. rotundata* (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist, 78*, 235–246.

Bartomeus, I., Park, M. G., Gibbs, J., Danforth, B. N., Lakso, A. N., & Winfree, R. (2013). Biodiversity ensures plant–pollinator phenological synchrony against climate change. *Ecology Letters, 16*, 1331–1338.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beattie, A. J., Breedlove, D. E., & Ehrlich, P. R. (1973). The ecology of the pollinators and predators of *Frasera speciosa*. *Ecology, 54*(1), 81–91. https://doi.org/10.2307/1934376

Benkendorf, R. C., Woodworth, E. J., CaraDonna, P. J., Ogilvie, J. E., Taddeo, S., & Fant, J. B. (2025). Improving plant DNA metabarcoding accuracy with ecological filters and Angiosperms353: Field and pollen microscopy validation. *Applications in Plant Sciences, 13*(5), e70026. https://doi.org/10.1002/aps3.70026

Bronstein, J. L., Alarcón, R., & Geber, M. (2006). The evolution of plant–insect mutualisms. *New Phytologist, 172*, 412–428. https://doi.org/10.1111/j.1469-8137.2006.01864.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal, 9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

CaraDonna, P. J., Burkle, L. A., Schwarz, B., Resasco, J., Knight, T. M., Benadi, G., Blüthgen, N., Dormann, C. F., Fang, Q., Fründ, J., Gauzens, B., Kaiser-Bunbury, C. N., Winfree, R., & Vázquez, D. P. (2021). Seeing through the static: The temporal dimension of plant–animal mutualistic interactions. *Ecology Letters, 24*(1), 149–161. https://doi.org/10.1111/ele.13623

Dotson, A. (2024). *Seasonal variation in abundance and thermal tolerance of bumble bees (Bombus) in Grand Teton National Park* [Doctoral dissertation, University of Wyoming].

Elliott, S. E., & Irwin, R. E. (2009). Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi*. *American Journal of Botany, 96*, 912–919. https://doi.org/10.3732/ajb.0800260

Heinrich, B., & Esch, H. (1994). Thermoregulation in bees. *American Scientist, 82*(2), 164–170.

Høye, T. T., & Forchhammer, M. C. (2008). Phenology of high-arctic arthropods: Effects of climate on spatial, seasonal, and inter-annual variation. *Advances in Ecological Research, 40*, 299–324.

Iler, A. M., Inouye, D. W., Høye, T. T., Miller-Rushing, A. J., Burkle, L. A., & Johnston, E. B. (2013). Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Global Change Biology, 19*(8), 2348–2359.

Inouye, D. W. (1986). Long-term preformation of leaves and inflorescences by a long-lived perennial monocarp, *Frasera speciosa* (Gentianaceae). *American Journal of Botany, 73*(11), 1535–1540. https://doi.org/10.2307/2443919

Irwin, R. E., Bronstein, J. L., Manson, J. S., & Richardson, L. (2010). Nectar robbing: Ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution, and Systematics, 41*, 271–292. https://www.jstor.org/stable/27896224

Iserbyt, S., & Rasmont, P. (2012). The effect of climatic variation on abundance and diversity of bumblebees: A ten years survey in a mountain hotspot. *Annales de la Société Entomologique de France, 48*, 261–273.

Kevan, P. G., & Baker, H. G. (1983). Insects as flower visitors and pollinators. *Annual Review of Entomology, 28*, 407–453.

Koenig, W. D., Knops, J. M. H., Carmen, W. J., & Pearse, I. S. (2015). What drives masting? The phenological synchrony hypothesis. *Ecology, 96*(1), 184–192.

Lenth, R., & Piaskowski, J. (2026). *emmeans: Estimated marginal means, aka least-squares means* (R package version 2.0.4). Comprehensive R Archive Network. https://CRAN.R-project.org/package=emmeans

Maia-Silva, C., da Silva Pereira, J., Freitas, B. M., & Hrncir, M. (2021). Don't stay out too long! Thermal tolerance of the stingless bees *Melipona subnitida* decreases with increasing exposure time to elevated temperatures. *Apidologie, 52*, 218–229.

Michener, C. D. (1953). *The biology of a leafcutter bee (Megachile brevis) and its associates* (Mc. Paper 105).

Michener, C. D. (1974). *The social behavior of the bees: A comparative study*. Harvard University Press.

Morgan, K. R., & Heinrich, B. (1987). Temperature regulation in bee- and wasp-mimicking syrphid flies. *Journal of Experimental Biology, 133*(1), 59–71. https://doi.org/10.1242/jeb.133.1.59

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., De Cáceres, M., Durand, S., Evangelista, H., Hannigan, G., Hill, M., Lahti, L., Martino, C., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., & Weedon, J. (2026). *vegan: Community ecology package* (R package version 2.7-5). Comprehensive R Archive Network. https://CRAN.R-project.org/package=vegan

Prather, R. M., Underwood, N., Dalton, R. M., Barr, B., & Inouye, B. D. (2023). Climate data from the Rocky Mountain Biological Laboratory (1975–2022). *Ecology, 104*(11), e4153. https://doi.org/10.1002/ecy.4153

R Core Team. (2026). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rering, C. C., Franco, J. G., Yeater, K. M., & Mallinger, R. E. (2020). Drought stress alters floral volatiles and reduces floral rewards, pollinator activity, and seed set in a global plant. *Ecosphere, 11*(9), e03254. https://doi.org/10.1002/ecs2.3254

Soler, R., Espelta, J. M., Lencinas, M. V., Peri, P. L., & Martínez Pastur, G. (2017). Masting has different effects on seed predation by insects and birds in Antarctic beech forests with no influence of forest management. *Forest Ecology and Management, 400*, 173–180. https://doi.org/10.1016/j.foreco.2017.06.014

Szymkowiak, J., Bogdziewicz, M., Celary, W., Piechnik, Ł., Ledwoń, M., Szarek-Łukaszewska, G., Żywiec, M. (2026). Dynamic pollinator networks maintain pollination efficiency during mast flowering in an insect-pollinated tree. *Oikos, 2026*(2), e11682.

Taylor, O. R., & Inouye, D. W. (1985). Synchrony and periodicity of flowering in *Frasera speciosa* (Gentianaceae). *Ecology, 66*(2), 521–527. https://doi.org/10.2307/1940400

Whitney, H. M., Dyer, A., Chittka, L., Rands, S. A., & Glover, B. J. (2008). The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. *Naturwissenschaften, 95*(9), 845–850. https://doi.org/10.1007/s00114-008-0393-9

figures

	Both	Nectar	Pollen
BOMB	0.260	0.969	0
MEGA	0.050	0.341	0.607

Table 1.Contingency table of *Bombus* & *Megachile*

	ratio	SE	p-value
Both / Nectar	0.207	1.865	0.1489
Both / Pollen	0.281	2.826	0.0131*
Nectar / Pollen	1.22	0.107	0.0610

Table 2. estimated marginal means comparison of foraging patterns across pollinator guilds

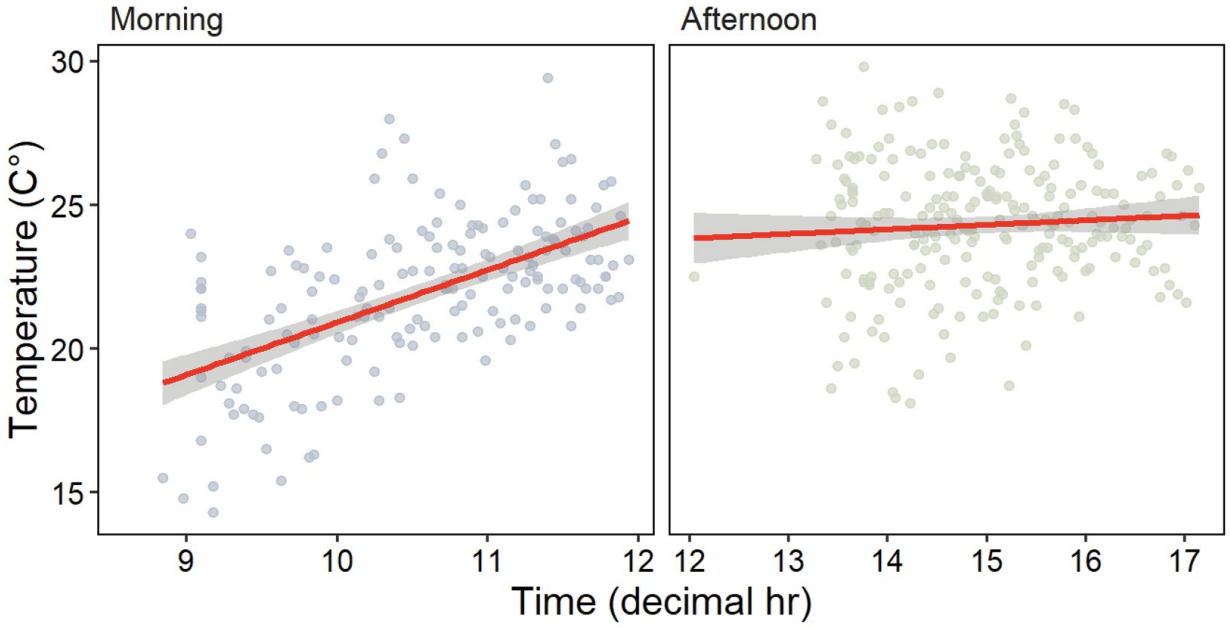

Figure 1. Temperatures across morning and afternoon time-blocks.

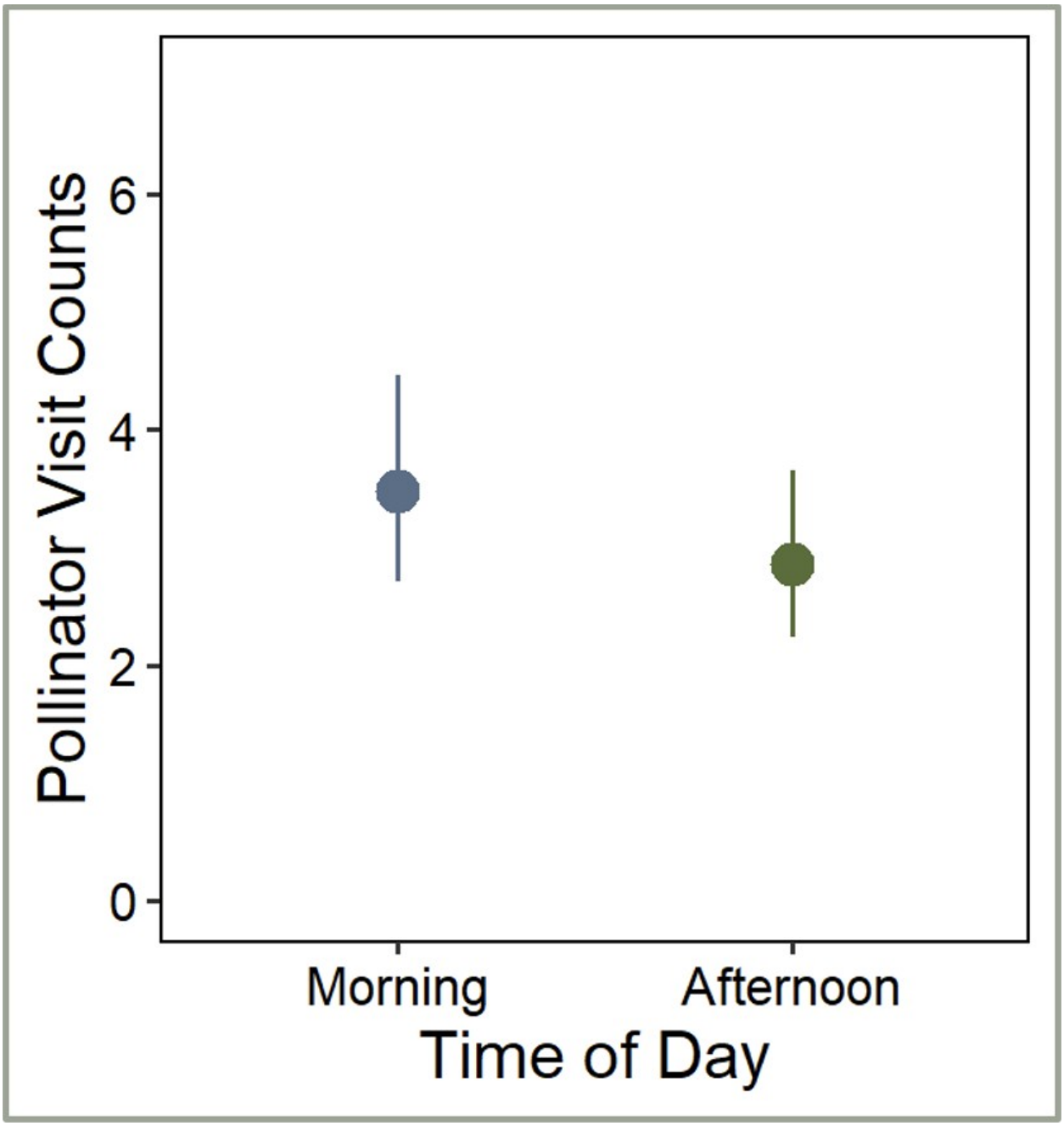

Figure 2. Morning and Afternoon observations comparing pollinator visit counts.

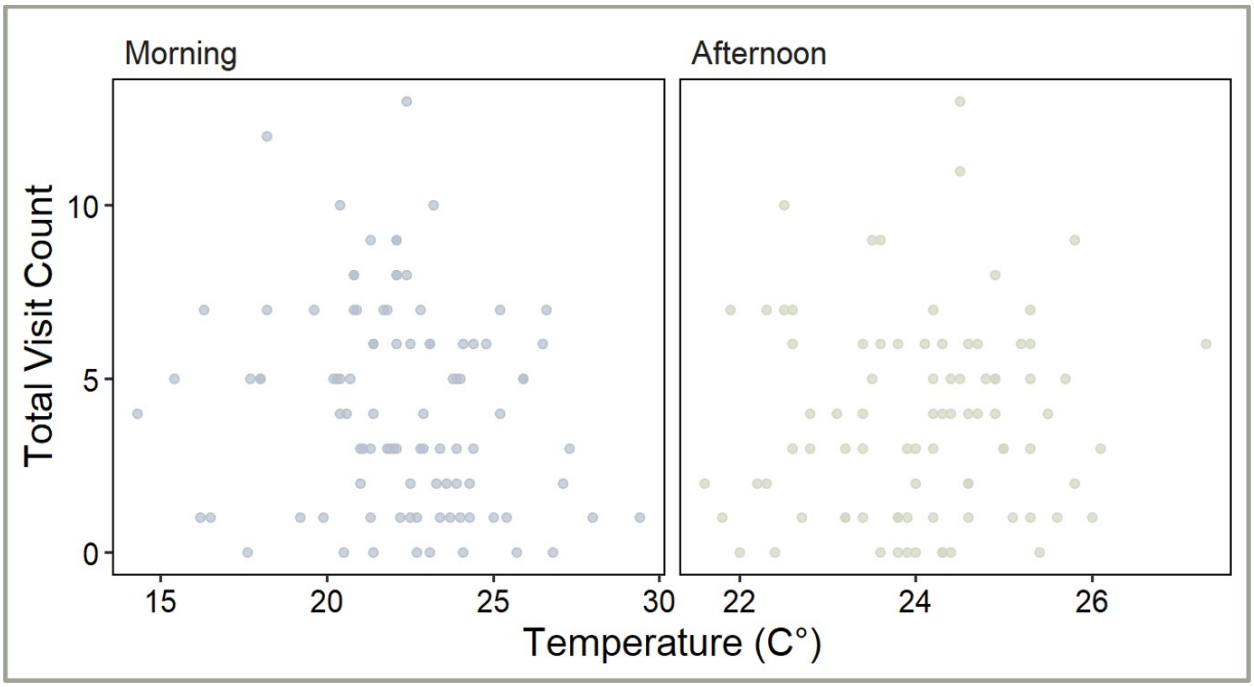

Figure 3. No effect of temperature on total visit count in the morning or afternoon.

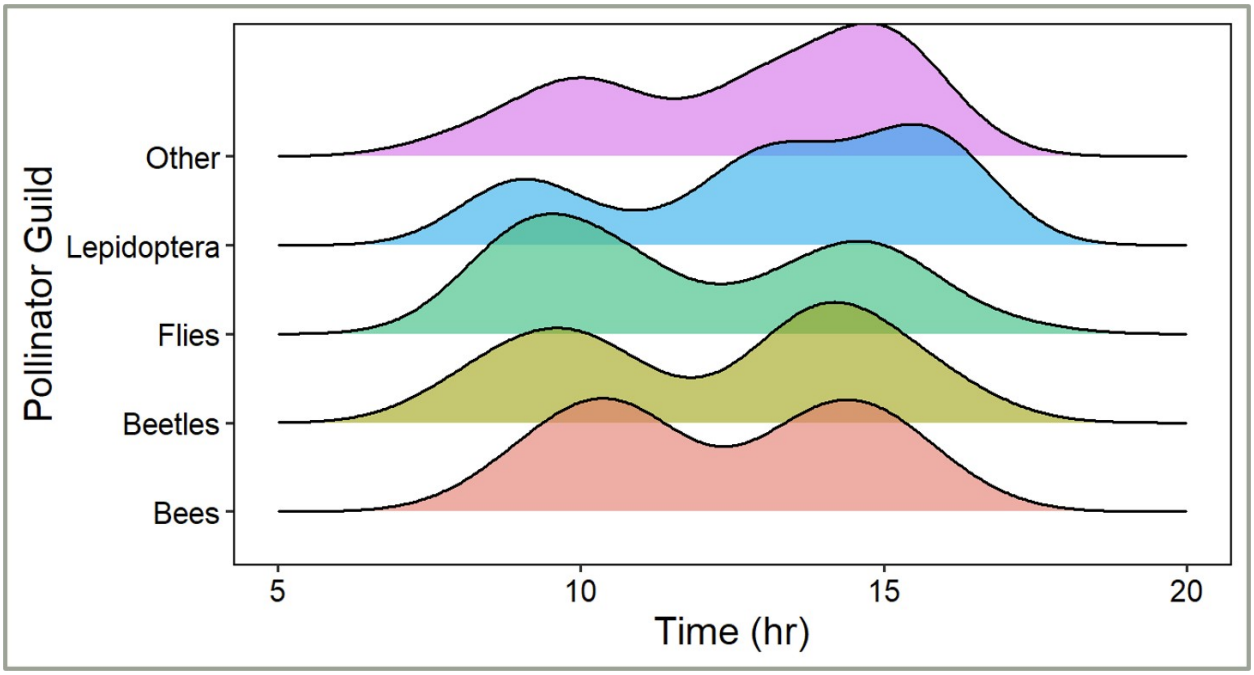

Figure 4. Activity density plot across the five pollinator guilds.

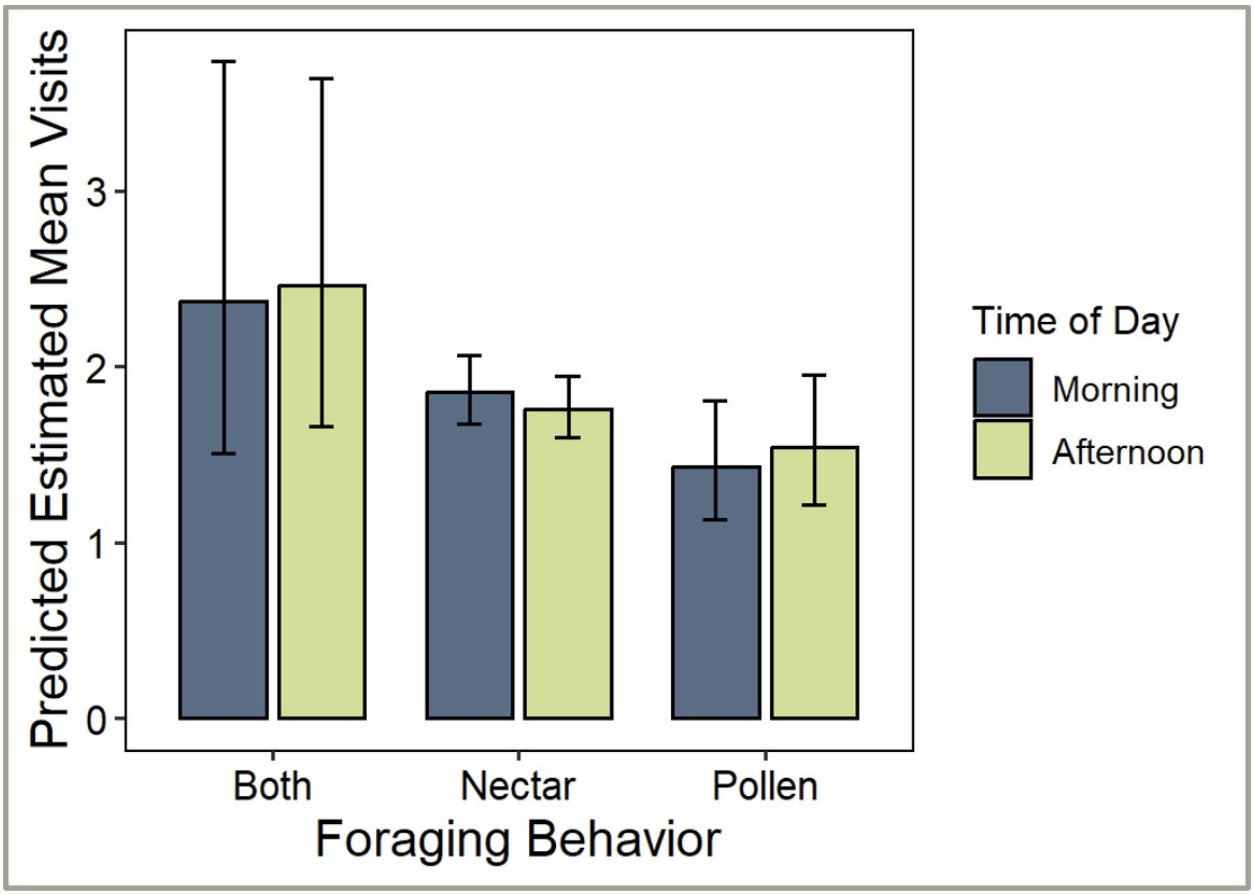

Figure 5. Time of day had no effect on foraging behavior patterns.

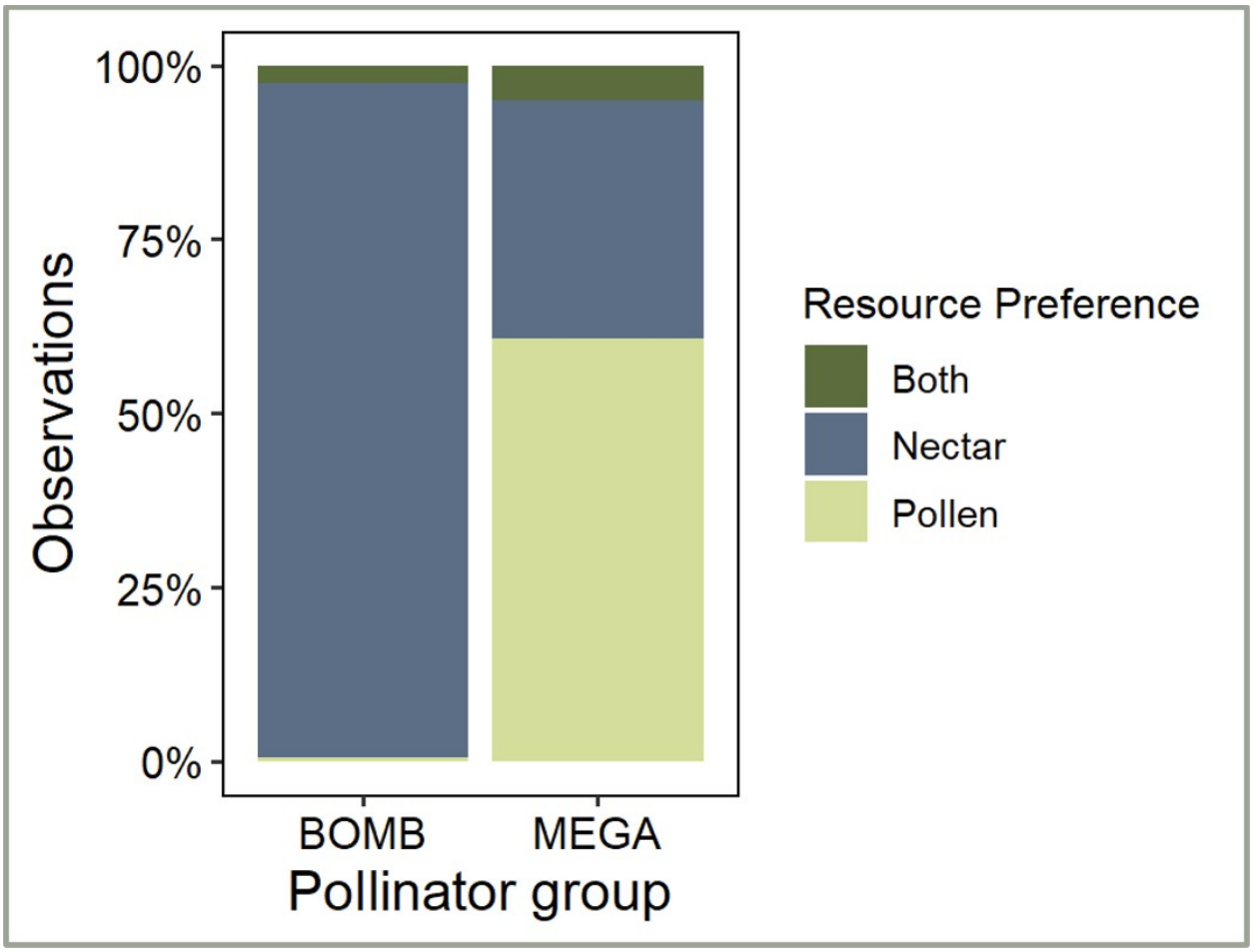

Figure 6. *Bombus* and *Megachile* foraged significantly different from each other on *Frasera* .