

Testing the Marginal Value Theorem on *Bombus appositus* and *Bombus nevadensis*

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Kaila in the field

Abstract

Previous studies on bumblebee foraging behavior found that bumblebees often exhibit optimal foraging behavior when collecting nectar and pollen. A popular theory is that bumblebee foraging can be represented by the marginal value theorem (MVT). This summer, I observed the foraging behavior of *Bombus appositus* and *Bombus nevadensis* workers in Gothic, Colorado, to analyze whether bumblebee foraging decisions on naturally occurring *Delphinium barbeyi* patches are consistent with the MVT. Specifically, I investigated 1) Do *B. appositus* and *B.*

nevadensis workers spend more time foraging in denser patches of *D. barbeyi*, 2) do *B. appositus* and *B. nevadensis* workers visit proportionally fewer flowers in denser patches of *D. barbeyi*, and 3) are these trends less apparent at the end of the summer when all patches are *D. barbeyi* are more sparse. After following bumblebees throughout their foraging bouts and tracking their foraging decisions with a voice recorder, I found that patch flower density explains a significant amount of variation in the patch residence time and proportion of flowers visited by *B. appositus* workers. I found that patch flower density explains a significant amount of variation in the patch residence time, but not the proportion of flowers visited by *B. nevadensis* workers. Finally, I found that foraging behavior is not significantly different later in the summer when all *D. barbeyi* patches are more sparse.

Introduction

Bumblebees are one of the primary pollinators of wildflowers, among several other insects and birds (Pleasants, 1989). Bumblebees incidentally pollinate flowers while foraging for pollen and nectar, which are their primary food sources (Goulson, 1999). Therefore, plant-pollinator interactions are critical for the reproductive fitness and long-term survival of both organisms.

Bumblebees forage to maximize their rate of net energy intake (RNEI) during a foraging bout (Cibula & Zimmerman, 1984). Specifically, the amount of pollen and nectar available at a given flower patch, which I will refer to as patch quality, influences a pollinator's decision to visit that patch, the duration of time they spend there, and their selection of the next patch (Lovett Doust & Lovett-Doust, 1990). Bumblebees infer patch quality using visual cues such as sex, color, shape, and symmetry (Goulson, 1999), and scent cues such as markers left by other pollinators telling the bumblebee if a particular patch has already been depleted of its resources (Goulson, 1999). Previous studies have hypothesized that the duration of time bumblebees spend foraging at a patch, called patch residence time, can be explained by the marginal value theorem (MVT) which states that they will leave the patch after the quality of the patch drops below the average quality of the overall habitat (Charnov, 1976; Goulson, 1999, 2000; Pleasants, 1989). For example, if the average amount of nectar available in patches for a given environment is 50 units, and a bumblebee begins foraging in a patch with 100 units, the bumblebee will remain at

that patch until it has depleted the amount of nectar to 50 units. Essentially, bumblebees will forage at a patch until it's no longer energetically beneficial to remain.

Two studies conducted in Gunnison County found that, consistent with the MVT, bumblebees spend more time foraging but visit proportionally fewer flowers at patches with higher flower density (Cibula & Zimmerman, 1984; Pyke, 1982). The phenomenon of fewer flowers visited in denser patches occurs because bumblebees try to avoid visiting the same flower more than once to maximize their RNEI (Goulson, 1999; Pyke, 1982). These results were obtained by observing *B. flavifrons* on experimentally manipulated patches of *Delphinium nelsonii* (Cibula & Zimmerman, 1984) and *Bombus flavifrons* and *Bombus appositus* workers foraging on naturally occurring patches of *Aconitum columbianum* (Pyke, 1982).

In my study, I will investigate whether the same result, that bumblebees spend more time foraging but visit proportionally fewer flowers in patches with high flower density, is observed for *Bombus appositus* and *Bombus nevadensis* workers foraging in patches of naturally occurring *Delphinium barbeyi* in Gothic, Colorado. The goal of this is to observe whether bumblebee foraging is consistent with the MVT in a natural system, where variation in the density of flowers is caused by seasonal flowering phenology. Further, I hypothesize that this result may be less apparent in the later season when all patches of *D. barbeyi* have relatively low flower density. If the MVT is observed in patches of naturally occurring *D. barbeyi*, a model can be created and used to make predictions on how changes in the flowering phenology of *D. barbeyi* may influence the foraging behavior of *B. appositus* and *B. nevadensis* workers.

Methods & Study Site

During summer 2025, I collected empirical data with graduate student Sabine Dritz, from mid-June to the end of July, which is the time that *B. appositus* and *B. nevadensis* workers are actively foraging. We sampled in a 5,500 square foot study meadow at Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO (see map). In this meadow, *D. barbeyi* patches are abundant throughout the summer, and while there are other plant species available to forage on, they are all less preferred by *B. appositus* and *B. nevadensis*.

Data collection followed protocols established by Dritz for her graduate research project (Dritz, n.d.). Four days a week, Dritz and I collected observational data on bumblebee foraging bouts. To do so, we walked random paths until encountering a bumblebee worker. Once



encountered, we tracked the bumblebee along its foraging bout and marked each patch it visited with a flag for up to twenty patches or until the bumblebee was lost or left the boundaries of our study meadow. A new patch is defined as a switch in flower species visited or a movement of foraging location greater than one meter. At each patch along the foraging bout, we counted the number of flowers visited and stated when the bee arrived and left that patch in a voice recorder. After each foraging bout, we recorded the location of flagged patches using a ten-centimeter accuracy GPS Trimble.

Additionally, every other day, Dritz flew a drone across the study site to capture high-resolution images of the meadow, which will allow us to approximate the flower density in each patch using an object detection algorithm (Dritz, n.d.). I helped develop a training dataset for this algorithm during the 2024-2025 academic year. To locate the flower patches in which we tracked bumblebees in the drone images, we used their GPS locations. To ensure the accuracy of flower density estimates, we hand-counted flowers in six patches a day using a 1x1 meter transect. In this analysis, I only included the subset of patches for which we hand-counted flowers. However, upon completion of the object detection algorithm during the next academic year, I will rerun the analysis using all patches of *D. barbeyi* visited by *B. appositus* and *B. nevadensis* workers.



1 x 1 meter transect used for ground truthing



. Example of a 1 x 1 meter drone image

Data Analysis

I used generalized linear models in R to analyze the relationship between patch flower density, patch residence time, and the proportion of flowers visited for *B. appositus* and *B. nevadensis* workers foraging on *D. barbeyi*. I conducted the analysis for each bumblebee species independently to account for possible behavioral differences arising from factors such as body size. I developed two linear models to quantify the impact of patch flower density on patch residence time and proportion of flowers visited, respectively. For each linear model, I performed a likelihood ratio test (LRT) to determine if patch flower density explains a significant amount of variation in patch residence time and the proportion of flowers visited.

I filtered out data collected at the first patches along bumblebees' foraging bouts because the arrival time to these patches is unknown, and therefore, patch residence time and the proportion of flowers visited are also unknown. Further, to remove patches that bumblebees sampled but did not choose to forage in, I filtered out patches where the patch residence time was less than 5 seconds.

To analyze whether the relationships between patch flower density, patch residence time, and proportion of flowers visited are less apparent later in the season when all patches of *D. barbeyi* are more sparse, points on the plot were color coded to represent how many days had passed since snowmelt in the study site, using information composed in Dr. Ian Breckheimer's snowmelt maps (Ian Breckheimer, n.d.).

Results

Patch Density vs Foraging Time

Conducting an LRT revealed that for both *B. appositus* and *B. nevadensis* workers, patch flower density explains a significant amount of variation in patch residence time, given p-values of $2e-6$ and $1.062e-8$, respectively (Table 1). The coefficients for patch flower density in the linear models for *B. appositus* and *B. nevadensis* were 0.524 and 0.529, which demonstrates that the effect of patch flower density on patch residence time is positive for both bumblebee species (Fig. 1). The snowmelt data reveal no clear difference between the patch time of bumblebees followed at the beginning and end of summer.

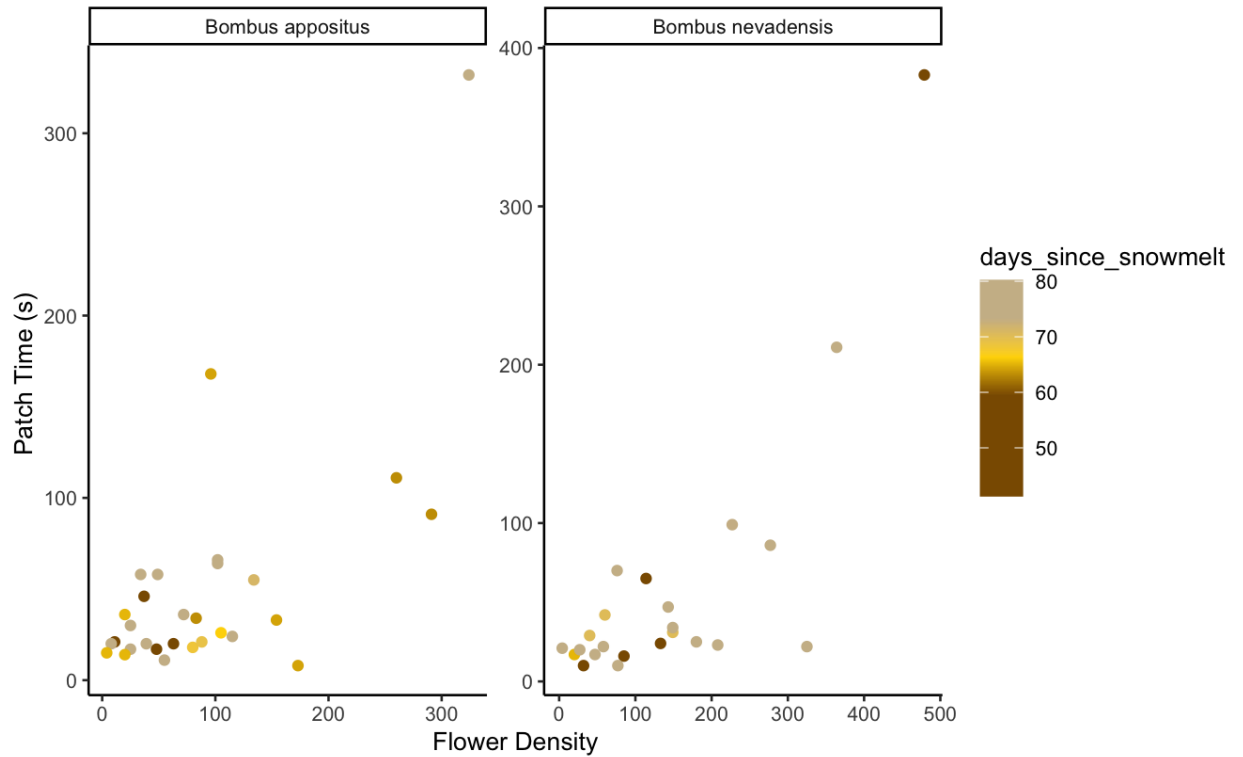


Fig 1. Plot of Flower Density and Patch Time.

Table 1. LRT results (response = patch time) *indicates level of significance.

Bee Species	Coefficient of Patch Flower Density	Df	P value
<i>B. appositus</i>	0.524	1	2e-6***
<i>B. nevadensis</i>	0.529	1	1.062e-8***

Patch Density vs Proportion of Flowers Visited

Conducting an LRT revealed that for *B. appositus* workers, patch density explains a significant amount of variation in the proportion of flowers visited, given a p-value of 0.0328. (Table 2). On the other hand, an LRT test also revealed that for *B. nevadensis* workers, the patch density does not explain a significant amount of the variation in the proportion of flowers visited,

given a p-value of 0.113 (Table 2). The coefficients for patch flower density in the linear models for *B. appositus* and *B. nevadensis* were -0.0011 and -6.79e-4, which demonstrates that the effect of patch flower density on the proportion of flowers visited is negative for both bumblebee species (Fig. 2). The snowmelt data reveals no clear difference between the proportion of flowers visited for bumblebees followed at the beginning and end of summer.

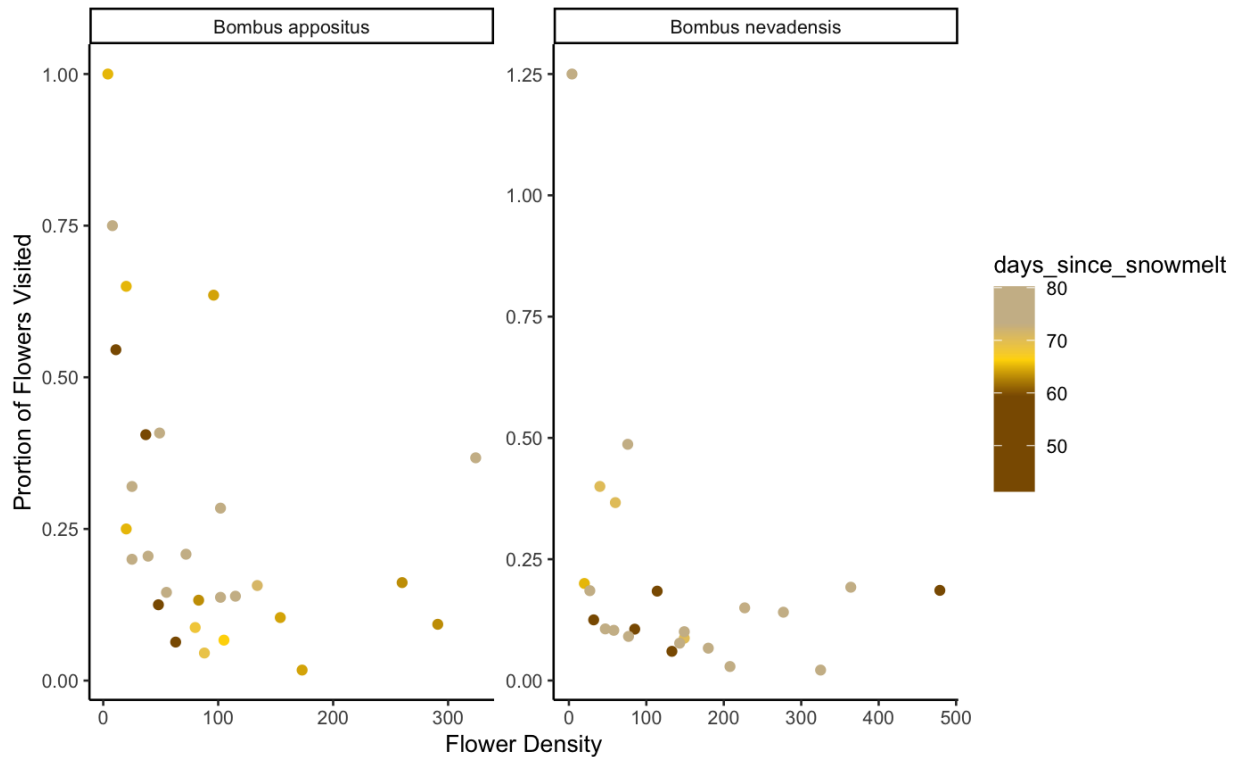


Fig 2. Plots of flower density and proportion of flowers visited,

Table 2. LRT results (response = proportion of flowers visited) *indicates level of significance

Bee Species	LR Chi Sq	Df	P value
<i>B. appositus</i>	-0.0011	1	0.0328 *
<i>B. nevadensis</i>	-6.79e-4	1	0.113

Discussion

Patch time

As hypothesized, these results reveal that *B. appositus* and *B. nevadensis* workers will spend more time foraging in patches with greater flower density. These results are consistent with those found in a previous study observing *B. flavifrons* and *B. appositus* foraging on *Aconitum columbianum* (Pyke, 1982). The reason this result arises is that the number of flowers visited increases in more dense patches, and visiting more flowers takes more time.

Proportion of flowers visited.

As hypothesized, these results suggest that *B. appositus* workers will visit proportionally fewer flowers in patches with greater flower density. These results are consistent with previous studies, which demonstrated that the fraction of flowers visited by bumblebee workers declines as the number of available flowers (or density) increases (Cibula & Zimmerman, 1984; Pyke, 1982). The reason this result occurs is that in less dense patches, there is a smaller likelihood of a bumblebee revisiting a flower it has already depleted. On the other hand, these results suggest that the foraging behavior of *B. nevadensis* workers demonstrate no relationship between patch flower density and the proportion of flowers visited. It is possible that the size differences between species contributed to differences in foraging behavior, as studies on size polymorphism have shown that larger bumblebee foragers carry larger nectar loads (Spaethe & Weidenmüller, 2002). Since *B. nevadensis* is a larger species, it is possible that their decision to visit more flowers in denser patches reflects their ability to obtain and hold more nectar rather than leaving to avoid the risk of revisiting flowers. Further, it is possible that different bumblebee species have different memories or different strategies to maximize their RNEI such as risk-sensitive foraging (Cartar & Dill, 1990).

MVT trends throughout the summer

Originally, I predicted that the MVT trends would be less apparent at the end of the summer due to all patches having a lower density of *D. barbeyi* and therefore less variation between patches in the meadow. However, the results show that there is no clear difference in the foraging decisions of bumblebees earlier in the summer compared to those later in the summer. In fact, at the end of the summer, when observing bumblebees foraging at patches with very low *D. barbeyi* density, they often visited every flower, which is consistent with the predictions of the MVT (Goulson, 1999; Pyke, 1982). This may be because low resource availability encouraged the bumblebees to maximize their RNEI by visiting every flower available to them.

Conclusion

Previous studies at RMBL found that changes in snowmelt and temperature have an impact on the variation in the density and spatial distribution of *D. barbeyi* (Inouye et al., 2002). Since my study demonstrates that the MVT is relevant in natural systems, in the future, a model can be created to predict how climate-driven variation in flower density may impact foraging decisions, such as patch residence time, which ultimately impacts annual resource acquisition and population size the following year. This model can be used to predict the ability of bumblebee populations to adapt to a changing environment. Future experiments and observations should be conducted to test this trend on different ecosystems to determine if this model can be generalized.

Bibliography:

1. Cartar, Ralph V., & Dill, Lawrence M. (1990). Why are bumble bees risk-sensitive foragers? *Behavioral Ecology and Sociobiology*, 26(2).
<https://doi.org/10.1007/BF00171581>
2. Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9(2), 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)
3. Cibula, D. A., & Zimmerman, M. (1984). The Effect of Plant Density on Departure Decisions: Testing the Marginal Value Theorem Using Bumblebees and *Delphinium Nelsonii*. *Oikos*, 43(2), 154. <https://doi.org/10.2307/3544763>
4. Dritz, S. (n.d.). *The functional response of bumblebee foraging rate to floral resources across spatial scales*.
5. Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, 2(2), 185–209. <https://doi.org/10.1078/1433-8319-00070>
6. Goulson, D. (2000). Why do pollinators visit proportionally fewer flowers in large patches? *Oikos*, 91(3), 485–492. <https://doi.org/10.1034/j.1600-0706.2000.910309.x>
7. Ian Breckheimer. (n.d.). *RMBL Snow Persistence Forecast Map* [Map].
<https://www.arcgis.com/apps/instant/sidebar/index.html?appid=47f93365a1d040e59e9a7ed8385640a9&locale=en¢er=-106.9733;38.9323&level=13&hiddenLayers=187293eb4bc-layer-10;187293b331a-layer-8;187293ad4d2-layer-6;187293b0f96-layer-7;1874e800380-layer-14;1874e80132f-layer-15>
8. Inouye, D. W., Morales, M. A., & Dodge, G. J. (2002). Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): The roles of

snowpack, frost, and La Niña, in the context of climate change. *Oecologia*, 130(4), 543–550. <https://doi.org/10.1007/s00442-001-0835-y>

9. Lovett Doust, J., & Lovett-Doust, L. (Eds.). (1990). *Plant reproductive ecology: Patterns and strategies* (1. issued as an Oxford University Press paperback). Oxford University Press.
10. Pleasants, J. M. (1989). Optimal Foraging by Nectarivores: A Test of the Marginal-Value Theorem. *The American Naturalist*, 134(1), 51–71. <https://doi.org/10.1086/284965>
11. Pyke, G. H. (1982). Foraging in bumblebees: Rule of departure from an inflorescence. *Canadian Journal of Zoology*, 60(3), 417–428. <https://doi.org/10.1139/z82-057>
12. Spaethe, J., & Weidenmüller, A. (2002). Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insectes Sociaux*, 49(2), 142–146. <https://doi.org/10.1007/s00040-002-8293-z>