Understanding Impact of *Bombus spp.* Intraspecific Body Mass Variation on Foraging Behavior on *Delphinium barbeyi*

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Rocky Mountain Biological Laboratory Education Program 2026:

Full Time Independent Research

ABSTRACT

Bumble bee workers vary widely in body size, influenced by resource availability and temperature during larval development. This variation allows for success in a range of abiotic and biotic conditions, and informs different foraging strategies. As anthropogenic climate change increases temperatures and bee body sizes decrease, understanding the impact of body size on specific features of their foraging paths including inter-patch flight distance, inter-patch travel time, patch residence time, and patch floral density and ii) foraging path fidelity is critical. I found that larger bumble bees travel farther distances between foraging patches, as well as take longer flights between foraging patches. With decreasing body size, potentially corresponding to a decrease in inter-patch travel time and flight distances, bees may be vulnerable to missing better resourced patches that are isolated. This decline might limit their resource acquisition and negatively impact the successful growth and development of bumble bee colonies. The effect on pollinators can have a rippling effect outward to the entire meadow ecosystem, further accentuating the importance of understanding bumblebee foraging ecology.

INTRODUCTION

Eusocial insects, such as bumble bees, are organized into castes, with each caste performing specialized, complementary functions and therefore varying widely in body size (O'Donnell, 2021). However, bumble bee body size also varies significantly within the worker caste in response to resources available and environmental conditions during larval development. Specifically, at higher brood temperatures, bumble bees tend to be smaller (Guiraud et al., 2021). As a result, anthropogenic climate change, by producing warmer temperatures, has decreased bumble bee body size distributions, over time (Fitzgerald et al., 2022). A decrease in bumble bee body size, seen in multiple species across North America and Europe, is correlated with an increase in temperature (Nooten & Rehan, 2020; Oliveira et al., 2016; Theodorou et al., 2021). These trends beg the question of how foraging ecology of worker bumble bees will respond to the shifting size distributions.

Size variation among workers allows them to efficiently forage in a range of environmental conditions (Fitzgerald et al., 2022). For instance, larger body sizes correlate with larger foraging ranges (Greenleaf et al., 2007), allowing these bigger bees to explore more foraging habitat. Additionally, large-bodied bees can travel greater distances at higher speeds (Ohashi et al., 2008) and have better eyesight leading to more efficient foraging (Spaethe & Chittka, 2003) and the exploitation of low light foraging times (Hall et al., 2021). Furthermore, larger bodied bumble bees can afford to take risks that smaller bees cannot, such as foraging on patches with a lower flower density (Foster & Cartar, 2011). Understanding how body size impacts foraging behavior is important, given that any changes could have cascading effects across plant-pollinator communities in alpine meadows.

Beyond general features of bumble bee foraging, bumble bees demonstrate specific foraging strategies to maximize efficiency when foraging in patchy landscapes. Bumble bees often return to the same patches to forage. One relevant study found that around two-thirds of bumble bees visiting a montane flower species returned to the site over the following three days (Ogilvie & Thomson, 2016). Further, bumble bees frequently repeat their foraging paths even when the quantity of floral resources available along those patches shift by drawing on knowledge from past foraging experiences. (Thomson, 1996). To my knowledge, previous studies have not investigated how body size impacts these specific features of bumble bee foraging strategy.

In this study, I investigated how intraspecific variation in bumble bee body size impacts i) features of their foraging paths including inter-patch flight distance, inter-patch travel time, patch residence time, and patch floral density and ii) foraging path fidelity. I hypothesized that bees with a larger body size will have longer inter-patch flight distances, inter-patch travel times, and shorter residence times. Additionally, because they are

better provisioned, allowing them to take more risks, I further hypothesized that larger bees would exhibit greater divergence from reliable foraging paths over time.

METHODS

Study Site

The study area was a flat, 70m x 70m meadow southeast of Gothic, Colorado with a heterogenous distribution of flowers that turnover rapidly throughout the summer season. Our team visually surveyed the meadow for *Bombus spp*. workers foraging on patches of *Delphinium barbeyi,* a later flowering species with zygomorphic, dark purple flowers (Williams et al., 2001). *D. barbeyi* plants grow in a patchy distribution across meadows and provide principally nectar resources to their pollinators. The pollinator species seen most frequently on *D. barbeyi* were *B. nevadensis, B. appositus, B. flavifrons, B. occidentalis,* and *B. californicus*.

Field Methods

When I spotted an unmarked bumble bee visiting *D. barbeyi*, I caught it with an insect net and transferred it to a "bee squeezer," a restraining apparatus to identify and mark individuals (Kearns, 2001). I gave each bee a unique three-color ID in a triangular pattern on its intertegular region with Sharpie brand oil-based paint pens. I then recorded the intertegular distance (used as a proxy for body mass) with the internal jaw of a digital caliper while the paint dried. After 20 seconds of drying, I released the bumblebee back into the environment. With the method, a marked bee could be easily identified upon resight without recapture. However, color code identity was not a foolproof method—some colors wore off and lightened over time. Due to this, there were some instances of misidentification.

When a team member and I spotted a marked bumble bee, one of us began a voice recording, counting each flower that the bumble bee visited at the patch and adding "new" each time the bee moved to a flower on a different inflorescence. When the bee left the patch, the voice recorder noted "left" and followed the bee to its next patch, saying "next patch" when the bee began foraging at the first flower of the next patch. The other team member placed a numbered flag in the middle of each patch after the bee left, in numerical order (1-30). After the bee finished the foraging bout, left the survey boundary, or escaped the eyeline of the follower, we retraced the foraging route and recorded the GPS coordinates of each flagged patch with a Trimble.

Every sample day, a team member executed a drone mission to survey floral density of patches in the meadow. Prior to the mission, all ground control points were cleared by using shears to trim back any plants that have grown over the point or may obscure the drone's view. During the mission, the drone took photos every 0.7 seconds, totaling about 2,000 images. Our team also counted the flower density of all flower species present at three representative patches using a 1x1 meter quadrat which served as our ground truth.

Data Processing

Upon returning to the lab, we transcribed the data from the voice recordings, noting the number of flowers and inflorescences visited at each patch, as well as arrival and departure times of each patch. Inter-patch travel time and distance were calculated as the time elapsed and distance traveled between selected patches, respectively. I defined a selected patch as one in which the bee spent at least 10 seconds foraging, thereby filtering out patches that were briefly sampled.

Next, we put the drone images into a convolutional neural network to count *D. barbeyi* inflorescences at each patch. Inflorescence counts were transformed to flower density using a statistical model trained on the ground truth data.

Finally, I converted the intertegular distance (ITD) to an estimated body mass, using the following: $m = (\frac{ITD}{.77})^{\frac{1}{.405}}$ (Cane, 1987).

Data Analysis

We completed all analyses in R version 6.4.1. For the following analysis I only considered *B.*

nevadensis and *B. appositus* because we observed too few visits by other bumblebee species.

I performed my analysis with generalized linear mixed effects models fit by maximum likelihood, or a Laplace approximation with the glmer function from the lme4 package in R. Continuous variables including foraging time of day, days from start of the sampling, body mass, and inter-patch distance, were scaled to improve model convergence. I made eight models, for four response variables (inter-patch travel time, inter-patch distance, residence time, and patch floral density) for two bumble bee species, *B. appositus* and *B. nevadensis*. Each model was run through the Anova function from the car package which uses Likelihood Ratio tests to evaluate the significance of fixed effects. Details on the individual models are available in appendix Table 1.

I defined patch revisits as all GPS points clustered within a circle of 0.5 meter radius using the dbscan function from the dbscan package in R. We observed fewer patch revisits between foraging paths than expected. Therefore, I did not quantify foraging path dissimilarity as originally proposed but instead reported summary statistics on patch revisits.

RESULTS

Throughout four survey weeks, we followed 65 unique bumblebees on their foraging bouts.

To investigate a possible shift in body mass throughout the course of the season, I created a linear model that established a weak negative relationship (slope = -0.014275) between marking date and body mass for *B. appositus* (p = 0.00188). It also established a weak positive relationship (slope = 0.06778) between marking date and body mass for *B. nevadensis* (p = <2.2e-6).

Inter-patch travel time between selected patches was not significantly predicted by body mass for *B. appositus* but was for *B. nevadensis*, with an estimated coefficient of 2.0685 and a p-value of 0.00127 (Fig. 1).

Inter-patch distance was similarly not significantly predicted by body mass for *B. appositus* but was *B. nevadensis* with an estimated coefficient of 0.26643 and a p-value of 3.31e-07 (Fig. 2). Additionally, days from start of sampling was a significant predictor of inter-patch distance with an estimated coefficient of 0.13119 and a p-value of 0.0114. Therefore, days from start of sampling was a potential confounding variable positively impacting both body mass and inter-patch flight distance. As a result, I included a categorical date variable having both random intercept and slope effects on the coefficient of body mass. We found that on each date, all slopes were positive. In other words, after stratifying by date, we still found a significant positive relationship between body mass and inter-patch distance.

Patch residence time was not significantly predicted by body mass for either *B. appositus* or *B. nevadensis*. Instead, for *B. nevadensis,* patch residence time was significantly predicted by foraging time of day, with an estimated coefficient of -3.747 and a p-value of 0.00127. Patch density was also not significantly predicted by body mass for either *B. appositus* or *B. nevadensis*.

Of the 65 bees followed, 36 were followed more than once (55%). Of the 382 bees marked, 113 were seen at least once more after marking (30%). Despite this, there were fewer patch revisits between foraging paths than originally expected. Therefore, I did not analyze path dissimilarity with beta diversity. Instead, I summarized the frequency of bumble bee resights and patch revisits in the following paragraphs (Table 1).

The maximum number of days an individual bee was seen throughout the season was 6, with a mean of 1.9. The maximum number of foraging paths an individual followed throughout the season was 13, with a mean of 3.3. The maximum number of patches an individual foraged on throughout the season was 199, with a mean of 30.2.

The maximum number of days where an individual revisited the same foraging patch was 4, with a mean of 1.1. The maximum number of foraging paths where an individual revisited the same foraging path was only 5, with a mean of 1.2. The

maximum number of times a foraging patch was revisited by an individual was 8, with a mean of 1.3.

DISCUSSION

In this study, I found that larger body masses correlate with longer inter-patch flight distances and travel times for *B. nevadensis* but not *B. appositus*. Larger bees having longer travel times and flight distances is supported by previous literature (Greenleaf et al., 2007; Ohashi et al., 2008). However, I did not find a relationship between body mass and patch flower density or residence time for either *B. nevadensis* or *B. appositus*. Instead, residence time for *B. nevadensis* was best explained by foraging time-of-day, given that as the day went on, flowers were likely depleted of nectar resources.

We resighted 29.6% of the bees we marked, echoing Ogilvie and Thomson's findings of bumble bee site fidelity (Ogilvie & Thomson, 2016). Our resight rate was lower than in their original study, likely because we surveyed in a 70x70m meadow instead of a 2.25x2.25m patch. We did not find evidence of the path fidelity documented by Thomson in 2008 because, in general, we observed few patch revisits. This may also be due to our large survey meadow reducing the likelihood of observing the same individual in the same area. However, the number of bumble bee resights and patch revisits across days and paths leads me to believe that future work in flight path fidelity within an observational environment is achievable.

We may have observed more foraging patch and path fidelity if observation was focused on a smaller area. This would allow us to observe how individual bees behave in the same area among the same patches. However, a smaller survey area may have also resulted in fewer bumble bee resights during the four-week observation period. As a result, it may have been difficult to collect sufficient data for analysis in one summer. Altogether, more summers of observation would be necessary to elucidate the flight-path patterns of bumble bees within the meadow.

In conclusion, as bumble bee body mass decreases with rising temperatures, potentially corresponding to a decrease in inter-patch travel time and flight distances, bees may be vulnerable to missing better resourced patches that are isolated. This decline might limit their resource acquisition and negatively impact the successful growth and development of bumble bee colonies. The effect on pollinators can have a rippling effect outward to the entire meadow ecosystem, further accentuating the importance of understanding bumblebee foraging ecology.

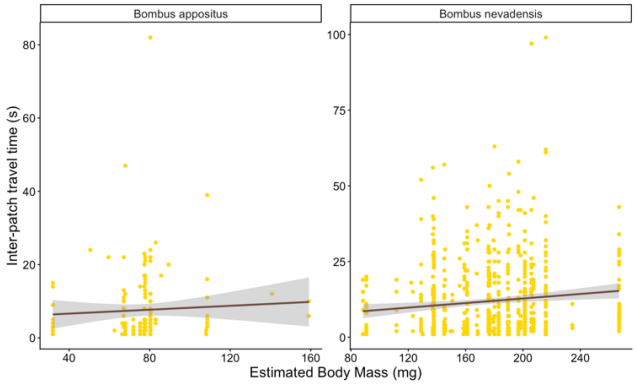

Figure 1. Each point represents travel time between two consecutive selected patches as a function of body mass. Each panel shows this for a specific *Bombus* species.

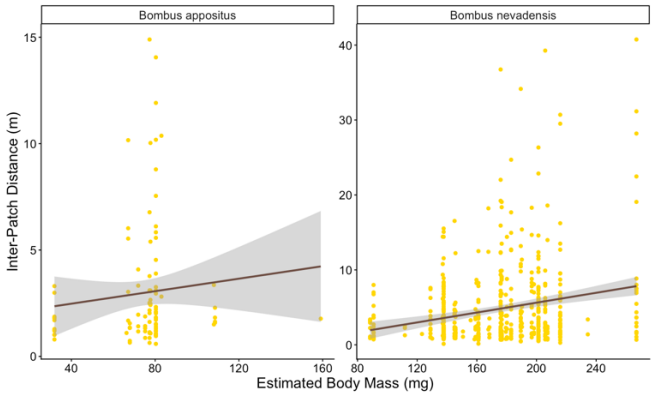

Figure 2. Each point represents distance between two consecutive selected patches as a function of body mass. Each panel shows this for a specific *Bombus* species.

Table 1. A summary of repetition of individual bee behaviors and similarity across days, paths and patches.

	Days		Foraging Paths		Patches	
	Max	Mean	Max	Mean	Max	Mean
Total	6	1.9	13	3.3	199	30.2
Including patch revisits	4	1.1	5	1.2	8	1.3

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