

The Impact of *Delphinium nuttallianum* and *Ipomopsis aggregata* Phenology on Broad-tailed Hummingbird (*Selasphorus platycercus*) Visitation Patterns

Leila Granier and Joe Ugliandolo

High Meadows Environmental Institute, Princeton University

Rocky Mountain Biological Laboratory Education Program

Full-Time Independent Research

Mentors: Dr. Mary Caswell Stoddard, Audrey Miller, and Katja Kochvar

August 13, 2024

Abstract

Biological interactions reliant on synchronized phenology are being thrown into disarray with warming temperatures and an earlier onset of spring. Migrating Broad-tailed Hummingbirds (*Selasphorus platycercus*) in Gothic, Colorado tend to arrive and breed in alignment with wildflower flowering phenology, fostering important plant-pollinator interactions. Two wildflower species, *Delphinium nuttallianum* and *Ipomopsis aggregata*, form a large part of the hummingbirds' diet and bloom in sync with arrival and breeding milestones. Since both hummingbirds and wildflowers benefit from a synchronized schedule, phenological mismatch would likely decrease hummingbird population persistence through food resource limitation. For this project, we investigated whether weekly changes in Broad-tailed Hummingbird wildflower visitation patterns correspond to changing wildflower phenology in 2022, an earlier-than-average snowmelt year, and 2023, a later-than-average snowmelt year. Due to climate change, years like 2022 with earlier snowmelt are expected to become more common. Using floral phenology transect data and hummingbird visitation data for *D. nuttallianum* and *I. aggregata*, we determined that Broad-tailed Hummingbirds adjust their foraging behavior to align with the phenology of their food sources, a behavior that may help prevent the phenological mismatches projected to occur with climate change.

Keywords: phenology, phenological mismatch, climate change, plant-pollinator interactions, Broad-tailed Hummingbirds, foraging ecology

The Impact of *Delphinium nuttallianum* and *Ipomopsis aggregata* Phenology on Broad-tailed Hummingbird (*Selasphorus platycercus*) Visitation Patterns

Early spring milestones are accelerating in ecosystems across the world due to climate change (Parmesan, 2007). On average, the onset of spring is 2.8 days earlier every decade in the Northern Hemisphere (Parmesan, 2007). This shift has a dramatic impact on phenology, defined as the timing of cyclical natural events ranging from migration to plant reproduction. Phenological mismatch occurs when organisms dependent on synchronized milestones adapt to environmental changes, such as climate change, at different rates, causing their reproductive, feeding, and/or migration patterns to become asynchronous (Ovaskainen, 2013). For plants and their pollinators, synchronized schedules are necessary to ensure that plants can successfully reproduce and pollinators can successfully access their food sources.

Due to the relatively contemporary nature of climate-change-related studies, the factors that influence phenological mismatches between migratory bird species and their food sources have only recently been investigated. Past studies have demonstrated that some migratory bird species have the ability to shift key life cycle milestones, like arrival dates and peak breeding times, in response to phenological and environmental shifts influenced by climate change. Other species have been far less successful. A study by Covino et al. (2020) found that in response to earlier leaf-out dates in eastern deciduous forests, the Black-throated Blue Warbler (*Setophaga caerulescens*) arrived earlier at deciduous-forest breeding sites to maintain its ability to utilize traditionally available resources. In contrast, birds that cannot shift their behavior to accommodate phenological shifts may suffer. For example, Both et. al 2006 found that Dutch populations of the migratory European Pied Flycatcher

(*Ficedula hypoleuca*) had plummeted 90% due to their inability to arrive synchronously with earlier leaf-out times and peak caterpillar abundance. The difference between adapting or failing to adapt to phenological shifts could determine whether migratory bird populations thrive like Black-throated Blue Warblers or suffer like European Pied Flycatchers (Covino et al., 2020, Both et al., 2006).

For this project, we investigated the phenological relationship between migratory Broad-tailed Hummingbirds (*Selasphorus platycercus*) and seasonally blooming wildflowers. From late spring through the summer, the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado hosts a population of breeding Broad-tailed Hummingbirds in a subalpine meadow ecosystem. Broad-tailed Hummingbirds are plant pollinators, feeding primarily on nectar from wildflowers and transferring pollen between flowers (Waser, 1978). Since both hummingbirds and wildflowers benefit from a synchronized schedule (Waser, 1976), it is likely that a phenological mismatch would have detrimental effects on both hummingbirds and wildflowers. Such a mismatch would likely decrease Broad-tailed Hummingbird fitness by limiting their food resources, which would negatively impact the population's persistence (McKinney, 2012). This would also negatively affect wildflower populations, as they would face diminished pollination due to an asynchronous relationship with hummingbirds.

We investigated weekly shifts in Broad-tailed Hummingbird wildflower visitation patterns at RMBL from 2022, an earlier-than-average snowmelt year, to 2023, a later-than-average snowmelt year (2022: 0 cm of snow on the ground in Gothic by May 12th; 2023: 0 cm of snow on the ground by May 26th) (barr, 2024). Since the first hummingbird food source wildflowers typically begin to bloom around two weeks after snow is absent from the ground (McKinney, 2012), we expect that this two-week difference in snowmelt will lead to a significant change in flower phenology from 2022 to 2023.

We chose to investigate the relationship between floral phenology and hummingbird visitation patterns over these two years for two main reasons: 1) a contrast in climatic conditions between 2022 and 2023, and 2) the availability of detailed transect data on weekly flower abundance from the Stoddard Lab's "HummerFlowerWatch" project (HFW). We investigated whether weekly changes in hummingbird visitation patterns corresponded to changing wildflower phenology for these two years, allowing us to draw parallels between any signs of phenological mismatch we observed and those projected to occur with climate change.

We focused on two common wildflowers that serve as crucial food sources for Broad-tailed Hummingbirds. These species, Nuttall's larkspur, *Delphinium nuttallianum*, and scarlet gilia, *Ipomopsis aggregata*, are both found in dry meadows and flower sequentially to avoid interspecific pollination by hummingbirds (Waser, 1978). After Broad-tailed Hummingbirds migrate from their wintering grounds in Mexico, they arrive at RMBL just before the first flowering of *D. nuttallianum* (McKinney, 2012), and there is some evidence suggesting they time their nesting soon after its first flowering (Waser, 1978). Once *D. nuttallianum* approaches the end of its flowering season, *I. aggregata* begins to bloom. *I. aggregata* then serves as a reliable source of nectar, as its peak abundance aligns with the peak of the hummingbird brooding period (Waser, 1976). Because these wildflower species serve as crucial food sources during important milestones in the Broad-tailed Hummingbirds' life cycle, hummingbird breeding behavior may be affected by phenological mismatches with these wildflowers. Broad-tailed Hummingbirds are the only common pollinator of both wildflower species, so sequential flowering synchronized with the hummingbirds' breeding cycle is beneficial to all three organisms (Waser, 1978). However, Broad-tailed Hummingbirds are projected

to arrive at RMBL after the first flowering of *D. nuttallianum* by the mid-21st century (McKinney, 2012), which may result in a phenological mismatch. Any shifts in flowering or migratory phenology would likely negatively impact Broad-tailed Hummingbird populations and could drive them to arrive earlier or find a new habitat with more reliable wildflowers to maintain access to crucial food sources.

To investigate the adaptability of hummingbird foraging patterns, we utilized floral phenology transect data and hummingbird visitation data to determine if Broad-tailed Hummingbirds adjust their foraging behavior to align with the phenology of their food sources. We aimed to answer the following questions: How did weekly hummingbird wildflower visitation patterns change from an earlier-than-average snowmelt year (2022) to a later-than-average snowmelt year (2023)? Do any changes correspond to changes in wildflower phenology? Our null hypothesis is that Broad-tailed Hummingbirds did not alter their visitation rate in response to changing wildflower abundance, while our alternative hypothesis is that Broad-tailed Hummingbirds altered their visitation patterns in accordance with changing wildflower abundance. We predicted that hummingbird visitation patterns would align with our alternative hypothesis – namely, that hummingbirds fed on flowers at an increasing rate as they became abundant regardless of phenological timing. We anticipate that the results from this study will add to the growing literature on phenological match and mismatch and provide valuable insight into the long-term stability of Broad-tailed Hummingbird populations in and around Gothic.

Methods

To answer our research questions, we analyzed transect and camera trap data collected from the Stoddard Lab's HummerFlowerWatch (HFW) project, a long-term study of Broad-tailed Hummingbird foraging patterns at RMBL. Beginning in early June of 2022 and 2023, transect data was collected at two field sites in the area surrounding RMBL (Fig. 1). These transect lines take counts of a variety of wildflower species found within two meters of the transect – including *D. nuttallianum* and *I. aggregata* – that are presumed food sources for Broad-tailed Hummingbirds. For a complete list of wildflower species in the HummerFlowerWatch Project, see Supplementary Table 1. Three transects are located on the Judd Falls trail from Gothic Road to Judd Falls; three more are located on the Stupid Falls trail from the Gothic townsite to Stupid Falls. All transects are 50 meters in length with the exception of Judd Falls Transect 3, which is 25 meters long. We collected transect data at each of these sites in six-day intervals, using clickers to count *D. nuttallianum* and *I. aggregata* flowers.

Camera data was sourced from 20 Brinno TLC200 cameras (2.5 x 1.8 x 4.2 inches) with waterproof cases that were positioned on small tripods to record hummingbird-relevant wildflowers in the area around RMBL. Every day from early June to mid-August, members of the HFW team set up cameras on blooming flowers at one of three research sites (Judd Falls, Stupid Falls, and the Gothic townsite). 32GB SD cards and batteries were replaced before locating a new flower to record for the next three days. Precise camera location was documented using a Garmin GPSMAP tagger accurate to 5-10 meters; the coordinates and notes on the physical location were recorded for future reference. We prioritized flowers that had newly bloomed and/or had buds, as this increases the likelihood of recording fresh flowers that are appealing to hummingbirds. The rechargeable batteries in the cameras

last approximately three days, so working at one field site each day allowed us to create a rotating schedule in which cameras are repositioned on the day they run out of battery.

We used raw camera data consisting of time-lapse footage (1 picture per second recorded from 5:00am to 9:00pm for 3 days per flower) from the 2022 and 2023 summer seasons. Once SD cards were retrieved, the timelapse footage was uploaded onto a hard drive containing our data. This footage was processed by the program DeepMeerkat, a deep machine learning algorithm trained with ~29,000 images to detect those that may contain hummingbirds and add them to a folder for further review (Weinstein, 2018). We then parsed the flagged images, selecting only those that contained hummingbirds feeding on the target flowers. See Supplementary Figure 1 for an example of an image that was positively identified as a hummingbird visiting a target flower.

To calculate hummingbird visitation rate and abundance for each flower, we first sorted the data into eleven weeks spanning the summer season. For consistency, similar dates were used for 2022 and 2023, with those in 2023 shifted forward by one day to ensure that we had consistent data throughout the season. To calculate hourly visitation rate, we divided the total number of visits on each flower species in each week by the total hours of footage on that flower species for the week. We multiplied this value by 15, the number of daylight hours recorded by the cameras per day, to get the daily visitation rate (visits/day). To calculate floral abundance, we divided the total number of *D. nuttallianum* and *I. aggregata* flowers found across all transects for that week by the area (in square meters) of transects that contained that flower for that week. This gave us our floral abundance, expressed in flowers/m². We also approximated species diversity by counting the total number of species recorded in each week's transects as a way to measure the overall floral landscape beyond just

our two study flowers. Our species diversity counts included every hummingbird-relevant flower contained within our transect data and consisted of raw counts of how many species were present in each survey week.

Analyzing our data involved comparisons of week-to-week visitation and flower abundance data between 2022 and 2023 using R programming (R Core Team, 2021, Wickham, 2016). Because our goal was to measure whether hummingbirds shift their feeding patterns in response to phenological changes, we compared the relationship between floral abundance and visitation rate for each week between June and August in 2022 with the same week in 2023. We first checked for normality using the Shapiro-Wilk normality test of visitation and abundance separated by year and flower species. Then, we checked for linearity by making scatterplots with visitation rate and abundance on the axes separated by year and flower species. Depending on whether the assumption of normality was met, we assessed the correlation between floral abundance and daily visitation rate using either the Pearson correlation coefficient (normal: *D. nuttallianum* 2022, *I. aggregata* 2022 and 2023) or Spearman's rank correlation coefficient (not normal: *D. nuttallianum* 2023).

Results

We found that there was a weak correlation between visitation rate and floral abundance for *D. nuttallianum* in 2022 (Fig. 2a, $\text{cor} = .74$, $p = .09$) and no correlation in 2023 (Fig. 2c, $\text{cor} = .19$, $p = .68$). We found that visitation rate and floral abundance for *I. aggregata* were not correlated in 2022 (Fig. 2b, $\text{cor} = .003$, $p = .99$) and weakly negatively correlated in 2023 (Fig. 2d, $\text{cor} = -.34$, $p = .40$). All correlations were statistically non-significant, with p-values greater than .05.

The graphs of weekly visitation rate and abundance for *I. aggregata* in 2022 and 2023 appear to display an inverse relationship between visitation rate and abundance (Fig. 3a), though this pattern was not demonstrated in the previously mentioned correlation calculations. The graphs for *D. nuttallianum* (Fig. 3b) also illustrate this inverse relationship to some extent. Despite higher abundance for *D. nuttallianum* (compared to *I. aggregata*) in both years, visitation rate for *D. nuttallianum* remained far lower than that of *I. aggregata* (Fig. 3b).

In line with the years' snowmelt data, both flowers bloomed earlier in 2022 than 2023 (Fig. 4). In 2022, our transect data began too late to measure the first half of the *D. nuttallianum* flowering season, which had likely begun weeks before our data was collected. The overlap between *D. nuttallianum* and *I. aggregata* was 2 weeks longer in 2022 (week 23-27) than in 2023 (week 26-28). As soon as *I. aggregata* entered the floral landscape, hummingbirds immediately began to feed on it at rates significantly higher than those of *D. nuttallianum*, despite the latter's higher abundance (Fig. 4). As *I. aggregata* reaches peak abundance, visitation rate drops slightly. Visitation rate for *I. aggregata* was at its lowest in week 28 in 2022 and in week 29 in 2023. During the last few weeks, as *I. aggregata* became less abundant, visitation rate once again increased.

We observed similar trends in both years for overall species diversity (Fig. 4). Both *Mertensia ciliata* and *Erythronium grandiflorum* were present from the first week of transect data, with *D. nuttallianum* serving as the key early-season difference between the two years. *D. nuttallianum* was counted in our transects from the beginning in 2022, but took two more weeks to emerge in 2023. Species diversity peaked during the week of June 22nd in 2022 and the week of July 5th in 2023. From the peak to the end of the summer, species counts ranged from 8 to 13 in 2022 and from 9 to 14 in

2023. This increase from 2022 to 2023 was largely because our 2023 transect data was expanded to include a few more wildflowers.

Discussion

The aim of our study was to find evidence of phenological match or mismatch between Broad-tailed Hummingbirds and two of their key wildflower food sources, *D. nuttallianum* and *I. aggregata*, in years of different snowmelt timing. Our results did not initially support our alternative hypothesis that Broad-tailed Hummingbirds alter their visitation patterns in accordance with changing wildflower phenology in the manner we expected. We found no significant correlation between visitation rate and floral abundance for either of our flowers or years. However, our results revealed a clear pattern across temporal scales in support of our alternative hypothesis in that hummingbirds fed on certain flowers as soon as they emerged.

Hummingbirds began feeding on *I. aggregata* as soon as it appeared in the floral landscape in both years and on *D. nuttallianum* as soon as it emerged in 2023. In 2022, our camera data began after *D. nuttallianum* emerged, so we cannot draw meaningful phenological match/mismatch conclusions for *D. nuttallianum* in 2022. The effect of snowmelt on floral emergence was also supported by our findings, as *D. nuttallianum* had already peaked by June 1st (when our transect data began) in 2022, but didn't emerge until the week of June 14th in 2023. This also occurred for *I. aggregata*, which emerged during the week of June 22nd in 2022 and the week of July 5th in 2023. This two-week gap in emergence for both flowers is in line with our predictions of the effect of snowmelt on flowering phenology (McKinney, 2012). Further, we propose that the earlier snowmelt in 2022 likely

contributed to the 5-week overlap in flowering between *D. nuttallianum* and *I. aggregata*, greater than the 3-week overlap in 2023 with later snowmelt. Because we observed such drastic phenological variation between the two years, we can use our hummingbird visitation data to draw meaningful conclusions about Broad-tailed Hummingbirds' ability to adapt to phenological changes in the floral landscapes.

The year-to-year phenological changes we observed impacted the length of flowering time for both *D. nuttallianum* and *I. aggregata*, leading to potential differences in the pollination window for each flower. Hummingbirds appeared to feed on *I. aggregata* as soon as it emerged, prioritizing it over *D. nuttallianum*. Since these two wildflowers are competing for the same pollinator, *D. nuttallianum* benefits from periods when it is abundant and *I. aggregata* is not yet present (Waser, 1978). With later snowmelt in 2023, *D. nuttallianum* was present for just three weeks before *I. aggregata* first emerged. In 2022, *D. nuttallianum* was present for at least two weeks before *I. aggregata*, but likely more than three weeks since our data did not capture the first half of *D. nuttallianum* flowering. For both flowers, especially *D. nuttallianum*, the shorter overlap in 2023 was likely beneficial due to fewer opportunities for interspecific pollination and a longer period of individual species abundance.

One of the most interesting findings from our results was an inverse relationship between weekly visitation rate and abundance for *I. aggregata*. In both 2022 and 2023, our data displays a clear pattern in which visitation rate on *I. aggregata* is highest when abundance is lowest. As *I. aggregata* progresses towards its peak, visitation rate gets lower, and as it passes its peak, visitation rate climbs yet again. We propose a number of possible explanations for why this may occur. First, the presence of a greater number of *I. aggregata* flowers may provide hummingbirds with a wider selection of

individuals to choose from, such that they feed on each individual plant less. Since our cameras only focus on one plant, we would expect to observe a lower visitation rate when abundance of a flower is highest since visits are more diluted across a larger population. During the beginning and end of *I. aggregata*'s flowering season, the smaller floral population means that the plants we record represent a larger proportion of the whole population, resulting in higher visitation rates as hummingbirds concentrate their visits among a small number of flowers. Second, we investigated the possibility that increased species diversity around the time of peak *I. aggregata* abundance may decrease visitation rate by presenting hummingbirds with a greater variety of food options, encouraging lower visitation rate on *I. aggregata*. For all species and years excluding *D. nuttallianum* in 2022 ($\text{cor} = -.8, p = .04$), we found no correlation between species diversity and visitation rate ($|\text{cor}| < .2, p > .8$). Since our data collection began near the peak of *D. nuttallianum*'s flowering season in 2022, we only captured the period of declining abundance after the peak. This meant that our data only accounted for *D. nuttallianum*'s decline as well as an overall increase in species diversity as the season progressed towards summer. As such, the strong negative correlation we observed may have resulted from the missing earlier weeks when *D. nuttallianum* was likely increasing in abundance and species diversity was low. Since our data does not include early-season *D. nuttallianum* flowering data for a year with early snowmelt, further research is needed to clarify the relationship between species diversity and visitation rate of *D. nuttallianum*.

Another interesting conclusion from our results is that visitation rates on *D. nuttallianum* were consistently far lower than visitation on *I. aggregata* by roughly one order of magnitude. Daily visits on *D. nuttallianum* consistently ranged between 0 and 0.5 visits/day, while those for *I.*

aggregata were consistently between 2 and 5 visits/day, with some weeks even higher. Our data supports this trend by demonstrating that as soon as *I. aggregata* entered the floral landscape in both years, hummingbirds began feeding on it at rates far higher than *D. nuttallianum*. This immediate reaction to the presence of *I. aggregata* also supports our alternative hypothesis, suggesting that Broad-tailed Hummingbirds have the ability to quickly adapt to changing floral landscapes. It is entirely possible that the extremely high abundance of *D. nuttallianum* (reaching as high as 6 flowers/m² in some cases, while *I. aggregata* never surpassed 0.75 flowers/m²) produces a similar effect to that discussed above for *I. aggregata*, in which the sheer number of flowers makes it difficult to capture individual visits to a single plant. Regardless, we suggest that further studies incorporate a way to measure population-level visitation to better understand the relationship between Broad-tailed Hummingbirds and *D. nuttallianum*.

Our study was limited by various factors. First, only two years of transect data were available, some of which were incomplete or inconsistent. Since the methods for collecting transect data had not yet been refined, some weeks had fewer transects than others and some flowers were not counted in 2022. We attempted to resolve the first issue by using flowers/m² rather than total flowers, and the latter issue had little impact on our species diversity counts.

Second, we observed extreme floral abundance at peak season for *D. nuttallianum*, making it difficult for our finite number of cameras to accurately measure visitation rates, especially at the population level. With only twenty cameras spread across multiple species, there were times when only five or six cameras were available to capture overall visitation to *D. nuttallianum* flowers, despite thousands of such flowers being in bloom. As such, the low visitation rates we observed on

D. nuttallianum may have been a byproduct of methodological limitations, not floral irrelevance. We experimented with calculating population-level visitation by multiplying visitation rate by total number of flowers, but enough cameras observed no visits at all that this metric was of limited use. Future studies might find other ways to gauge population-level visitation on *D. nuttallianum*, perhaps through direct visual observation, drone footage, or pollen samples taken during banding. Assuming the low visitation rates we observed accurately reflect hummingbird behavior, these studies may allow us to recontextualize the relationship between Broad-tailed Hummingbirds and *D. nuttallianum*.

Third, our study was conducted across relatively similar elevations. Elevation at our sites ranges from 9,300 feet at Stupid Falls to 9,900 feet at Judd Falls, a relatively narrow band in a county that ranges from 7,500 feet near the town of Gunnison to over 14,000 feet in the Elk Mountains. Anecdotally, we have observed Broad-tailed Hummingbirds feeding at up to 12,000 feet near some of the peaks within three miles of the Gothic townsite, suggesting that the local population spans across a wider elevation gradient than what we studied. This presents the possibility that hummingbirds at RMBL may be visiting flowers at higher elevations not accessible by our cameras. If so, the hummingbirds could adapt to changing phenology at RMBL by feeding on the same flowers at higher elevations later in the season, a possibility that our data did not capture.

Finally, our conclusions are slightly tempered by the lack of reliable Broad-tailed Hummingbird breeding surveys in and around Gothic. RMBL has an annual Breeding Bird Survey that provides some valuable information, but does not often encounter the many hummingbird nests surely present in the area. Detailed surveys could provide insight as to whether hummingbirds are flexible in their foraging patterns but unable to adjust breeding season milestones to correspond with

floral phenology. This would likely lead to lowered nesting success and population viability.

Alternatively, such surveys could show that, like the Black-throated Blue Warblers studied by Covino et al. (2020), the hummingbirds were taking advantage of longer flowering seasons in years with early snowmelt by raising multiple broods rather than their usual single brood. Were the hummingbirds to adopt such a behavior, it would further push back against the notion of a phenological mismatch-based population decline and support the idea that RMBL's Broad-tailed Hummingbirds are increasing in population.

Conclusion

Our results supported our alternative hypothesis by demonstrating that Broad-tailed Hummingbirds have some capacity to adapt to changes in floral phenology across temporal scales, whether year-to-year with snowmelt changes or week-to-week as the floral landscape changes over the course of the summer season. This adaptability could help them avoid the phenological mismatch that often accompanies climate change and persist despite their projected arrival at RMBL after the first flowering of *D. nuttallianum* by the mid-21st century (McKinney, 2012). There is currently limited evidence (McKinney, 2012) that Broad-tailed Hummingbirds are adjusting their migration timing to account for earlier floral phenology as other birds have done (Covino et al., 2020). However, the hummingbirds' ability to improvise and feed on whichever flowers are present in the floral landscape throughout the breeding season should allow them to adapt regardless of migration timing.

Future studies focusing on measuring population-level visitation would add to our existing work, allowing us to better understand hummingbird visitation patterns on wildflowers.

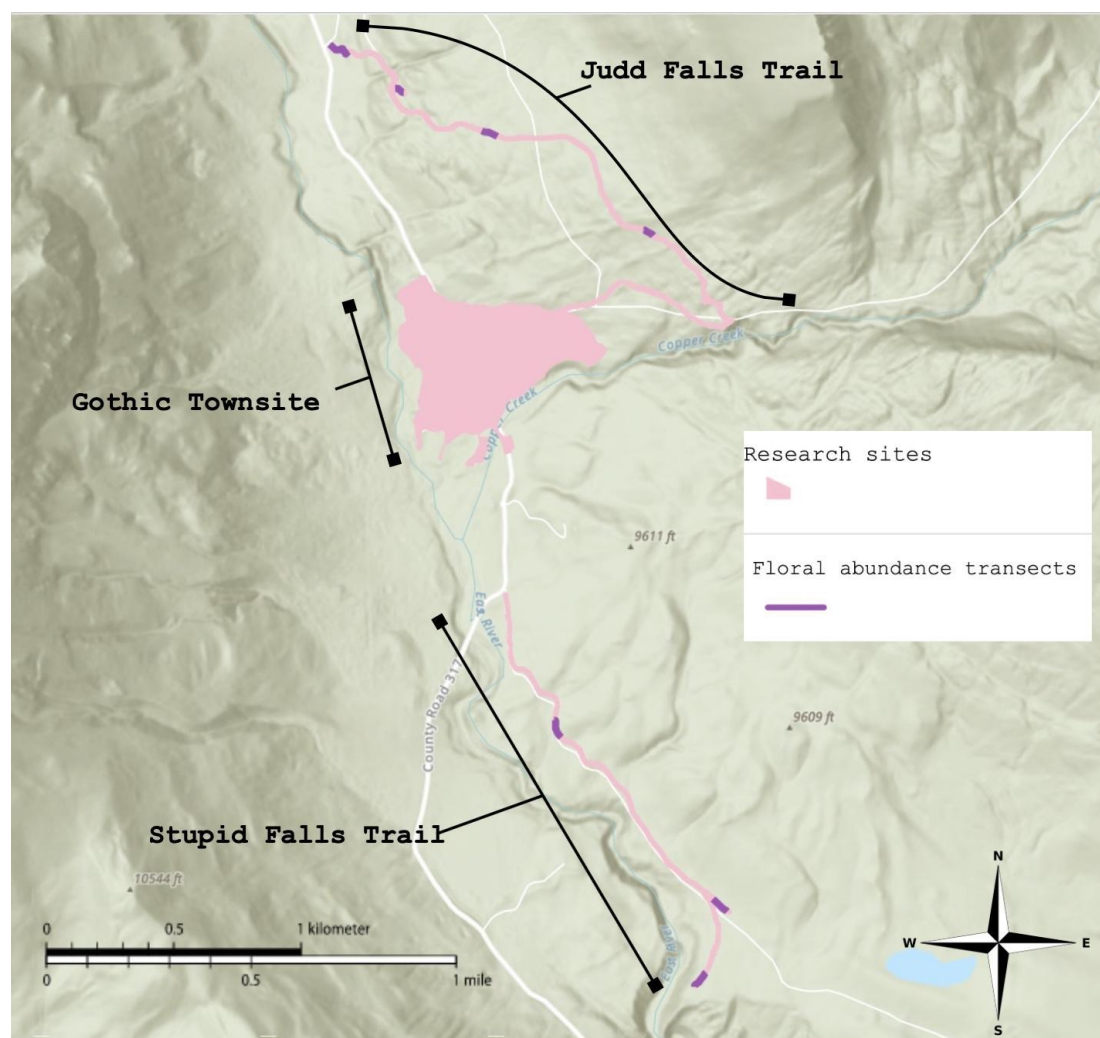
Continuation of our current methods across future years would give us a larger sample size with more variation in snowmelt timing over which to investigate the relationship between hummingbird visitation and floral abundance. Such a study could also be extended to other species of wildflowers present at different points during the hummingbirds' breeding season, creating a more detailed portrait of phenological changes and responses. Hummingbirds may be more or less flexible in adapting their behavior to the phenology of other flowers that also make up an important part of their diet at RMBL. Flowers like *Castilleja miniata*, *Delphinium barbeyi* and *Linaria vulgaris* also have relatively high visitation rates and are worth investigating to gain a more comprehensive picture of hummingbird foraging behavior. Some of these flowers begin to bloom later than *I. aggregata*, corresponding more closely with juvenile emergence and the arrival of the more aggressive Rufous Hummingbird (*Selasphorus rufus*) (Camfield, 2006). These influential breeding season events should be studied in a similar manner to the ones chosen in our study. All in all, this study's use of hummingbird visitation and flower abundance data provides a promising foundation for future research on contextualizing behavioral shifts in Broad-tailed Hummingbirds and other pollinators faced with the possibility of phenological mismatch.

References

- barr, billy. (2024). *Gothic Weather Long Term Weather Data: Snowfall, by Month, in cm, 1974-2024* [Dataset]. <https://www.gothicwx.org/long-term-snow.html>
- Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089), 81–83.
<https://doi.org/10.1038/nature04539>
- Camfield, A. F. (2006). Resource value affects territorial defense by Broad-tailed and Rufous hummingbirds. *Journal of Field Ornithology*, 77(2), 120–125.
<https://doi.org/10.1111/j.1557-9263.2006.00031.x>
- Covino, K. M., Horton, K. G., & Morris, S. R. (2020). Seasonally specific changes in migration phenology across 50 years in the Black-throated Blue Warbler. *The Auk*, 137(2).
<https://doi.org/10.1093/auk/ukz080>
- Egar, A. (2021). *Responses of Broad-tailed Hummingbird Foraging Behavior to Climate Change Across Multiple Temporal Scales* [Unpublished thesis]. Princeton University.
- McKinney, A. M., CaraDonna, P. J., Inouye, D. W., Barr, B., Bertelsen, C. D., & Waser, N. M. (2012). Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology*, 93(9), 1987–1993. <https://doi.org/10.1890/12-0255.1>
- Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E., & Delgado, M. D. M. (2013). Community-level phenological

- response to climate change. *Proceedings of the National Academy of Sciences*, 110(33), 13434–13439. <https://doi.org/10.1073/pnas.1305533110>
- Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13(9), 1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org/>.
- Waser, N. M. (1976). Food Supply and Nest Timing of Broad-Tailed Hummingbirds in the Rocky Mountains. *The Condor*, 78(1), 133–135. <https://doi.org/10.2307/1366943>
- Waser, N. M. (1978). Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology*, 59(5), 934–944. <https://doi.org/10.2307/1938545>
- Weinstein, B. G. (2018). Scene-specific convolutional neural networks for video-based biodiversity detection. *Methods in Ecology and Evolution*, 9(6), 1435–1441. <https://doi.org/10.1111/2041-210X.13011>
- Wickham, H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Tables and Figures

Figure 1*Transect Locations for Judd and Stupid Falls*

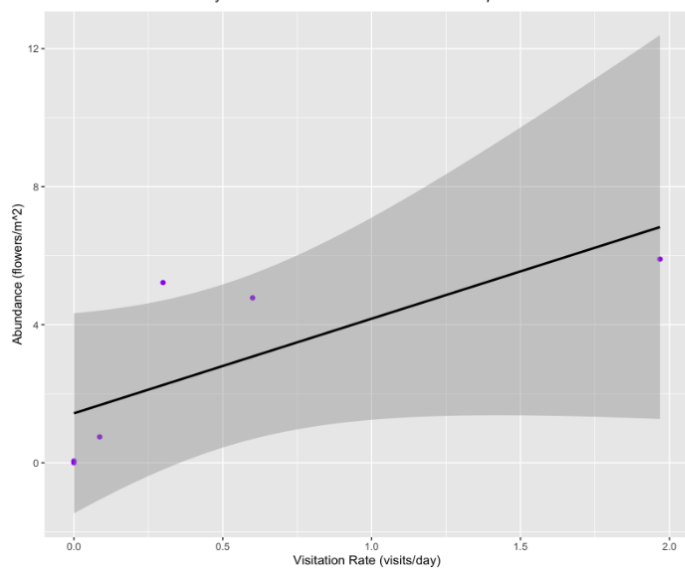
Note. This map shows the location of the research sites and the seven wildflower transects. All transects are 50 meters long with the exception of Judd Falls Transect 3, which is 25 meters long.

Figure 2

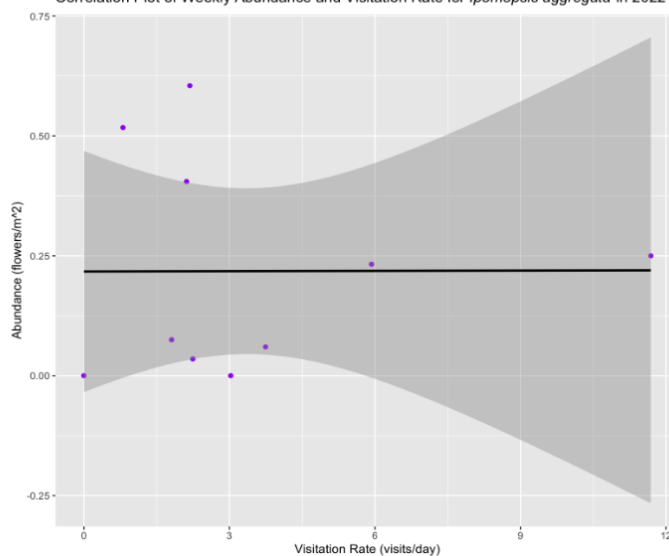
Correlation Plots of Weekly Abundance and Visitation Rate by Species and Year

Figure 2a

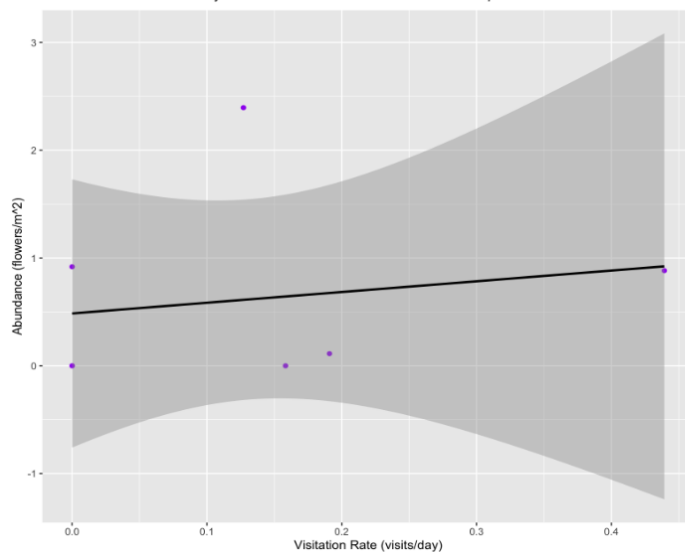
Correlation Plot of Weekly Abundance and Visitation Rate for *Delphinium nuttallianum* in 2022

**Figure 2b**

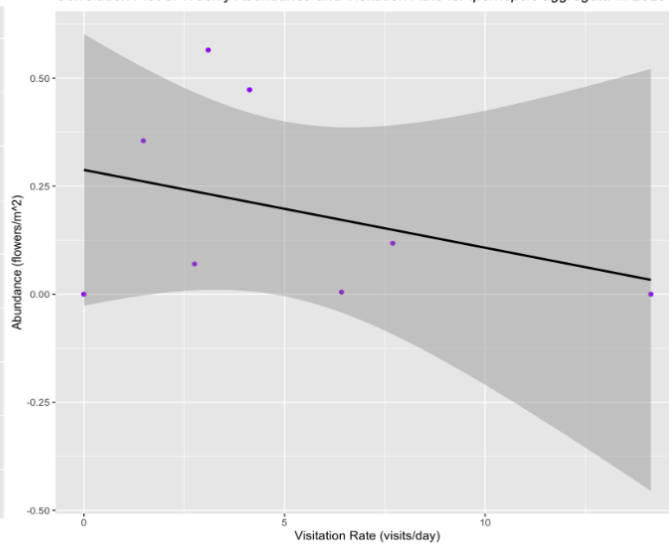
Correlation Plot of Weekly Abundance and Visitation Rate for *Ipomopsis aggregata* in 2022

**Figure 2c**

Correlation Plot of Weekly Abundance and Visitation Rate for *Delphinium nuttallianum* in 2023

**Figure 2d**

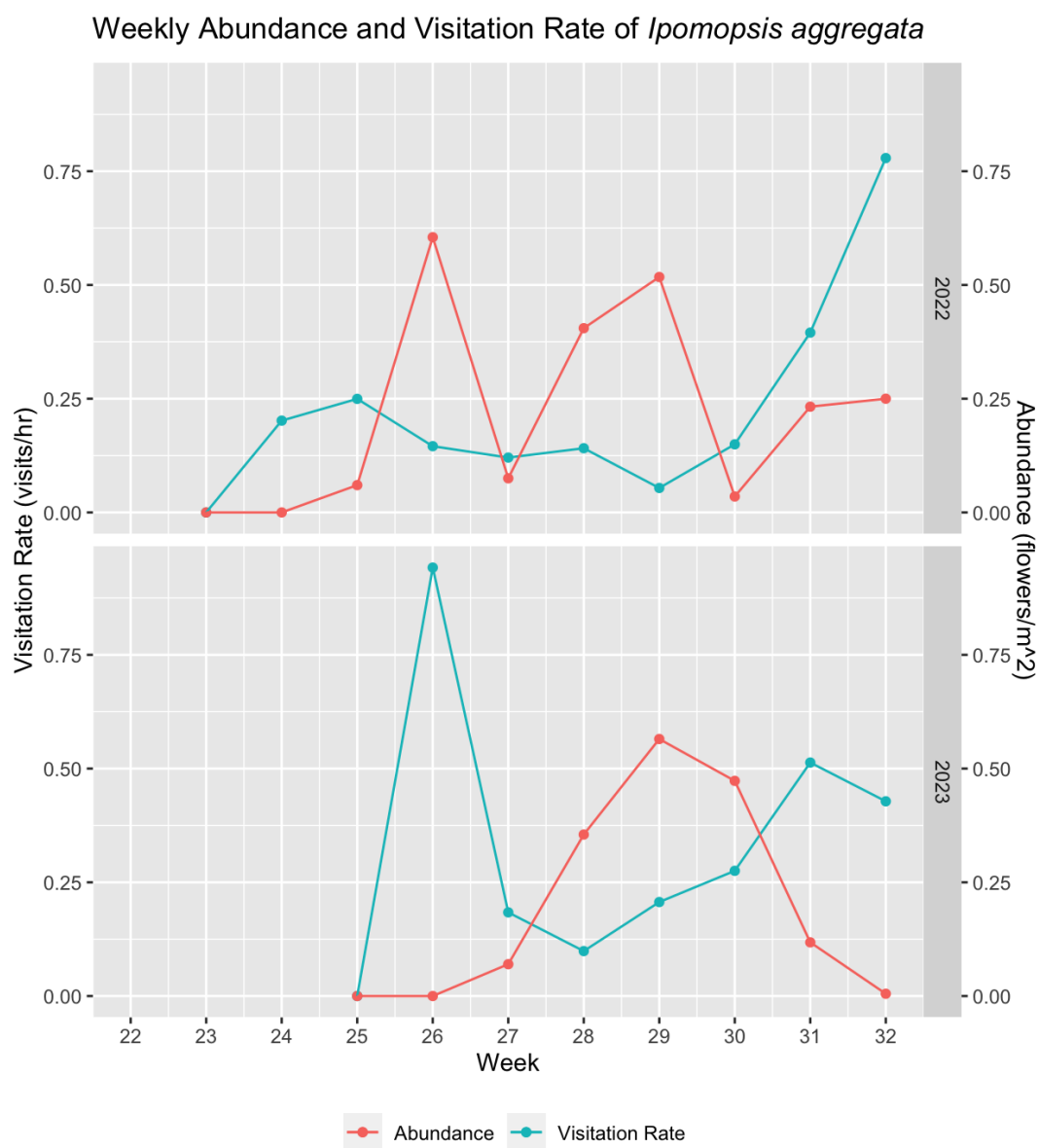
Correlation Plot of Weekly Abundance and Visitation Rate for *Ipomopsis aggregata* in 2023



Note. Correlation plots of weekly abundance and visitation rate of *Delphinium nuttallianum* and *Ipomopsis aggregata* for 2022 and 2023 where we observed no significant linear correlations between our variables (from left to right: p-value=0.09, p-value=0.99, p-value=0.68, p-value=0.40).

Figure 3a

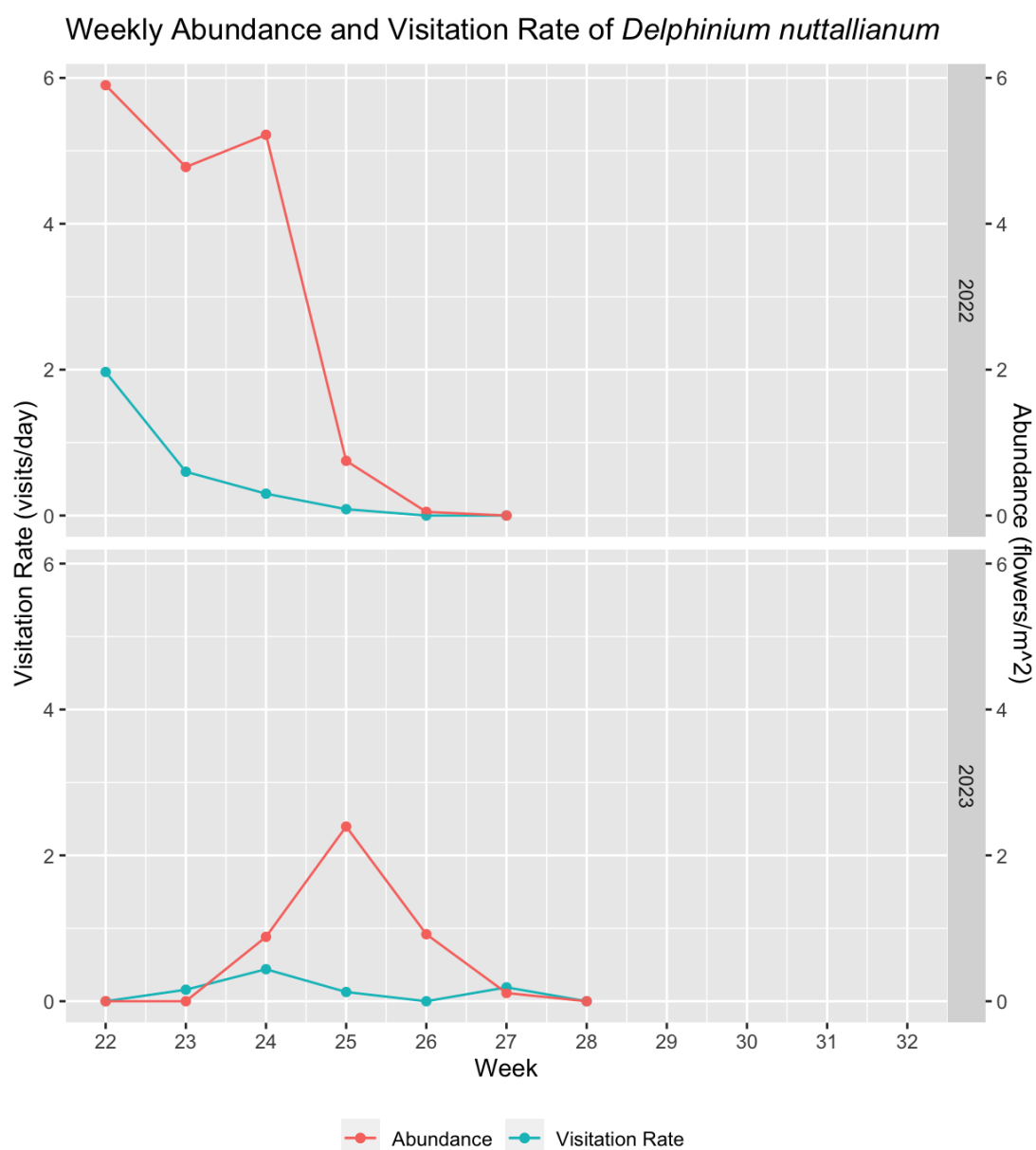
Weekly Abundance and Visitation Rate of Ipomopsis aggregata



Note. This graph displays the abundance and visitation rate for *I. aggregata* across the weeks present in our dataset. For *I. aggregata*, we chose to display visitation rate as visits/hour to better illustrate changing trends since visits/day occurred at a scale that would be difficult to display on a graph containing comparatively smaller abundance data.

Figure 3b

Weekly Abundance and Visitation Rate of Delphinium nuttallianum



Note. This graph displays the abundance and visitation rate for *D. nuttallianum* across the weeks present in our dataset. For *D. nuttallianum*, we chose to display visitation rate as visits/day to better illustrate changing trends since visits/hour occurred at too small a scale to be easily discriminable.

Figure 4

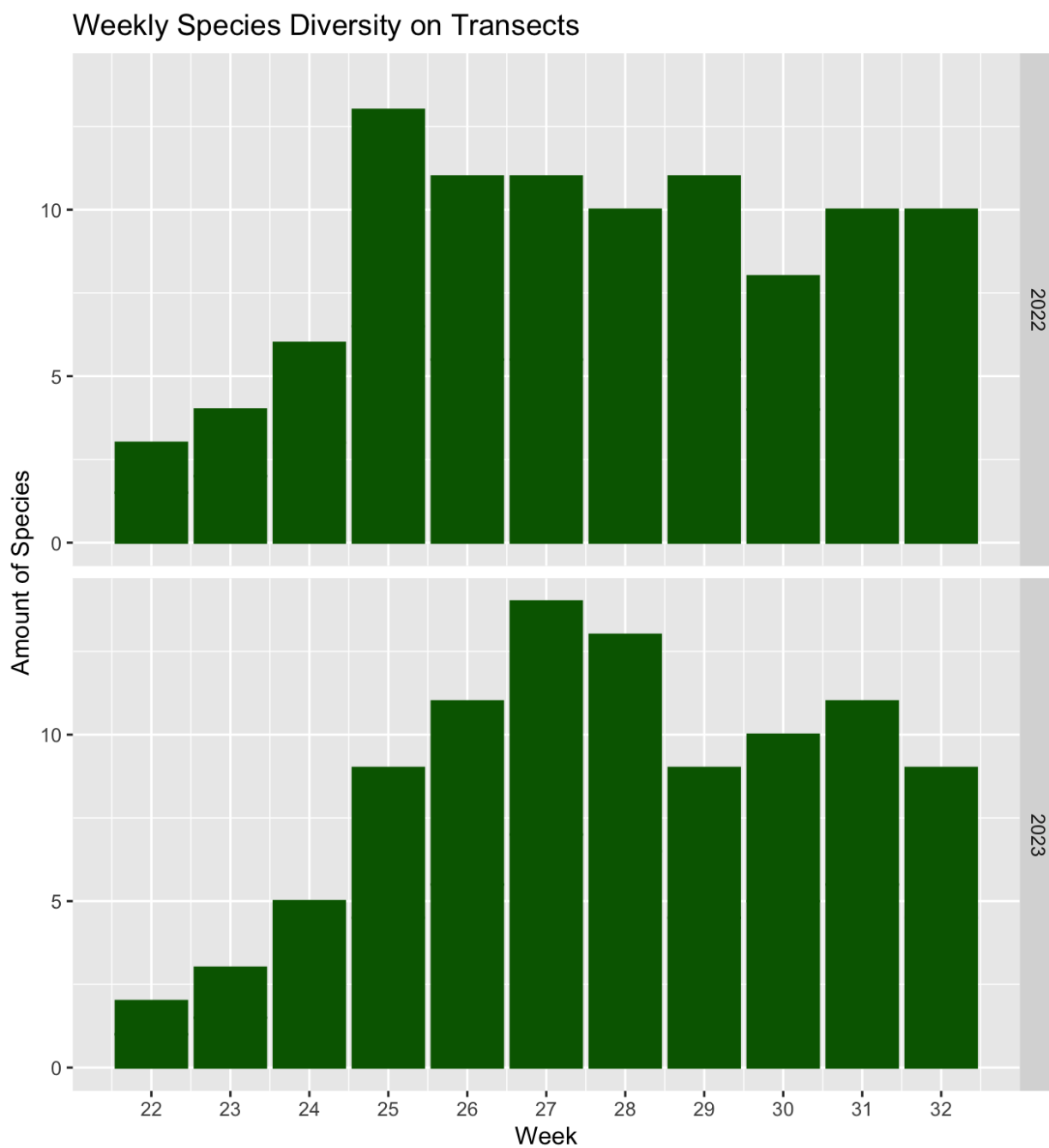
*Scaled Weekly Abundance and Visitation Rate for *D. nuttallianum* and *I. aggregata**



Note. Abundance, visitation rate, and species diversity for *I. aggregata* and *D. nuttallianum* per week from early June to mid-August in 2022 and 2023, with all data scaled to 1 (where 1 is the largest value for that variable recorded for a given species and year). By scaling all data to 1, this graph allows for better comparison of the changing trends present in our data across years and species.

Figure 5

Weekly Species Diversity on Transects



Note. This graph displays a raw count of species diversity for all weeks across 2022 and 2023.

Supplementary Figures

Supplementary Figure 1

DeepMeerkat Positive Hummingbird Visitation Frame



Note. A single frame from the HFW camera data that had been processed through DeepMeerkat in 2018. This frame shows a positive identification by DeepMeerkat of a hummingbird visit to *I. aggregata*. The value in red in the top left shows the confidence value by deep meerkat that there is a hummingbird in the frame.

Supplementary Table 1

HummerFlowerWatch Surveyed Species

Columbian monkshood (<i>Aconitum columbianum</i>)	Rocky Mountain columbine (<i>Aquilegia caerulea</i>)
Western red columbine (<i>Aquilegia elegantula</i>)	Parry's bellflower (<i>Campanula parryi</i>)
Harebell (<i>Campanula rotundifolia</i>)	Wyoming paintbrush (<i>Castilleja linariifolia</i>)
Giant red Indian paintbrush (<i>Castilleja miniata</i>)	Sulphur Indian paintbrush (<i>Castilleja sulphurea</i>)
Fireweed (<i>Chamerion angustifolium</i>)	Thistle (<i>Cirsium spp.</i>)
Tall/Subalpine larkspur (<i>Delphinium barbeyi</i>)	Nuttall's larkspur (<i>Delphinium nuttallianum</i>)
Western wallflower (<i>Erysimum capitatum</i>)	Glacier lily (<i>Erythronium grandiflorum</i>)
Monument plant (<i>Frasera speciosa</i>)	Autumn gentian (<i>Gentianella amarella</i>)
Parry's gentian (<i>Gentiana parryi</i>)	Fringed gentian (<i>Gentianopsis thermalis</i>)
Ballhead waterleaf (<i>Hydrophyllum capitatum</i>)	Fendler's waterleaf (<i>Hydrophyllum fendleri</i>)
Scarlet gilia (<i>Ipomopsis aggregata</i>)	Yellow toadflax (<i>Linaria vulgaris</i>)
Twinberry honeysuckle (<i>Lonicera involucrata</i>)	Oregon grape (<i>Mahonia aquifolium</i>)
Mountain bluebells (<i>Mertensia ciliata</i>)	Bluebells (<i>Mertensia fusiformis</i>)
Bracted lousewort (<i>Pedicularis bracteosa</i>)	Giant lousewort (<i>Pedicularis procera</i>)
Rydberg's penstemon (<i>Penstemon rydbergii</i>)	Rocky Mountain penstemon (<i>Penstemon strictus</i>)
Towering Jacob's-ladder (<i>Polemonium foliosissimum</i>)	Currant (<i>Ribes spp.</i>)
Willow (<i>Salix spp.</i>)	

Note. List of all the hummingbird relevant wildflower species present in the HummerFlowerWatch study.