

Picky Eater?

**How Different Environmental Factors Affect Broad-tailed
Hummingbirds' (*Selasphorus platycercus*) Foraging Patterns in the
Rocky Mountains**

Trang Ngo

Department of Ecology and Evolutionary Biology

Princeton University

Professor Mary (Cassie) Stoddard

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HONOR CODE

This represents my own work in accordance with University regulations

Trang Ngo

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ABSTRACT

Plant and pollinator interactions are a form of mutualism requiring a careful balance between floral traits and pollinator behavior to maximize both pollination success and nectar consumption. This delicate relationship can result in detrimental effects on one party when the other shifts. Namely, global warming is causing phenological mismatches in many different ecosystems, where migratory species' resources are impacted due to advanced flowering phenology. For example, many studies conducted at the Rocky Mountains Biological Laboratory (RMBL) in Gothic, Colorado have shown that the breeding season of Broad-tailed hummingbirds (*Selasphorus platycercus*) is shortened due to advanced blooming of early season species and no extension in late species' blooming period. Moreover, climate change can affect environmental patterns like temperature, snowmelt timing or precipitation, which can alter resource availability for the hummingbirds within their breeding season. In this study, I analyzed the correlations between snowmelt date, daily temperature fluctuations, rainfall, floral abundance, nectar quality, and studied how these factors relate to hummingbird foraging patterns by analyzing available long-term data sets. In my results, I found little statistical evidence for a direct correlation between hummingbird visitation rate and these biotic and abiotic factors. However, I found many underlying patterns when looking at different combinations of variables. For example, temperature can increase or decrease nectar quality depending on the flower species, and the relationship between visitation rate for each species and daily temperature varies. This study reinforces the complex, interdependent way in which different abiotic and biotic factors interact to influence Broad-tailed hummingbirds' foraging patterns, highlighting how the cascading ecological effects of climate change on the plant-pollinator mutualism.

INTRODUCTION

Climate change and its effects on ecosystems

Climate change is driving increasingly irregular weather patterns all over the world. Global warming often evokes the image of melting ice caps and coral bleaching in the tropics due to high temperatures, and climate monitoring confirms that the warming rate of Earth's surface temperature has tripled since 1982 (Lindsey et al. 2024). Some environments, such as those at higher altitudes, exhibit more pronounced temperature fluctuation patterns compared to lowland areas (Beniston et al. 1997). Warmer temperatures also accelerate water evaporation in the atmosphere, causing drastic precipitation patterns: more intense droughts and storms across the globe (Trenberth 2011). Additionally, for montane ecosystems, global warming can lead to earlier snowmelt (Karl et al. 1993).

Literature reviews suggest these irregularities are impacting ecosystems as a whole rather than targeting individual organisms (Walther 2010). For example, mountainous plants and animals are shifting their ranges to higher elevations due to rising temperatures in lower elevations, in which those species do not thrive as optimally, altering community compositions and dynamics (Breshears et al. 2008; Sekercioglu et al. 2007). Another major effect is on phenology, the seasonal timing of life-history events of species triggered by environmental cues such as temperature or photoperiod (Walther 2010). A system highly dependent on tight seasonal synchrony is the plant-pollinator dynamic. Many studies have shown that both the onset of flowering and appearance of pollinators are advancing due to warming, but not necessarily at the same rate (Hegland et al. 2009), creating the risk of phenological mismatch (Visser and Gienapp 2019).

Climate change, phenological mismatch and the plant-pollinator dynamic

The plant and pollinator dynamic is a delicate relationship easily disrupted by phenological shifts. In many ecosystems, warmer temperatures are advancing snowmelt, consequently shifting the reproductive rhythms of certain plant species forward (Cleland et al. 2007). For instance, the flowering phenology of Canadian rockcress (*Boechea stricta*), a mustard plant found in the US Rocky Mountains, has advanced significantly within the span of 40 years (Anderson et al. 2012).

However, pollinator responses to earlier flowering vary. Some species can advance their own phenology to keep pace, such as various wild bee species across North America who are emergin roughly 10.5 days over the span of 130 years to keep up with plant phenology (Bartomeus et al. 2011). However, some high-altitude plants may not only shift flowering onset but also shorten phenophases (Inouye and Wielgolaski 2025). This can be detrimental to pollinators, because it means the flowers are in bloom for a shorter period of time, effectively shrinking the pollinators' window to access resources.

Some pollinators are not as fortunate as the wild bees in syncing up their pace with environmental changes. Migratory pollinators such as hummingbirds are particularly affected by phenological mismatch, where the arrival of the birds at the breeding site does not line up with flower blooming time, effectively reducing early breeding season resource availability, impacting breeding timing and foraging success (McKinney et al. 2012).

How Broad-tailed hummingbirds' foraging behavior is affected by climate change impact

A well-studied model species for studying the ecological effects of phenological mismatch is the Broad-tailed hummingbird (*Selasphorus platycercus*) (Figure 1). It is a species of mid-sized hummingbird that migrates from Central America to the Rocky Mountains every

summer to breed (Bent 1940). There is a non-migratory population in Guatemala, but this study focuses on the migratory population, and the breeding ground of choice is the Rocky Mountains Biological Laboratory (RMBL), situated at 9500ft (2900m) above sea level in Gothic, Colorado. As a research station established in 1928, RMBL and its scientists have studied the hummingbird population here as well as their surrounding ecosystem for decades. Apart from the later-arriving Rufous hummingbirds (*Selasphorus rufus*) in early July, Broad-tailed hummingbirds are the main species of hummingbirds at RMBL (Camfield 2006). This makes them one of the major pollinator species for a variety of flower species such as Scarlet gilia (*Ipomopsis aggregata*) and Giant red Indian paintbrush (*Castilleja miniata*) (Waser 1976). My study will build on prior work by examining direct and indirect effects of climate change on Broad-tailed hummingbird foraging behavior, namely by exploring:

- Abiotic factors: temperature, precipitation and snowmelt timing
- Biotic factors: floral abundance and nectar quality



Figure 1. Broad-tailed hummingbirds. Male (left) and female/juvenile male (right). Images: *All About Birds*, Cornell Lab.

Indirect effects of climate change on Broad-tailed hummingbirds' resource availability and quality

1. How snowmelt timing and phenology affects Broad-tailed hummingbirds' resource availability

There are many studies at RMBL documenting Broad-tailed hummingbirds' interactions with their environment and how phenological mismatch may affect their activities. For instance, Waser 1976 demonstrated that the birds' breeding seasons in 1972 and 1973 flexibly shifted along with peak abundance of floral resources (*Delphinium nelsoni/nuttallianum*, *Delphinium barbeyi*, *Ipomopsis aggregata* and *Castilleja miniata*), suggesting little phenological mismatch between the birds and the flowers in those two years.

However, a more recent work found contradictory results where early season flowers like *Erythronium grandiflorum* and *Delphinium nuttallianum* are blooming 4.6 ± 1.6 days and 4.3 ± 1.5 days earlier on average respectively, and the birds are arriving 1.5 ± 0.93 days earlier over the study's 37 years (McKinney et al. 2012). Arrival at the breeding site is a crucial time period for hummingbirds as males establish their territories and females prepare for peak brooding activity, which ideally coincides with peak blooming of major hummingbird species like *Ipomopsis aggregata* (McKinney et al. 2012; Waser 1976).

Resource scarcity at the start of their breeding season is especially detrimental to hummingbirds due to their small size yet extremely fast speed and high wing beat rate, meaning they are in a constant state of near starvation. In fact, they spend 11.3% of their day on foraging nectar, which provides 90% of their metabolism (Calder 1975; Carleton et al. 2006). Studies have shown they can be flexible in terms of diet, resorting to insects for amino acid supplementation when needed (López-Calleja et al. 2003; Waser 1976). However, nectar is still the bird's primary choice to best supply the high energy demands of hovering flight as they only spend 1.2% of their day catching insects (Suarez et al. 1990; Waser 1976).

Phenological mismatch can also directly affect the plants pollinated by hummingbirds. Studies have shown that increased overlap in blooming periods of hummingbird-pollinated

species like *Delphinium nuttallianum* and *Ipomopsis aggregata* can lead to more cross-pollination, decreasing seed set and reproductive success due to interspecies pollination (Waser 1978). Even without considering pollinators, plants' quality may decrease due to advanced phenology. When plants bloom earlier, their reproductive window is extended because leaf senescence is longer despite no change in flowering or fruiting period, and plants may have less time to allocate resources to the next season, therefore decreasing the quality (Collins et al. 2021). Consequently, reduced resource quality and availability then affects the hummingbirds, and a fragile relationship is imbalanced. Apart from influencing plant phenology, earlier snowmelt can also induce bud fatality in species sensitive to frost such as *Delphinium barbeyi*, again reducing overall plant abundance as hummingbirds' breeding season progresses (Inouye 2008).

Since the abundance of hummingbird flower species like *Delphinium nuttallianum* and *Delphinium barbeyi* in a season at RMBL correlates significantly with the amount of snowfall the previous year, snowmelt is a major driver in altering hummingbirds' foraging landscape throughout their entire breeding season (Inouye 2008; Inouye and McGuire 1991). Floral density, in turns, affects pollination efficiency: higher density means flowers are closer to each other, therefore decreasing the distance and frequency required for the pollinator to travel from one resource to the next, increasing foraging efficiency (Wolf et al. 1975). Past studies using similar data only analyzed one to two years of floral abundance, and found weak correlations with Broad-tailed hummingbird foraging behavior (Chang 2023, unpublished manuscript; Granier and Ugliarolo 2024, unpublished manuscript). Therefore, I am interested in investigating whether a variation in snowmelt timing across our three years of transect data collection will have an effect

on floral abundance throughout the birds' breeding seasons. Coupled with that, I will examine whether a flower density variation will prompt a difference in the birds' feeding patterns.

2. The role of nectar and 'typical' flowers in hummingbird foraging behavior:

Beyond influencing plant phenology and abundance throughout Broad-tailed hummingbirds' breeding season, climate change can affect the quality of the birds' resources. For example, Powers et al. 2021 discovered that snowmelt date has an effect on *Ipomopsis aggregata*'s morphology, from corolla length to nectar concentration. This is likely due to snowmelt timing's relationship with soil moisture: a year with earlier snowmelt tends to have drier soil moisture, which is an important factor in plant morphology development (Barnett et al. 2005; Powers et al. 2021). Temperature and rainfall also play key roles in altering soil and air humidity: higher temperature means dryer soil and air, but more precipitation means more moisture (Waser and Price 2016; Corbet et al. 1979; Powers et al. 2021).

Nectar quality plays a major role in the plant-pollinator relationship, a prime example of mutualistic coevolution where flowers evolve traits that maximize pollination and pollinators evolve traits and strategies to maximize nectar consumption. For example, bees extract nectar through a straw-like mouthpart using active suction, so they prefer flowers with higher nectar concentrations (~35% on average) to maximize energy gain (Kim et al. 2011; Pyke and Waser 1981).

Hummingbirds and the flowers they prefer also show strong signs of coevolution. "Typical" hummingbird flowers are ones with elongated corollas to match the birds' long beak, and vivid red coloring to both attract birds and deter bees (Cronk and Ojeda 2008). They also possess an optimal hummingbird nectar concentration of ~20-25% (Pyke and Waser 1981). This optimum reflects a trade off in efficiency in terms of foraging style. Hummingbirds rely on

capillary action to extract nectar while hovering, meaning they will benefit more from dilute nectar in terms of time:energy-gain trade-off since dilute nectar is faster to extract digest (Baker 1975). Moreover, hummingbirds do not consume water by itself, and obtain it purely from nectar; therefore, a higher water percentage in nectar would be beneficial when water loss from activity and high air temperature may affect osmotic homeostasis (Baker 1975, Calder 1979). Experiments have shown that hummingbirds decrease nectar volume intake as sucrose concentration increases, yet this does not change despite a drop in temperature, suggesting a physiological constraint in gut function and further emphasizing the importance of an optimal nectar concentration (McWhorter and Martínez del Rio 2000).

Nonetheless, hummingbirds still reach for atypical flowers quite often. Waser et al. 2018 has shown that these choices are not coincidental due to plant species range overlap; atypical flowers can be as energetically beneficial as typical ones when we take travel distance and type of flower (eg. bush) into consideration. Experiments have also shown that experimental birds preferred higher sucrose concentrations of 35-40% as opposed to their wild counterparts (Kim et al. 2011; Tamm and Gass 1986; Pyke and Waser 1981). This can be due to an laboratory setting where nectar is readily available in large quantities and temperature conditions are controlled as opposed to a natural setting, emphasizing the interaction between different environmental factors in the birds' foraging preferences.

Since there is little information on how nectar quality varies throughout Broad-tailed hummingbirds' breeding season, I will address this gap by collecting nectar concentration and volume data across the field season, and analyze how it correlates with hummingbird foraging patterns, and how it varies in relation to environmental factors like temperature and precipitation.

Direct effects of climate change on hummingbird foraging behavior due to dramatic weather patterns

1. Temperature

As mentioned above, temperature can affect phenology and resource availability for the hummingbirds during their breeding season by influencing snowmelt timing (Cleland et al. 2007). It can also play a more direct role in Broad-tailed hummingbirds' activities by affecting their thermoregulation. The birds' small body size results in a high surface area to volume ratio, allowing for more heat loss. Combined with little to no fat reserve in their body, along with a high daily energy expenditure due to their high wing beat rate, the birds have more difficulty with thermoregulation in lower temperatures. This can lead to a state of inactivity called 'torpor' when hummingbirds do not have enough energy reserve to keep warm, often occurring at night when temperatures drop (Calder and Booser 1973).

High temperatures also pose risks to the birds' homeostasis. Hummingbirds are diurnal: they are active during the day. These birds rely on nectar for both energy and hydration. The high surface area:volume again means the birds are more susceptible to dehydration in a dry and hot environment. For this reason, hummingbirds are not usually active during peak sun and heat hours (Calder 1975).

In a previous preliminary study, my colleagues and I found that temperature fluctuations by day and between year show no significant correlation with hummingbirds foraging patterns (Kim et al. 2023, unpublished manuscript). However, given the birds have a variable preferential window of activity (Calder 1975), I will be further analyzing how temperature fluctuations *by the hour* might correlate with Broad-tailed hummingbird feeding behavior, as well as how it correlates with other environmental factors.

2. Precipitation

Another weather factor affected by climate change is precipitation. Rainfall can decrease foraging time in birds as wet plumage can induce heat loss and impair flight capabilities (Stalmaster and Gessaman 1984; Ortega-Jimenez and Dudley 2012). Little is known about Broad-tailed hummingbirds' response to precipitation at RMBL. Therefore, I will be exploring whether a day with more precipitation can decrease hummingbird foraging rate, or in other words, how resilient they are against varying levels of rain.

Research questions and Hypotheses

One project focused on Broad-tailed hummingbirds at RMBL is called HummerFlowerWatch (HFW), organized by the Stoddard Lab in Princeton University's Department of Ecology and Evolutionary Biology. Every year since 2018, the lab has placed camera traps to document the feeding habits of the birds, from what flower species they prefer, to how often they feed on each. Since 2022, the project also includes collecting transect data, with 7 plots in total spread across our sites. Based on my literature review above, I have discovered that not many studies on Broad-tailed hummingbirds have scrutinized their foraging behavior on the basis of temperature, precipitation, snowmelt, floral abundance and especially nectar quality over multiple breeding seasons. I will integrate different datasets on these environmental factors to grasp a better understanding of Broad-tailed hummingbird foraging behavior. My hypotheses and predictions are as follows:

1. *Effects of different environmental factors on Visitation Rate:* I hypothesize that temperature, precipitation, snowmelt and floral abundance all have individual effects on Broad-tailed hummingbird visitation rate.
 - a. Temperature

I predict a negative relationship between temperature and hummingbird activity due to increased risk of dehydration. Since I am looking at temperature on an hourly basis, I predict less activity in hours with higher temperatures (noon-early afternoon) and more activity at dusk and dawn.

b. Precipitation

I would expect a negative correlation between precipitation and visitation rate due to impaired flight and thermoregulation.

c. Snowmelt and Floral Abundance

I expect earlier snowmelt years to correspond with higher early-season floral density. I also predict an inverse relationship between floral abundance and visitation rates due to the reduced need for frequent foraging.

2. *Variation of Nectar Quality throughout the breeding season and its relationship with hummingbird Visitation Rate:* I hypothesize that typical and atypical hummingbird flowers' nectar quality (volume, concentration) will differ throughout the 2024 field season.

a. Nectar Concentration vs. Nectar Volume

Typical hummingbird flowers will have lower nectar concentrations and higher volumes to suit the birds' capillary action feeding strategy. Atypical hummingbird flowers will have higher nectar concentrations and lower volumes because they do not cater to the birds' preference but rather different pollinators like bees, who prefer more sugary nectar.

b. Nectar vs. Visitation Rate

Typical flowers will receive more hummingbird visits. Atypical flowers will receive less hummingbird visits.

3. *How Nectar Quality ties in with other environmental factors*: I hypothesize that precipitation and temperature will affect nectar quality. Specifically:

a. Precipitation vs. Nectar Quality

I hypothesize that precipitation will increase soil and air moisture, diluting nectar.

Therefore, I expect a negative relationship between precipitation and nectar concentration, and a positive relationship between precipitation and nectar volume.

b. Temperature vs. Nectar Quality

I hypothesize that higher temperatures will cause water loss for the flowers. Therefore, I predict a positive relationship between average daily temperature and nectar concentration, and a negative relationship between temperature and nectar volume.

METHODS

HummerFlowerWatch camera trap data

Every summer, interns in the Stoddard Lab place camera traps along the project's three research sites: Stupid Falls, Judd Falls and Townsite (Figure 2). I contributed to data collection in the summers of 2023 (as a research intern) and 2024 (as a thesis student). We used Brinno TLC200 cameras starting in 2022 (Brinno, Taipei City, Taiwan), putting them in transparent waterproof cases rested on a tripod. For taller flowers such as *Delphinium barbeyi* and *Aconitum columbianum*, we attached the cameras onto a 1m stake, allowing for a better view of the plant.

We placed cameras on flowers in good condition: at least nearly full bloom and no signs of wilting. The flower species chosen are ones established in previous literature as hummingbird flowers, or through personal observations communicated by RMBL scientists and Stoddard Lab members (Table 1). Each time a camera was placed, we recorded the location coordinates on a Garmin GPS unit (Garmin GPSMAP 64s, Garmin Ltd., Olathe, KS, USA) to recover it in the next rotation. This also allows us to analyze location's effect on hummingbird feeding patterns.

We operated on a three-day rotating schedule, alternating between each site each day. For example, on a Judd Falls day, we collected cameras placed on the trail, changed the batteries and SD cards, and placed the cameras onto new plants. The next day, we repeated the same procedures for cameras placed on the Stupid Falls trail, and the day after, cameras placed around the townsite. The time-lapse cameras take a photo every second from 5AM to 9PM during sunlight hours. In 2024, the project had up to 21 cameras dispatched at any given point during the season.

To minimize potential confounders and disturbances, we took a few measures: Cameras of the same species are placed ~100m away from each other to account for location; they are

placed at least 50ft off trails and pointed away from the path to avoid human detection, especially on the public Judd Falls trails.

Afterwards, data in the collected SD cards are copied onto hard drives and run through *DeepMeerkat*, an AI program specialized in detecting hummingbird motion (Weinstein 2018). The data is further sifted through by Stoddard Lab members and volunteers to filter out false-positive images, and record additional information such as bird sex (if identifiable), date and time.

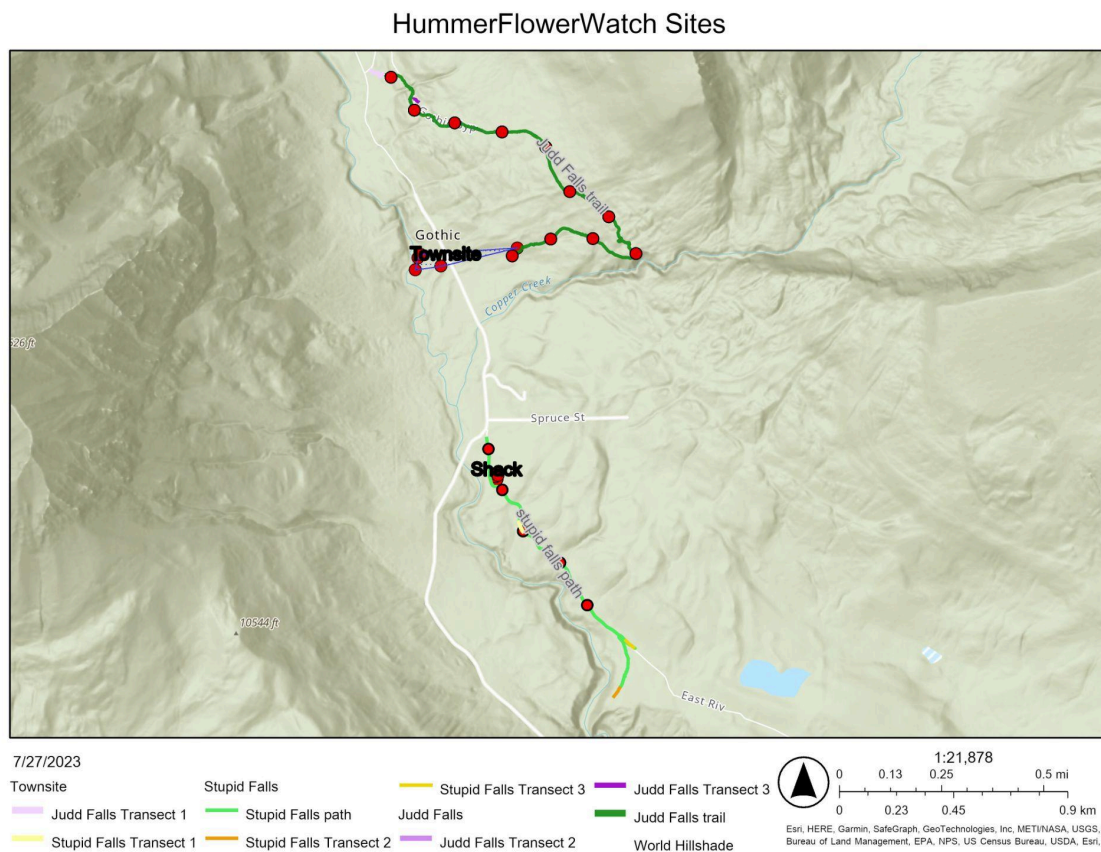
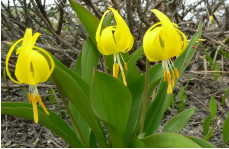


Figure 2. HummerFlowerWatch project's sites for camera trap and transect data collection (Kim et al. 2023).

FLOWER SPECIES IN HUMMERFLOWERWATCH CAMERA TRAP STUDY			
 Glacier lily (<i>Erythronium grandiflorum</i>) Late May - Early June	 Oregon grape (<i>Mahonia aquifolium</i>) Early June	 Creeping Oregon grape (<i>Mahonia repens</i>) Early June	 Bluebells (<i>Mertensia fusiformis</i>) Early June
 Nuttall's larkspur (<i>Delphinium nuttallianum</i>) Early June	 Willow (<i>Salix</i> spp.) Early June	 Western red columbine (<i>Aquilegia elegantula</i>) Mid-June	 Twinberry honeysuckle (<i>Lonicera involucrata</i>) Mid-June
 Rocky Mountain iris (<i>Iris missouriensis</i>) Mid-June	 Currant (<i>Ribes</i> spp.) Mid-June	 Western wallflower (<i>Erysimum capitatum</i>) Mid-June	 Mountain bluebells (<i>Mertensia ciliata</i>) Mid-Late June
 Scarlet gilia (<i>Ipomopsis aggregata</i>) Late June	 Bracted lousewort (<i>Pedicularis bracteosa</i>) Late June	 Monument plant (<i>Frasera speciosa</i>) Late June	 Towering Jacob's ladder (<i>Polemonium foliosissimum</i>) Late June - Early July

 Wyoming paintbrush (<i>Castilleja linariifolia</i>) Late June - Early July	 Giant red Indian paintbrush (<i>Castilleja miniata</i>) Late June - Early July	 Sulphur Indian paintbrush (<i>Castilleja sulphurea</i>) Late June - Early July	 Rocky Mountain penstemon (<i>Penstemon strictus</i>) Early July
 Rydberg's penstemon (<i>Penstemon rydbergii</i>) Early-Mid July	 Giant lousewort (<i>Pedicularis procera</i>) Early-Mid July	 Yellow toadflax (<i>Linaria vulgaris</i>) July	 Rocky Mountain columbine (<i>Aquilegia caerulea</i>) July
 Parry's bellflower (<i>Campanula parryi</i>) July	 Harebell (<i>Campanula rotundifolia</i>) July	 Columbian monkshood (<i>Aconitum columbianum</i>) July	 Tall/Subalpine larkspur (<i>Delphinium barbeyi</i>) July

 Fireweed (<i>Chamerion angustifolium</i>) July	 Thistle (<i>Cirsium spp.</i>) Early August	 Fringed gentian (<i>Gentianopsis thermalis</i>) Early August	 Parry's gentian (<i>Gentiana parryi</i>) Early August
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Table 1. Flower species included in the camera trap data collection. Species in red are included in 'Nectar measurements' data collection, but only highlighted species are ones considered in the analyses. Cells highlighted in pink are typical hummingbird flowers.

Temperature data

Since our project in 2023 did not find any correlation between hummingbird foraging patterns and daily average, minimum and maximum temperatures, I decided to look deeper into temperature fluctuations by hour (Kim et al. 2023, unpublished paper). For this, I used data from a weather station near RMBL (station AN097; Synoptic Data 2024). I also used the temperature data available in the same dataset in *Precipitation* for daily average temperatures.

Precipitation data

I used residential scientist billy bar's RMBL precipitation data on the Western Regional Climate Center website (WRCC 2024). Precipitation rate is measured in Inches/Hour.

Snowmelt data

I used RMBL residential scientist billy barr's data (barr n.d.). I used the date of first ground exposure at Gothic weather station as an index for snowmelt date, compared how early/late it is between the years of the study, and analyzed it with other variables.

Floral abundance data

We started collecting transect data in 2022. There are three transects established on the Stupid Falls trail and three on the Judd Falls trail; as of 2024, we added one more transect to the Judd Falls trail due to the high abundance of flowers on the trail (Table 2).

We collected transect data once a week for both locations, coinciding with every other rotation in *HummerFlowerWatch camera trap data*. We walked along each transect and counted the number of plants and the number of flowers on each 2m in from the path's edge. For bush plants like *Salix spp* and *Lonicera involucrata*, we estimated the volume in m³

(length*width*height) and the percent of flowers in bloom. We then calculated floral abundance using the formula $\frac{\text{Number of Flowers}}{\text{Area of Transect}}$.

Transect	Coordinates	Length (m)	Area (m ²)	Commonly found species	Description
Stupid Falls 1 (SF 1)	Start: N38.95024° W106.98667° End: N38.94984° W106.98647°	50	200	<i>Ipomopsis aggregata</i> , <i>Delphinium barbeyi</i> , <i>Mertensia fusiformis</i> *	On a high traffic path in tall grass with lots of sun.
Stupid Falls 2 (SF 2)	Start: N38.94434° W106.98209° End: N38.94396° W106.98246°	50	200	<i>Castilleja sulphurea</i> , <i>Campanula parryi</i> , <i>Delphinium barbeyi</i> , <i>Mertensia ciliata</i> ,	On a high traffic path with lots of sun.
Stupid Falls 3 (SF 3)	Start: N38.94603° W106.98189° End: N38.94569°	50	200	<i>Delphinium nuttallianum</i> , <i>Delphinium barbeyi</i> , <i>Mertensia fusiformis</i> *	Similar to SF 1 but little to no traffic

	W106.98137°				
Judd Falls 1 (JF 1)	Start: N38.96605° W106.99337° End: N38.96600° W 106.99289°	50	200	<i>Aconitum columbianum</i> , <i>Aquilegia caerulea</i> , <i>Castilleja miniata</i> , <i>Chamerion</i> <i>angustifolium</i> , <i>Cirsium</i> spp., <i>Delphinium barbeyi</i> , <i>Hydrophyllum capitatum</i> , <i>Hydrophyllum fendleri</i> , <i>Ipomopsis aggregata</i> , <i>Mertensia ciliata</i> , <i>Mertensia fusiformis</i> *, <i>Polemonium</i> <i>foliosissimum</i> , <i>Salix</i> spp.,	On a steep, rocky path with lots of traffic
Judd Falls 2 (JF 2)	Start: N38.96394° W106.98840° End: N38.96413° W106.98898°	50	200	<i>Aconitum columbianum</i> , <i>Aquilegia caerulea</i> , <i>Erythronium</i> <i>grandiflorum</i> , <i>Chamerion</i> <i>angustifolium</i> , <i>Delphinium barbeyi</i> , <i>Mertensia ciliata</i> , <i>Mertensia fusiformis</i> *,	On two sides of an open path with ample shade and traffic
Judd Falls 3 (JF 3)	Start: N38.96512° W106.99153° End: N38.96503° W106.99123°	30	120	<i>Aquilegia elegantula</i> , <i>Castilleja miniata</i> , <i>Castilleja sulphurea</i> , <i>Cirsium</i> spp., <i>Delphinium</i> <i>nuttallianum</i> , <i>Mertensia</i> <i>fusiformis</i> *,	A creek bed with ample shade
Judd Falls 4 (JF 4)	N/A	25	100	<i>Aconitum columbianum</i> , <i>Aquilegia caerulea</i> , <i>Chamerion</i> <i>angustifolium</i> , <i>Delphinium barbeyi</i> , <i>Delphinium</i> <i>nuttallianum</i> , <i>Mertensia</i> <i>fusiformis</i> *, <i>Mertensia</i> <i>ciliata</i> , <i>Hydrophyllum</i> <i>capitatum</i> ,	A muddy patch on a hill with ample sunlight and high traffic

Table 2. Description of each transect in the HummerFlowerWatch project. Traffic often refers to human activities in the paths that the transects surround, though can sometimes include vehicles. **Mertensia fusiformis* is only counted by the number of stalks

Nectar measurements

I collected nectar measurements of 12 species of flowers from June 26 to July 24, 2024 at the Stupid Falls and Judd Falls site as outlined in *HummerFlowerWatch camera trap data*. Data collection was conducted over a two-day rotating schedule between sites. Out of the 12 species, the four with most data points were *Castilleja* spp. (excluding the white *Castilleja sulphurea*, only the red *C. linariifolia* and *C. miniata*), *Delphinium barbeyi*, *Ipomopsis aggregata* and *Mertensia ciliata*. These four species represent both typical hummingbird flowers (*I. aggregata* and *Castilleja* spp.) and atypical hummingbird flowers (*D. barbeyi* and *M. ciliata*). Moreover, since the other species have a proportionately low percentage of data points, I decided to only consider this subset of flower species in my data analysis. Some data points are left out of concentration analyses due to failure of measurement, whether due to exceeding refractometer range or loss of microcapillary tube.

To ensure the nectar was not consumed by pollinators at the time of collection, I haphazardly selected plants and bagged them two days before collection. This entails wrapping an appropriately sized piece of white fine-mesh netting over the flower, and securing it with a rubber band. Even though bagging usually only requires 24h for the flowers to efficiently produce nectar, I waited two days for ease of following the rotation schedule. I selected flowers in good condition and started bagging on June 24 for Judd Falls and June 25 for Stupid Falls. The flowers I chose were near where cameras were placed to control for location differences in the observed data. The locations of netted flowers were also recorded on a Garmin GPS unit for

easy tracking and analyzing location data (Garmin GPSMAP 64s, Garmin Ltd., Olathe, KS, USA)

After two days, I removed the nettings and inserted a Drummond brand microcapillary 5µl or 10µl glass tube into the nectaries of the flowers, which uses capillary action to draw out the nectar. The exact collection methodology and size of the tube depends on the species (Table 3). I decided what tube size and which refractometer to use for each species through trial and error and through determining which species are hummingbird flowers, which tend to have higher volume and lower concentration, and bee flowers with lower volume and higher concentration (Kim et al. 2011, Cronk and Ojeda 2008). Volume is estimated as $(\text{Percentage of tube filled}) \times (\text{Volume capacity of tube})$. I then gently blew the nectar onto a handheld refractometer (Fisherbrand™, Fisher Scientific, Hampton, NH, USA) and read the concentration, measured in degrees Brix.

Apart from nectar volume and concentration, I recorded the net and nectar collection date of the flower and time of collection. Other variables recorded but not considered in the analyses are the approximate temperature and humidity at the site, for which I used a SensorPush HT1 Smart Sensor (SensorPush, Brooklyn, NY, USA). I also recorded the weather conditions (Sunny, Rainy, Windy, Cloudy, or a combination) as well as rain status (Normal, Rain and After Rain).

Species	Sample size	Number of nectaries	Tube volume (µl)	Refractometer capacity (%)	Special methodologies
<i>Aconitum columbianum</i>	18	2	10	28-62	Remove both nectaries from the flower if necessary; draw out nectar and add up the total volume
<i>Aquilegia caerulea</i>	32	5	10	0-32	Due to the extremely elongated and skinny nectaries, remove all five

					nectaries from the flower by grabbing onto the tails and gently pull them away from the rest of the flower. Squeeze the nectar up towards the opening, enough for the microcapillary tube to reach in, and extract the nectar
<i>Aquilegia elegantula</i>	8	5	10	0-32	Similar to <i>A. caerulea</i>
<i>Campanula rotundifolia</i>	4	1	5	28-62	Nectary is at the base of the style and stigma, covered by small, stiff flaps that need to be pried open to access nectar
<i>Castilleja spp.</i>	66	1	10	0-32	One red bulb is actually an inflorescence consisting of multiple flowers, and the red “petal” is actually a bract. The stigma, stamen, nectary, etc. are enveloped in a green petal. Remove a flower, peel off the bract, squeeze the nectar up from the base, insert the microcapillary tube and move it around until no more nectar is drawn out. A good way to tell when the flower has no more nectar is when the ovary (bulb at the base of the flower) is enlarged
<i>Castilleja sulphurea</i>	28	1	5	28-62	Similar to <i>C. linariifolia</i> except the inflorescence is white
<i>Delphinium barbeyi</i>	83	2	5	28-62	Elongated nectaries have two chambers; add up the nectar volume from both chamber
<i>Delphinium nuttallianum</i>	33	2	5	28-62	Similar to <i>D. nuttallianum</i>

<i>Erysimum capitatum</i>	2	1	5	28-62	Insert microcapillary tube into slightly elongated nectary at the base of the style
<i>Ipomopsis aggregata</i>	57	1	10	0-32	Remove elongated trumpet-shaped flower from the receptacle, holding the tip of the flower.
<i>Mertensia ciliata</i>	48	1	5	0-32	Similar to <i>E. capitatum</i>
<i>Pedicularis procera</i>	4	1	5	28-62	Insert the microcapillary tube into the bean pod shaped petal until it reaches the base; move the tube around until no more nectar is extracted

Table 3. Specific methodology on collecting and measuring nectar volume for each flower species. Highlighted rows are species considered in the analyses.

Analysis

Linear regression analyses and graphs are all done using RStudio (Posit Team 2024). From linear models, I extracted F-statistic p-values to indicate statistical significance, R^2 and adjusted R^2 values to analyze how well the models fit my data: a small p-value (<0.05) AND large R^2 values (≥ 0.5) would indicate a well-fitting model, suggesting strong correlation between my variables. For analysis purposes, I defined Broad-tailed hummingbird breeding season as the duration of the year where we have camera trap data: Early June - Mid August. Therefore, when a graph or analysis is ‘separated by year’, each year will only include June, July and August.

The main index I used to quantify hummingbird foraging patterns is visitation rate, which is calculated as

$$\text{Visitation Rate} = \frac{\text{Number of Visits}}{\text{Total Observation Duration}}$$

Specific analyses for each section is as follows:

Effects of different environmental factors on Visitation Rate

1. Temperature

To calculate visitation here, I opted for total visit duration, which is the sum (in seconds) of how long the birds were recorded on camera at a certain hour. I elected to use this measurement instead of visitation rate so that the reported rates would be easier to interpret, since hourly visitation rates resulted in very low values. I created time series graphs for each month of camera trap data collection from 2018 to 2024. I then regressed visit duration against temperature, as well as accounting for hour and year as interaction terms to see whether adding predictors will fit a better linear model.

2. Precipitation

I created a time series graph for *daily* visitation rate versus daily precipitation rate, faceted by year (2018-2022). Then, I created a linear regression model to see how well precipitation predicts visitation. Since precipitation had many outliers, I also made a linear regression excluding those outliers.

3. Snowmelt and Floral Abundance

Since species abundance varied by transect, and not all transects are counted on the same day, grouping density by day would introduce fluctuations masking the overall trend. Therefore, I calculated species abundance *weekly* as well as the corresponding visitation rates. I created a time series graph for floral density of each species, separated by year (2022-2024), along with *weekly* visitation rate and week with snowmelt date as a vertical line.

Variation of Nectar Quality throughout the breeding season and its relationship with hummingbird Visitation Rate¹

1. Nectar Concentration vs. Nectar Volume

I made a linear regression to see the relationship between nectar volume and nectar concentration across the four flower species of interest (*Castilleja spp.*, *Delphinium barbeyi*, *Ipomopsis aggregata* and *Mertensia ciliata*). I also make a regression looking at Volume vs. Concentration with Species as an interaction term.

2. Nectar vs. Visitation Rate

Here, I calculated visitation rate in this analysis by date and species, meaning it is not calculated using data from all species on a given day, but only by the species of interest. I then made separate linear regressions of concentration vs. visitation rate and volume vs. visitation rate, both paired by date, and added Species as an interaction term.

How Nectar Quality ties in with other environmental factors

1. Precipitation vs. Nectar Quality

The analyses here are similar to those in nectar vs. visitation rate, but with precipitation instead of visitation rate.

2. Temperature vs. Nectar Quality

Since I consider nectar measurements to be a *daily* and not hourly measurement, I decided to use average daily temperature, which is calculated by the mean high and low temperatures in a day. I further examined the relationship between temperature and visitation rate for these four species by creating a time series plot and linear regression model.

¹ Nectar data is only available in 2024; therefore the analyses including nectar will only be 2024 data, whether it is camera trap, temperature or precipitation.

RESULTS

Overview

After 7 years of data collection, the HummerFlowerWatch project has accumulated 78,880 hours of camera trap footage data (See Appendix. Supplemental Figure 1 for total observation duration broken down by species).

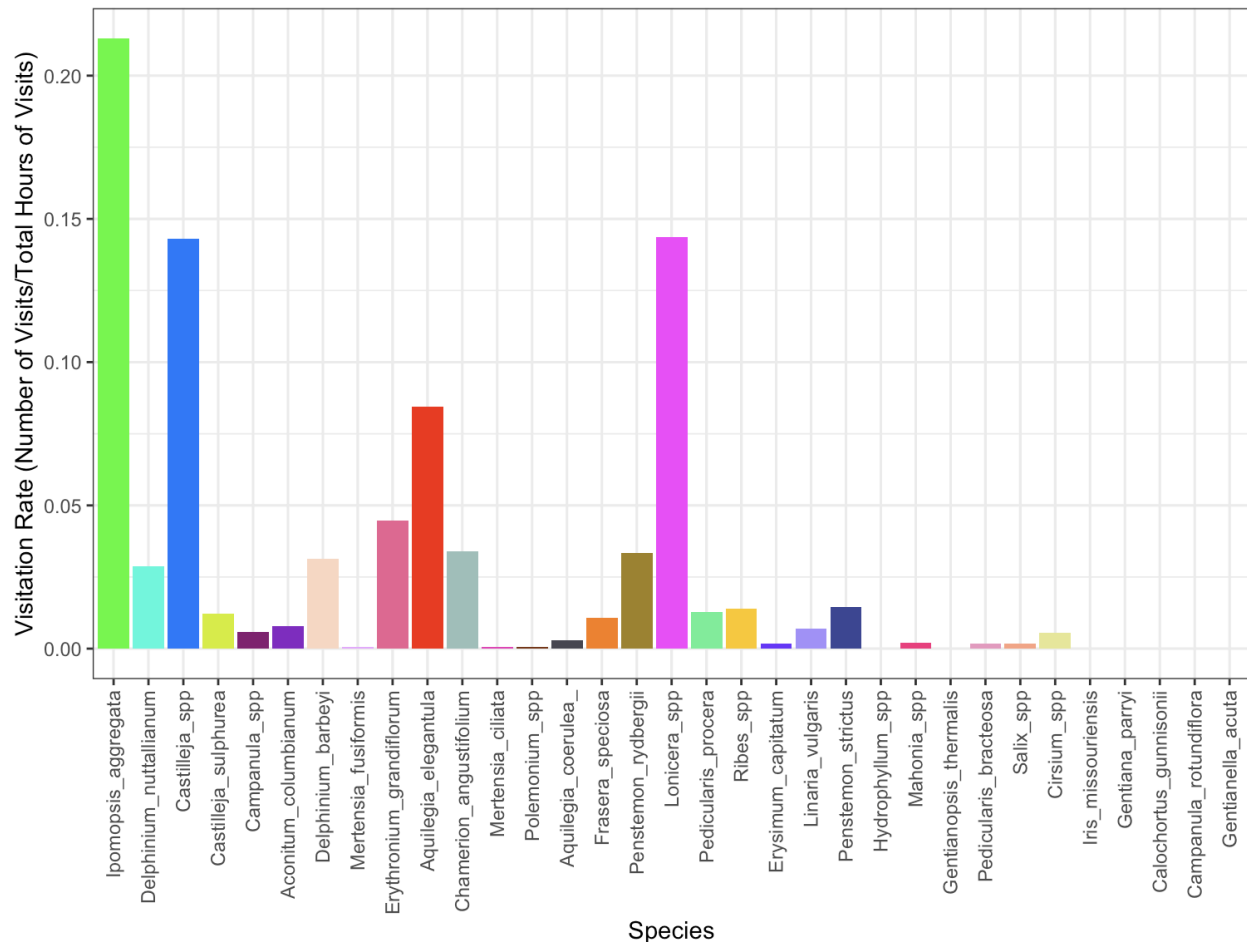


Figure 3. Visitation rate for species bar graph shows strong preference for typical hummingbird flowers. Top 10 most visited species in descending order are *Ipomopsis aggregata*, *Lonicera spp*, *Castilleja spp*, *Aquilegia elegantula*, *Erythronium grandiflorum*, *Chamerion angustifolium*, *Penstemon rydbergii*, *Delphinium barbeyi*, *Delphinium nuttallianum* and *Penstemon strictus*.

Results confirm Broad-tailed hummingbirds' bias for typical hummingbird flowers, with the top 4 species classified as typical hummingbird flowers (See Table 1): *I. aggregata* with a

visitation rate of 0.213, *Lonicera spp.* at 0.144, *Castilleja spp.* at 0.143 and *A. elegantula* at 0.0843.

Effects of different environmental factors on Visitation Rate

1. Temperature

Hourly temperatures follow a consistent pattern where the daily low is around 6am, and daily high around 4pm. Total visit duration pattern varies greatly by day, with some exhibiting peaks following the coldest morning hours and another peak roughly at the highest afternoon temperature hours (eg., 6/10/2018, 6/11/2018, 6/20/2018) (Figure 4). This trend is also seen across other months and years (Supplemental Figures 2-20).

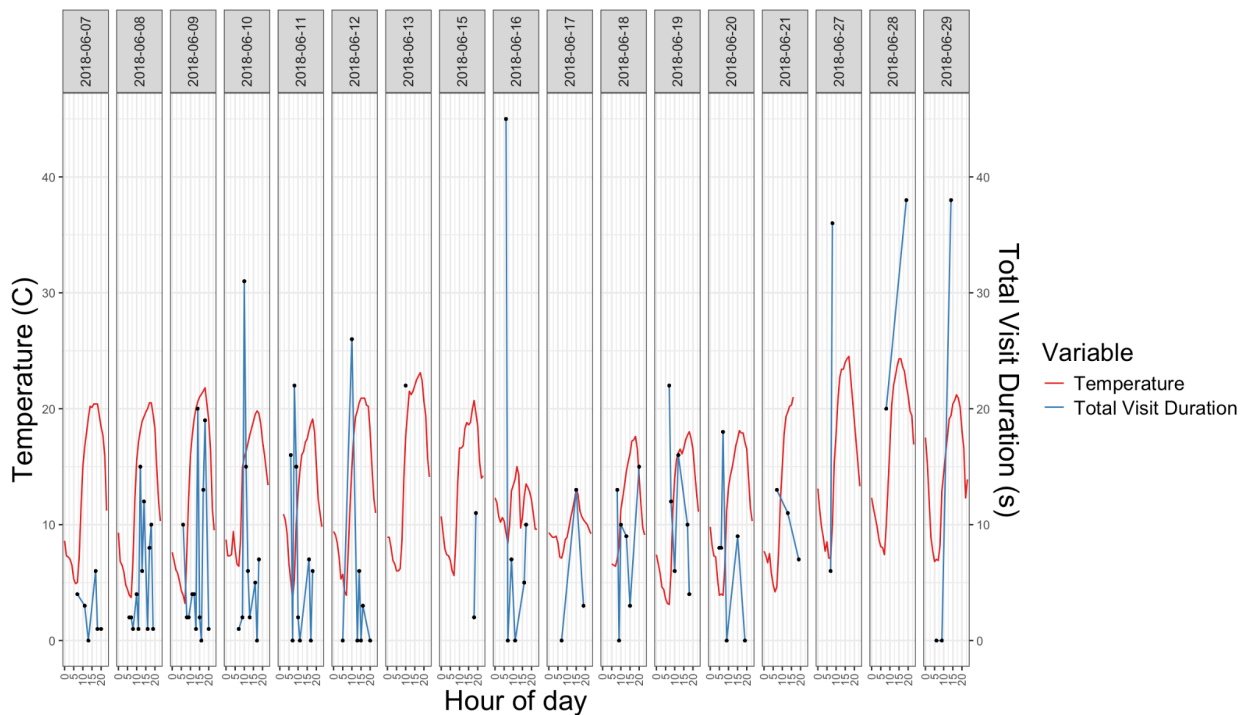


Figure 4. Time series graph for June 2018 of hourly temperature data (in Celcius, red line) against the total duration of visits (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs (See Supplemental Figures 2-20 to see graphs for 7/2018 - 8/2024). Statistics: visit duration and temperature: $p=0.183$, $R^2<0.001$, adjusted $R^2<0.001$; with hour as interaction term: $p=0.867$, $R^2=0.009$, adjusted $R^2=-0.004$; with hour and year as interaction terms: $p=0.087$, $R^2=0.104$, and adjusted $R^2=0.013$.

Despite some inherent behavioral patterns related to temperature, linear regression analyses reveal little statistical correlation between visit duration and temperature, even after fitting hour and year into the model. The linear model for visit duration and temperature has a p-value of 0.183 and low model fitting ($R^2 < 0.001$, adjusted $R^2 < 0.001$). With hour as an interaction term, F-statistic p-value=0.867, $R^2=0.009$, and adjusted $R^2=-0.004$. With both hour and year as interaction terms with temperature, p-value=0.087, $R^2=0.104$, and adjusted $R^2=0.013$.

2. Precipitation

Precipitation patterns varied substantially across seasons. Overall, daily rainfall at Gothic during the breeding season was fairly low (≤ 0.02 in/h). However, there are days such as 06/20/2021 where precipitation rate went up to 14.9in/h (Figure 5). Time series graphs show some mismatch between precipitation and visitation rate, more evident in 2020 and 2022. However, some visitation peaks align with precipitation, such as 08/02/2023 or 07/30/2019.

Daily precipitation rate correlates more with visitation rate if we omit outliers. With all data points included, the linear regression model does not fit our data as well, with $p=0.844$, $R^2 < 0.001$, and adjusted $R^2=-0.002$ (Figure 5). Without outliers, the model shows a slight negative correlation, with $p=0.020$, $R^2=0.014$, and adjusted $R^2=0.012$ (Figure 6). Adding year as an interaction term suggests no substantial difference in the relationship between visitation rate and precipitation across years despite great variation in both variables: with outliers, $p<0.001$, $R^2=0.122$, adjusted $R^2=0.099$; without outliers, $p<0.001$, $R^2=0.120$, adjusted $R^2=0.090$.

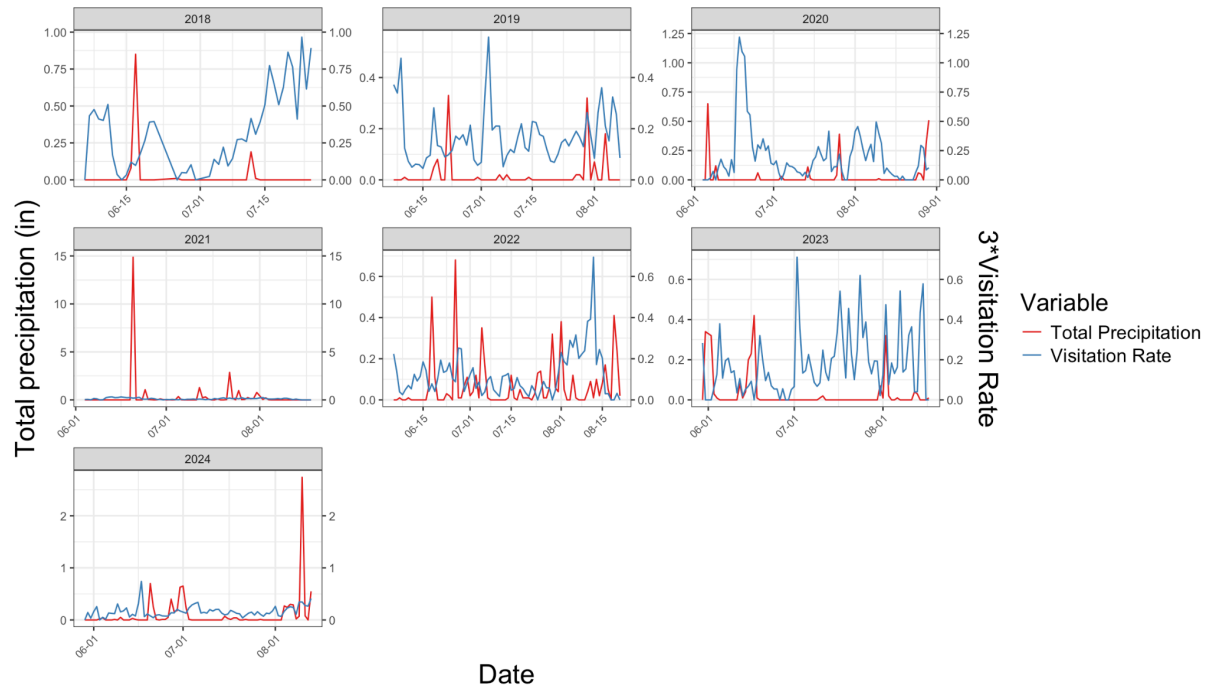


Figure 5. Time series graph of visitation rate (blue line) against total precipitation rate (red line) separated by year, with outliers. 2020 and 2022 show more inverse relationship between the two variables than other years, though some visitation peaks align with precipitation, such as 08/02/2023 or 07/30/2019. *Each year is scaled to fit the values available for easy viewing; neither axes are standardized. Visitation rate for all years is multiplied by 3 for scaling purposes.

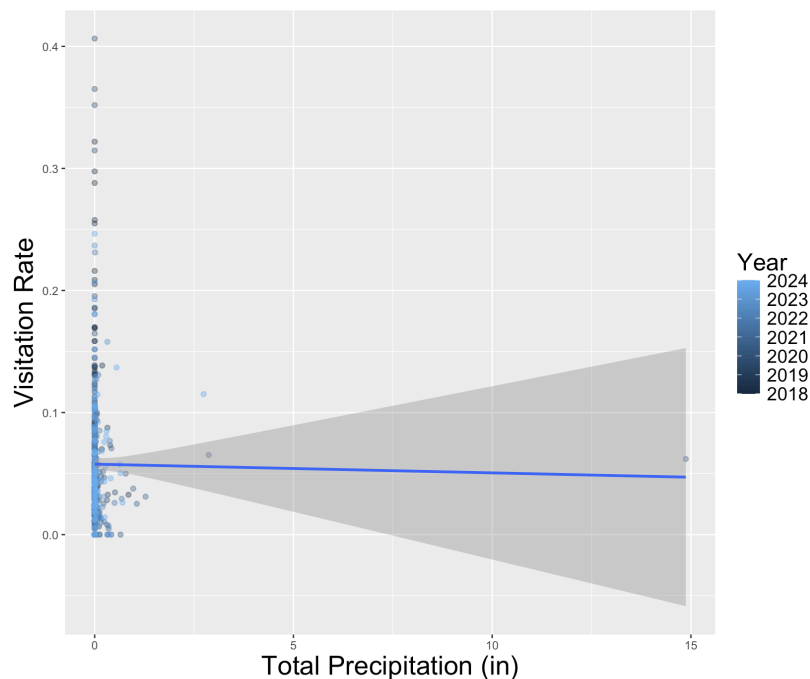


Figure 6. Linear regression (with outliers) for visitation rate against daily precipitation rate reveals no correlation (See Supplemental Figure 21 for the same graph excluding outliers). Statistics: $p=0.844$, $R^2<0.001$, adjusted $R^2=-0.002$.

3. Snowmelt and Floral Abundance

Figure 7 reveals the most abundant early season species is *Delphinium nuttallianum* and the most abundant late season is *Delphinium barbeyi* for all three years. Snowmelt date was earliest in 2022 on 5/12, latest in 2023 on 5/26, and 5/19 in 2024. Plant and flower density (Count per m²) vary greatly throughout those years (See Supplemental Figure 22 for plant density graphs).

In 2023 when snowmelt date is later, *Erythronium grandiflorum* and *D. nuttallianum* peaks are 2 weeks later than the other two years', and *D. nuttallianum* peak is shorter. Another early season species, *Mertensia ciliata*, saw large density at the start of the 2022 season, but not in the following years. There are no timing differences in *D. barbeyi*'s peak, though other late season species such as *Aconitum columbianum* saw a slight peak shift in 2023. 2024 saw higher density than 2022 and 2023 for *D. nuttallianum* early season, and *Aconitum columbianum*, *Aconitum columbianum*, *Castilleja spp*, *Mertensia ciliata*, etc. later in the season. Visitation rate showed mismatch with floral abundance, as seen around week 30 in 2022 and 2024, or week 27 in 2023. However, week 25 in 2024 and week 23-24 in 2022 showed both an increase in flower density and visitation rate.

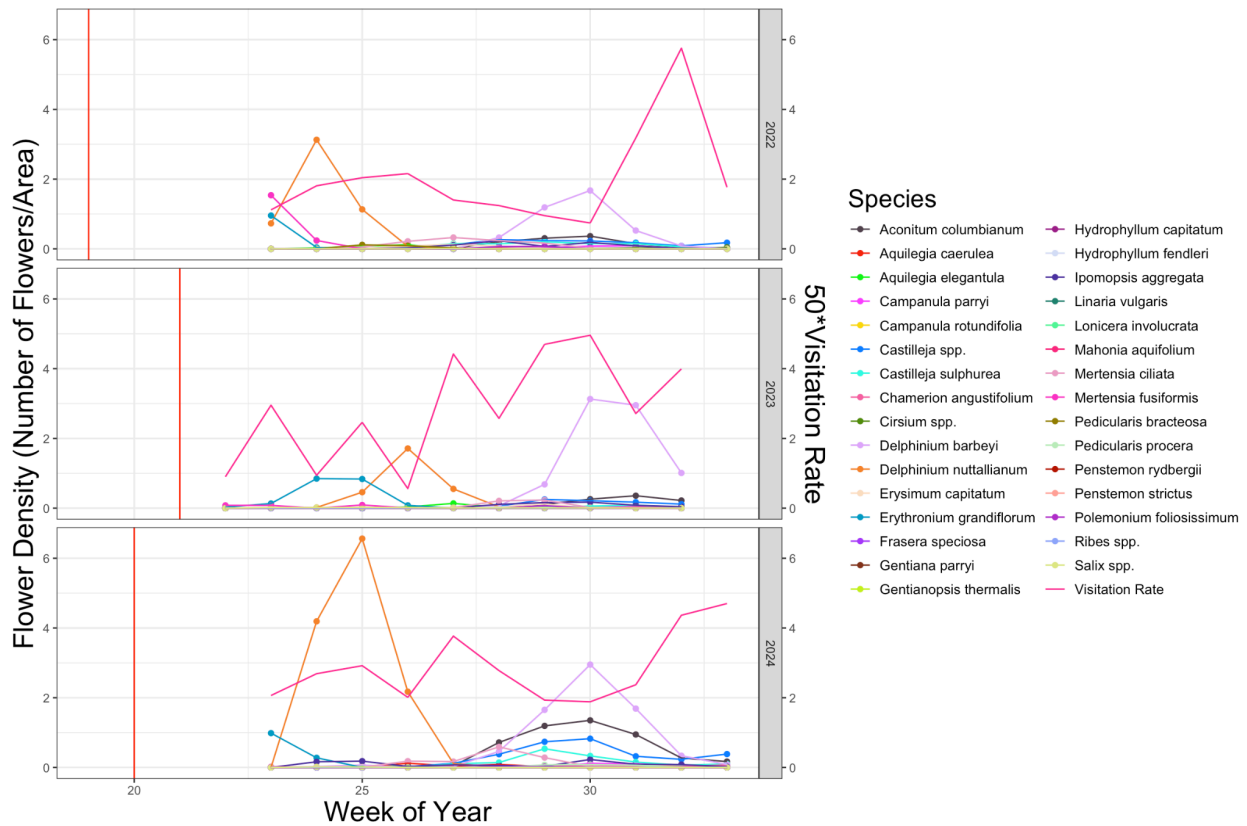


Figure 7. Flower density by species for each week of year. Snowmelt date is the red line, and weekly visitation rate is the magenta line. *D. barbeyi* is the most abundant species early in the season, and *D. barbeyi* is the most abundant later in the season. *Visitation rate for all years is multiplied by 50 for scaling purposes.

Variation of Nectar Quality throughout the breeding season and its relationship with hummingbird Visitation Rate

After 28 days of data collection, I obtained nectar measurements of 12 flower species and 384 flowers in total. The four species chosen for analyses (*Castilleja* spp., *Delphinium barbeyi*, *Ipomopsis aggregata* and *Mertensia ciliata*) showed varying visitation rates throughout the seasons (Figure 15).

Species	Number of flowers collected	Average Volume (μl)	Average Concentration (%)
<i>Delphinium barbeyi</i>	83	1.4	49.3

<i>Castilleja spp</i>	66	4.18	26.2
<i>Ipomopsis aggregata</i>	57	4.82	23.2
<i>Mertensia ciliata</i>	48	2.05	20.5
<i>Delphinium nuttallianum</i>	33	1.48	39.5
<i>Aquilegia caerulea</i>	32	16.8	26.3
<i>Castilleja sulphurea</i>	28	1.18	44.5
<i>Aconitum columbianum</i>	18	5.33	48.5
<i>Aquilegia elegantula</i>	8	4.16	18.1
<i>Pedicularis procera</i>	4	1.32	51.2
<i>Campanula rotundifolia</i>	4	2.3	33.8
<i>Erysimum capitatum</i>	2	0.2	53

Table 4. Count, average volume and average concentration for each species I collected nectar.

1. Nectar Concentration vs. Nectar Volume

There is a strong negative relationship between nectar volume and concentration for *Castilleja spp.*, *Delphinium barbeyi*, *Ipomopsis aggregata* and *Mertensia ciliata* all together (Figure 10). Broken down by species, *M. ciliata* and *D. barbeyi* show the same strong negative correlation, while *I. aggregata* show a weaker negative slope, and *Castilleja spp.*'s concentration remains constant despite volume (Figure 11).

It is also important to note that *D. barbeyi* flowers consistently had higher concentrations around 40-60% and low volumes of 0.5-2.5 μ l; *M. ciliata* has varied concentrations from 10-45% and low volumes of 0.1-4.5 μ l; *Castilleja spp.* has low-mid ranged volumes of 2-7.5 μ l and concentrations varying from 10-48%, and *I. aggregata* has the highest volumes from 3.5-11 μ l and concentrations of 17-36%.

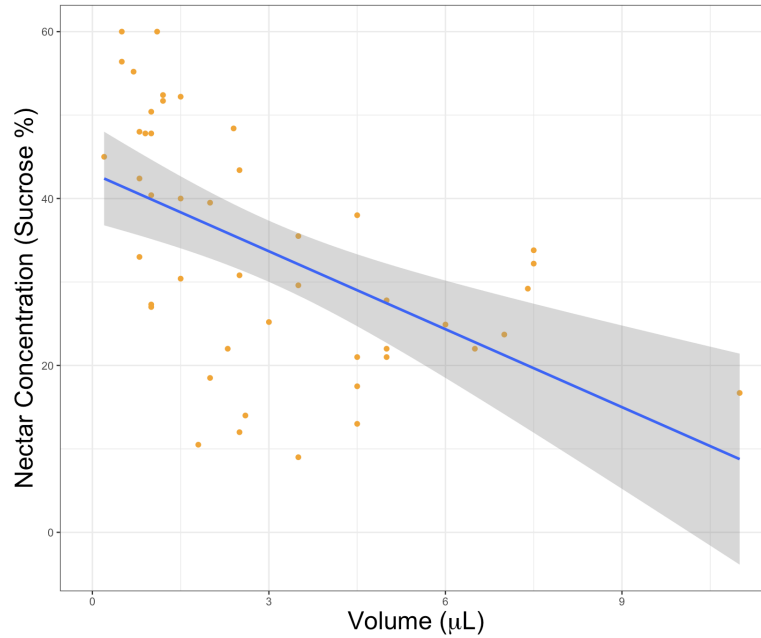


Figure 8. Linear graph of nectar volume vs. nectar concentration for *Castilleja spp.*, *Mertensia ciliata*, *Ipomopsis aggregata* and *Delphinium barbeyi*, showing a negative relationship. Statistics: $p < 0.001$, $R^2 = 0.281$, adjusted $R^2 = 0.265$.

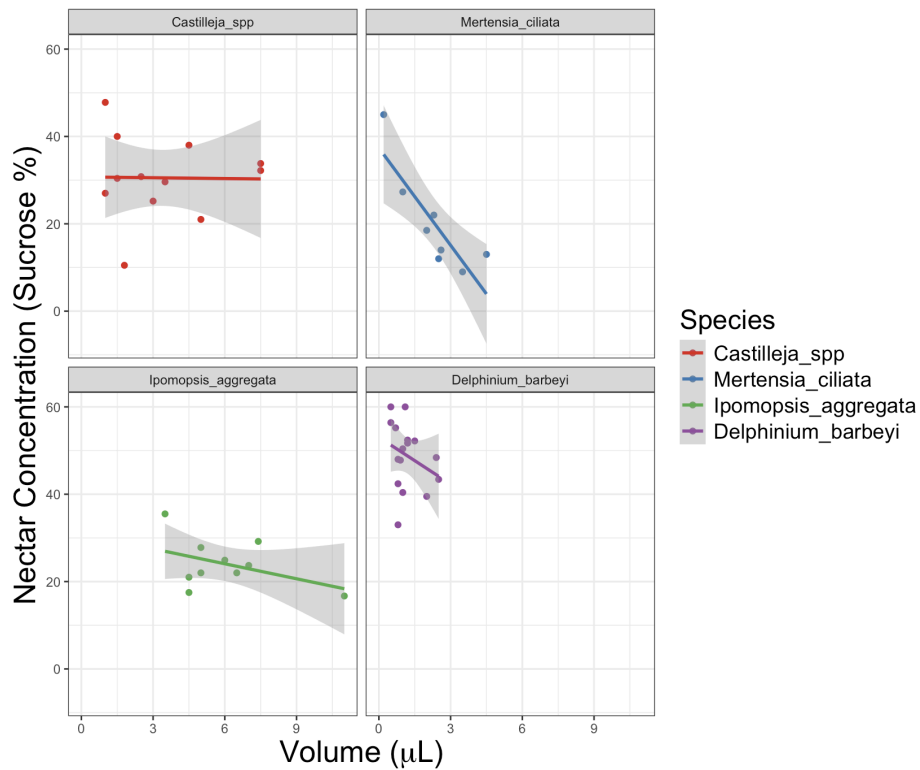


Figure 9. Linear graph of nectar volume vs. nectar concentration, broken down by the four species of interest, showing a negative relationship for all but *Castilleja spp.* Statistics: $p < 0.001$, $R^2 = 0.755$, adjusted $R^2 = 0.710$.

2. Nectar vs. Visitation Rate

Overall, nectar concentration had an inverse relationship with visitation rate while volume has a positive relationship with visitation rate with all 4 species (Figure 14). Visitation for *I. aggregata* increased with both nectar concentration and volume, while visits for *Castilleja spp.* slightly decreased for both nectar measurements. (Figure 15). There is a slight positive correlation for *D. barbeyi*'s concentration and visitation rate and a negative correlation for its volume and visitation rate.

It is important to note that on many nectar collection days for *D. barbeyi* and *M. ciliata*, we see no visitation for these two species; we recorded zero visits on *M. ciliata* over the duration of nectar collection and therefore see no trend for this species' nectar quality and visitation rate.

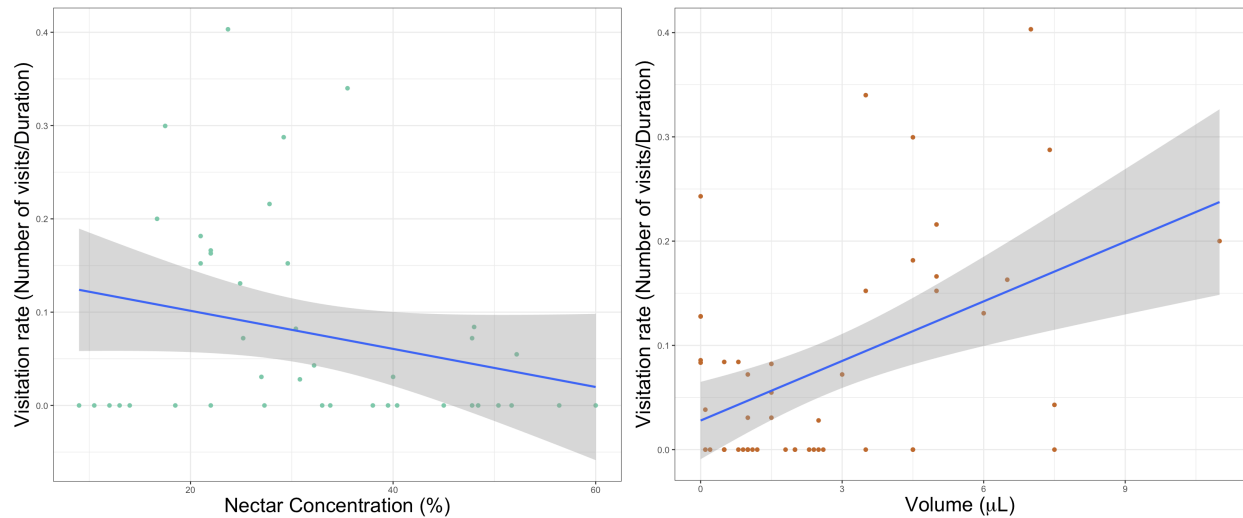


Figure 10. Nectar concentration for all four species has a negative correlation with visitation rate (left), while volume has a positive correlation (right). Concentration statistics: $p=0.106$, $R^2=0.066$, adjusted $R^2=0.042$. Volume statistics: $p<0.001$, $R^2=0.224$, adjusted $R^2=0.208$.

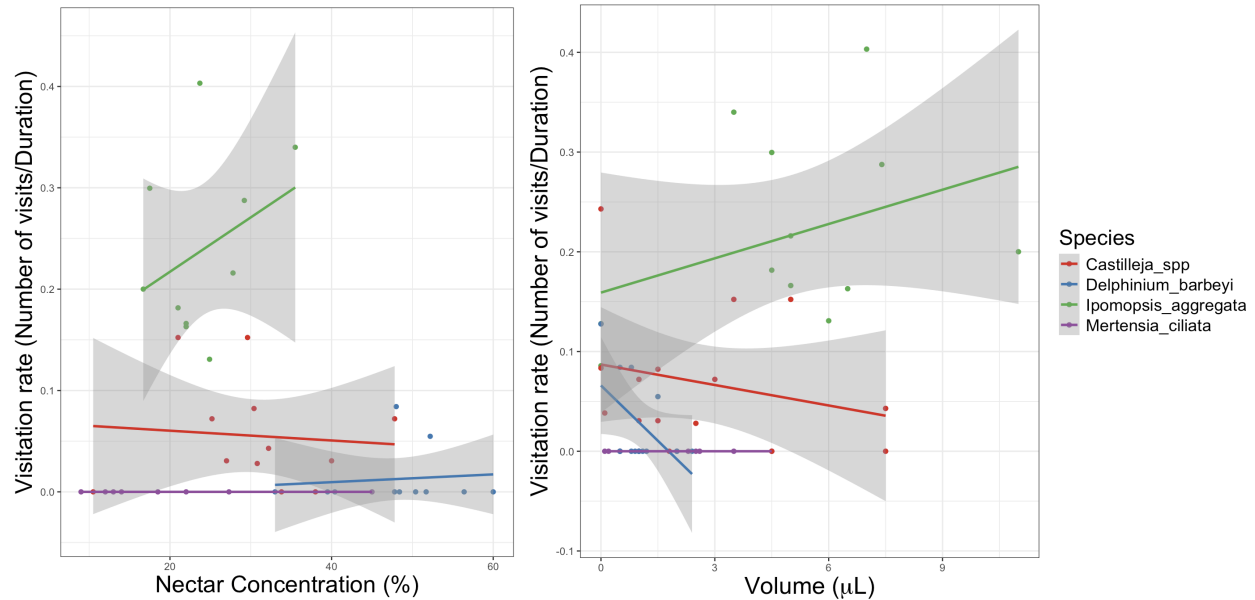


Figure 11. Nectar concentration (left) and volume (right) show varied relationships with visitation rate. Concentration statistics: $p < 0.001$, $R^2 = 0.783$, adjusted $R^2 = 0.737$. Volume statistics: $p < 0.001$, $R^2 = 0.682$, adjusted $R^2 = 0.631$.

How Nectar Quality ties in with other environmental factors

1. Precipitation vs. Nectar Quality

All four species together indicate a negative relationship between precipitation and nectar concentration, but no apparent trend for precipitation and volume (Figure 16). Individually, each species similarly shows a negative correlation for precipitation and concentration, while for volume, all but *D. barbeyi* indicate a negative relationship (Figure 17).

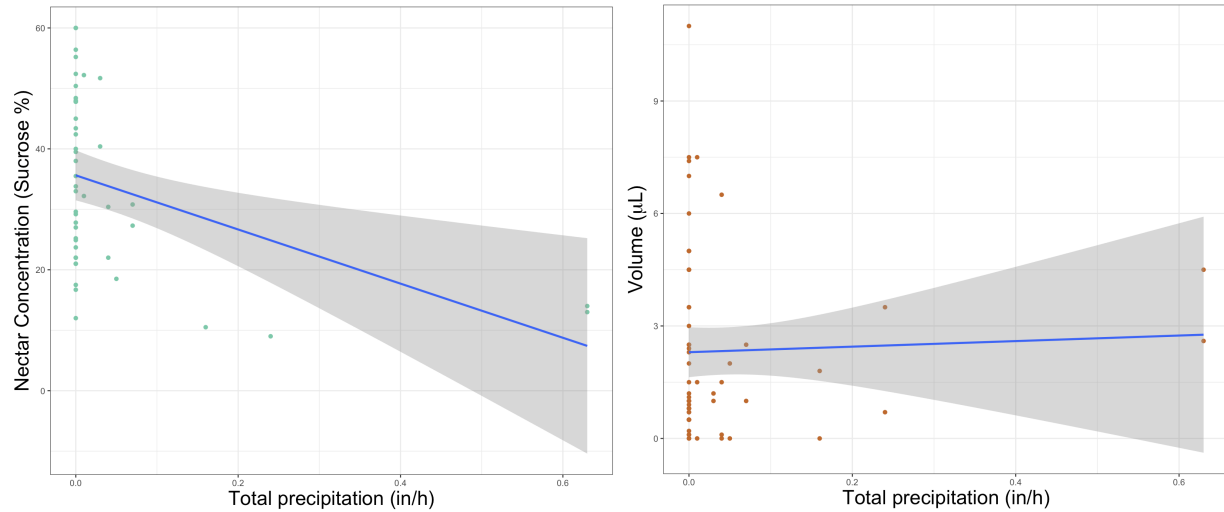


Figure 12. Nectar concentration for all four species has a negative correlation with precipitation rate (left), while volume has a slightly positive correlation (right). Concentration statistics: $p=0.004$, $R^2=0.174$, adjusted $R^2=0.155$. Volume statistics: $p=0.778$, $R^2=0.001$, adjusted $R^2=-0.016$.

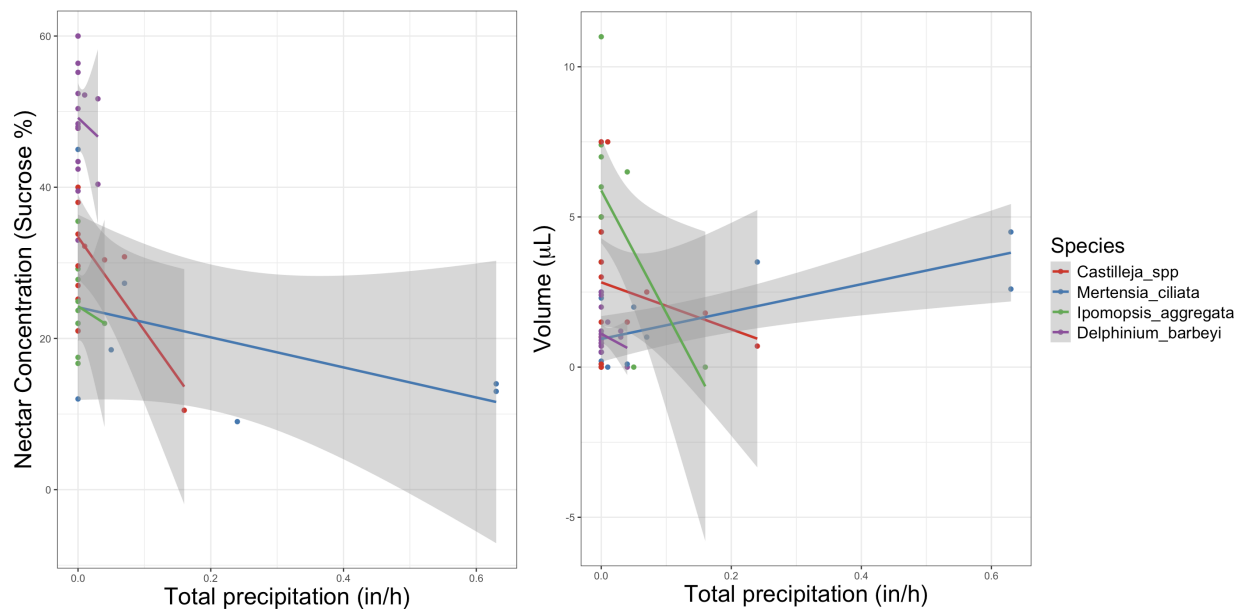


Figure 13. Nectar concentration for all four species has a negative correlation with precipitation rate (left), while volume has a slightly positive correlation (right). Concentration statistics: $p<0.001$, $R^2=0.733$, adjusted $R^2=0.684$. Volume statistics: $p<0.001$, $R^2=0.532$, adjusted $R^2=0.470$.

2. Temperature vs. Nectar Quality

For typical hummingbird flowers, nectar concentration does not correlate with temperature, but nectar volume shows a positive trend. Conversely, for atypical species, nectar

concentration shows a positive relationship with temperature, and a negative trend for nectar volume (Figure 19). Overall, concentration increases with temperatures for all four species, while volume shows no trend (Figure 18).

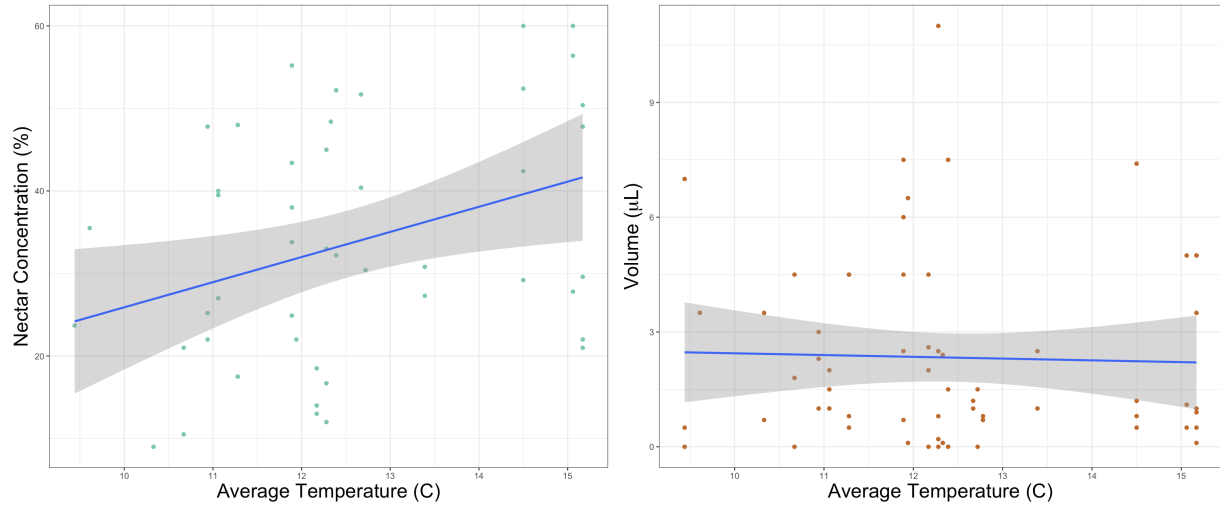


Figure 14. Nectar concentration for all four species has a positive relationship with average daily temperature (left). Volume shows no correlation with average daily temperature (right). Concentration statistics: $p=0.018$, $R^2=0.121$, adjusted $R^2=0.101$. Volume statistics: $p=0.810$, $R^2<0.001$, adjusted $R^2=-0.016$.

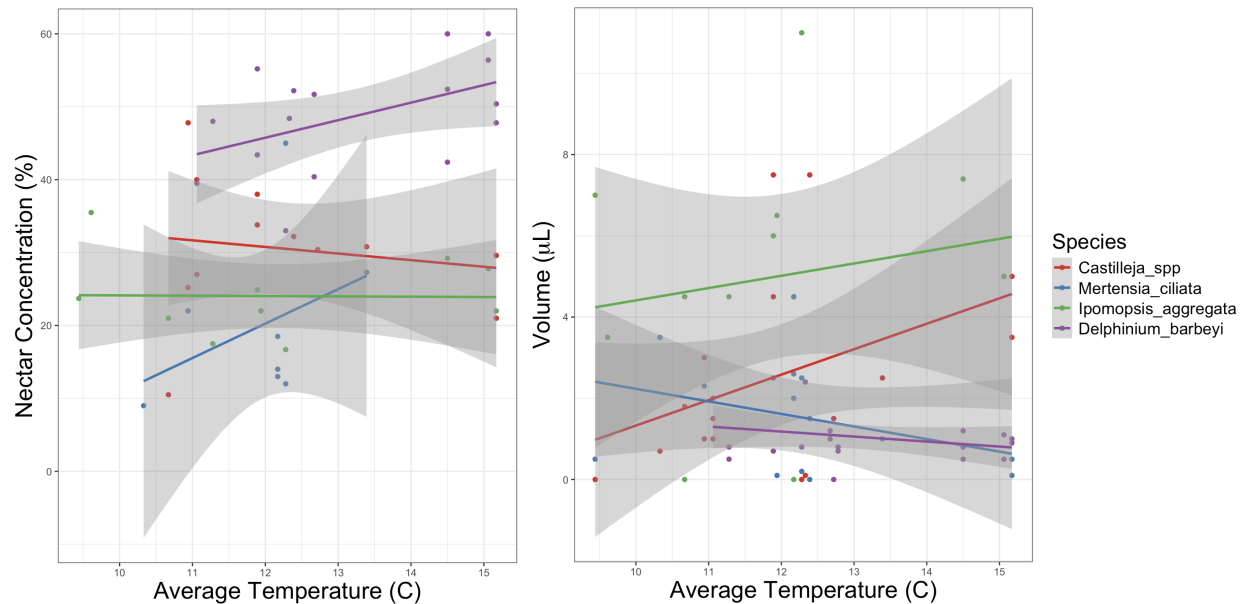


Figure 15. Nectar concentration (left) and volume (right) show varied relationships with average daily temperature. Concentration statistics: $p<0.001$, $R^2=0.705$, adjusted $R^2=0.651$. Volume statistics: $p<0.001$, $R^2=0.429$, adjusted $R^2=0.354$.

The time series plot for visitation rate with average daily temperature in the 2024 breeding season reveals mismatch between the two variables, particularly with the two typical hummingbird flowers. For example, DOY 186 shows a dip in temperature but a spike in visitation rate for *I. aggregata*, with a peak in *Castilleja spp.* and *D. barbeyi* a day before; day 216 shows the opposite where a temperature peak is present along with a drop in *I. aggregata* and *Castilleja spp.* visitation rate (Figure 20). The linear regression graph confirms this slight inverse relationship (Figure 21, bottom plot for 2024).

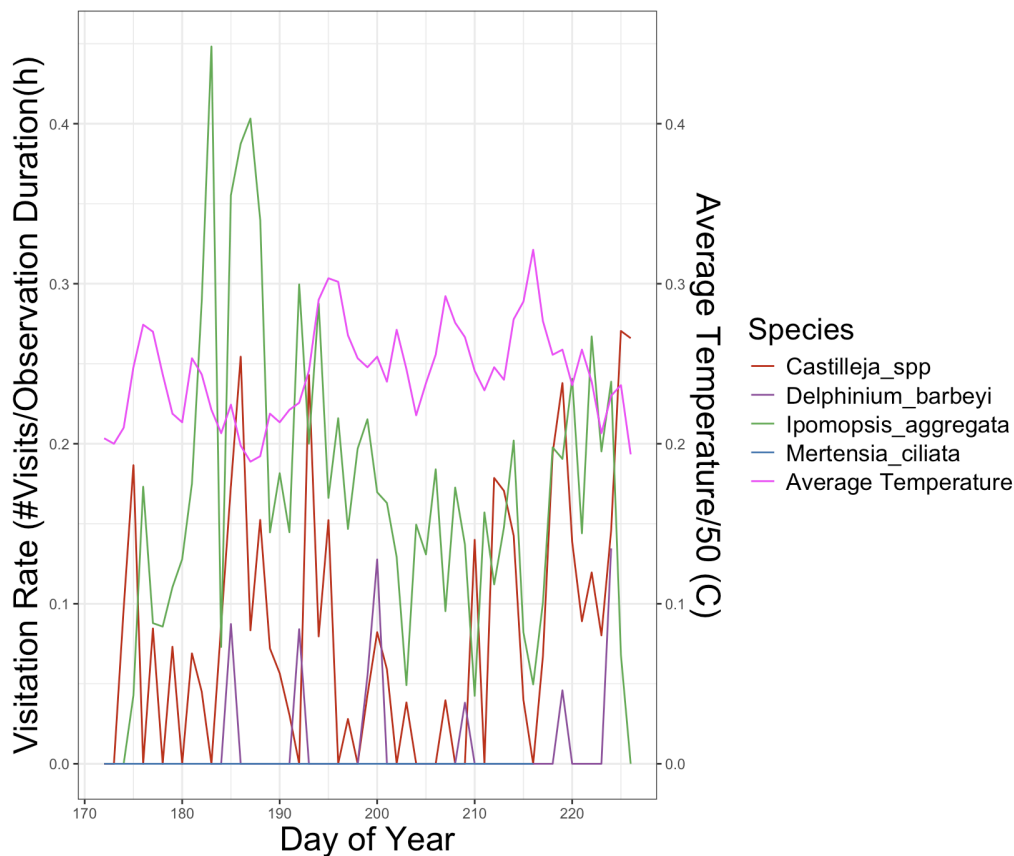


Figure 16. Time series graph for the four species' daily visitation rate in the 2024 breeding season reveals an inverse relationship with average daily temperature (magenta line). *Average temperature was divided by 50 for scaling purposes. Linear regression statistics for visitation rate against average daily temperature with species as an interaction term: $p < 0.001$, $R^2 = 0.511$, adjusted $R^2 = 0.492$.

However, this inverse relationship was not present in all years for all species: *I. aggregata*'s daily visitation rate increases as average temperature increases in 2018, 2019, 2021

and 2022 and decreases in 2020, 2023 and 2024 for example (Figure 21). A linear model predicting visitation rate based on average daily temperature from our data, accounting for species and year as an interaction term, yields adjusted $R^2=0.363$ and F-statistic $p<0.001$.

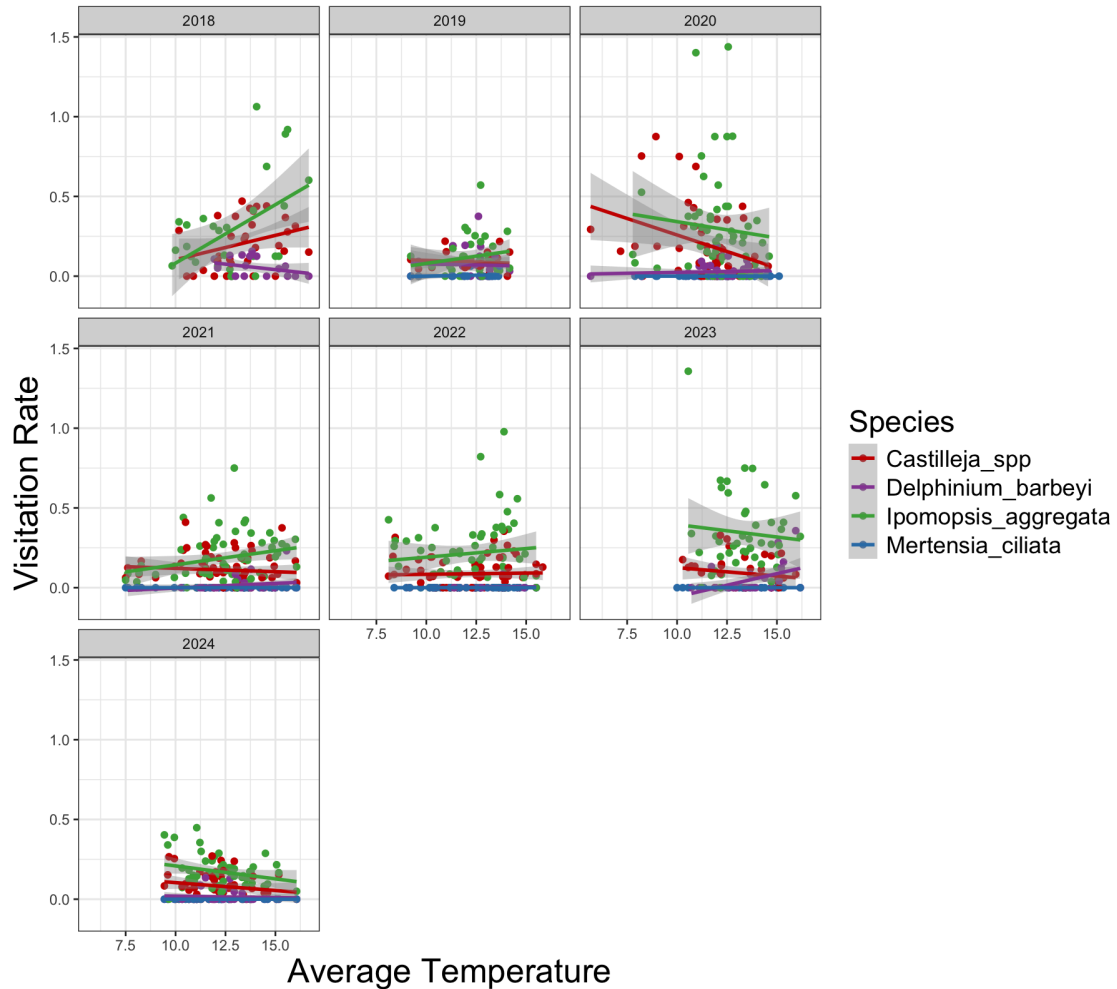


Figure 17. Linear regressions for the four species' daily visitation rate breeding season, all years, shows different relationships against average daily temperature depending on the year and species. Statistics: $p<0.001$, $R^2=0.394$, adjusted $R^2=0.363$.

DISCUSSION

Overview

This study is the first to analyze correlations between three abiotic environmental factors (temperature, precipitation snowmelt) and two biotic factors (floral abundance and nectar quality) using long-term datasets in conjunction with field nectar data collection. Past members in the Stoddard Lab and HummerFlowerWatch projects have individually explored average nectar concentrations, floral abundance and average daily temperature as factors influencing hummingbird visitation rate (Egar 2021, unpublished manuscript; Chang 2023, unpublished manuscript; Kim et al. 2023, unpublished manuscript). However, Egar et al. only compiled average nectar quality data of hummingbird flower species from pre-existing literature; Chang 2023 only analyzed one year of floral abundance data, and Kim et al. 2023 only examined temperature's effect on visitation on a daily basis. For my project, I expanded their findings by collecting nectar quality data over the field season, as well as utilizing the added years of data for camera trapping and transect, all while incorporating new variables like precipitation into the picture. I found many nuanced relationships between these variables, suggesting a complex, interconnected network of factors contributing to the birds' foraging decisions.

Effects of different environmental factors on Visitation Rate

1. Temperature

Hourly temperature fluctuations did not significantly correlate with Broad-tailed Hummingbird visitation rates across the breeding season. Statistical analyses show Broad-tailed hummingbird visits throughout the day were not correlated with temperature fluctuations (Figure 4). Prior studies suggested that hummingbirds are most active at sunrise to replenish after a cold night, and at sunset to fuel up for the night (Calder 1975). However, our results show even

though the birds do spend more time foraging at dawn, they spend more time mid-late afternoon than at sunset (Figure 4, Supplemental Figures 2-20).

Though the small R-squared values <0.001 and non significant F-statistic p-value of 0.183 do not suggest a strong deviation from the null hypothesis, it is important to note the small number of observations in each hour (Figure 4). Thus, the trend we see from the time series graphs can imply that hummingbirds prioritize foraging to make up for water loss rather than amassing energy to brace against the cold in contrast with Calder 1979, supporting part of my original hypothesis despite a lack of clear negative correlation between the variables.

2. Precipitation

There is little relationship between precipitation and Broad-tailed hummingbirds' visitation rate on a daily basis. Similar to hourly temperature, the linear regression models do not show much correlation between the two variables (Figure 6, Supplemental Figure 21). However, we can see in the time series graphs, especially including outliers, that higher visitation rate peaks tend to fall within periods of little to no rain, particularly at higher Precipitation Rates $>0.5\text{in/h}$ (Figure 5). Similar to observations by Stalmaster and Gessaman 1984 on the impact of rain on bird activity, our findings imply that heavy precipitation likely suppresses hummingbird foraging beyond a critical threshold; below that threshold, the birds' activity rate can vary depending on other factors. Therefore, the data supports my hypothesis that heavy rainfall decreases hummingbird foraging activity.

3. Snowmelt and Floral Abundance

Snowmelt timing significantly influenced early season flower phenology evident from only three years of floral abundance data, and consequently hummingbird visitation pattern throughout the breeding season (Figure 7). Results support my hypothesis as a year with earlier

snowmelt has earlier peak floral density; however, the relationship between floral abundance and hummingbird visitation rate varied across years and was not always consistent with initial expectations.

The 2023 season, characterized by later snowmelt, shifts early season species *E. grandiflorum* and *D. nuttallianum* peak abundance by a magnitude of week(s), corroborating findings in McKinney et al. 2012. The inverse relationship between floral density and visitation rate is more apparent in the latter half of the season in 2022 and 2024; visitation rate seems to increase with floral abundance at the beginning of the season, highlighting the need for newly migrated birds to refuel from their long-distance journey and perhaps prepare for the fluctuation cold temps at the time. However, 2023 deviates from this trend where the inverse relationship between visitation and flower density is more apparent at the start, and visitation seems to rise and fall with floral abundance later in the season, suggesting a shift in foraging pattern potentially due to delayed flowering and altered resource landscape. This corroborates earlier findings by Inouye 2008 and Inouye and McGuire 1991 linking higher snowpack to later snowmelt and shifted floral abundance.

Another point to note about 2024's higher floral abundance can be due to the addition of a new transect on our Judd Falls site. However, this transect's floral density is relatively low as the breeding season starts (Supplemental Figure 23). Therefore, this new transect only affected the *A. columbianum* peak late season; plot Stupid Falls 3 contributes the most to the *D. barbeyi* peak, and plot Judd Falls 3 contributed most to the *Castilleja spp.* peak. As a result, it is still reasonable to come to the inferences above about our floral abundance data despite the introduction of the new plot.

Variation of Nectar Quality throughout the breeding season and its relationship with hummingbird Visitation Rate

1. Nectar Concentration vs. Nectar Volume

Field-collected nectar data supports the hypothesis where *Castilleja spp.* and *I. aggregata* generally have lower concentrations and higher volumes than *D. barbeyi* and *M. ciliata*, reinforcing the hummingbird flower stereotype similar to findings in Pyke and Waser 1981 and Cronk and Ojeda 2008 (Figure 11; Figure 3). Species-specific regressions revealed that nectar quality was highly dependent on the species, with stronger model fits when species were regressed individually (Figure 9).

Notably, the atypical species show a strong negative slope, indicating a dilution effect, possibly driven by precipitation or temperature. In contrast, typical flowers show constant concentration regardless of volume change, perhaps maintaining a preferential optimum for their pollinators (Figure 9). I will discuss these effects further in the next sections.

2. Nectar vs. Visitation Rate

Analysis on the species level shows each's quality has a different correlation with visitation rate (Figure 11). Again, the linear regression model showed higher fit to the data if we incorporate species as an interaction term, suggesting visitation rate is also dependent on the species. Typical species exhibited overall higher Visitation Rate than the atypical species (Figure 11), contrary to the findings in Tamm and Gass 1986 where hummingbirds reached for more concentrated nectar in a laboratory setting, highlighting the importance of studying nectar preferences in a natural setting. These findings also align with the evolutionary expectation that hummingbirds prefer flowers that match their sensory and foraging adaptations (Cronk and Ojeda 2008; Pyke and Waser 1981).

How Nectar Quality ties in with other environmental factors

1. Precipitation vs. Nectar Quality

As predicted, nectar concentration decreases with increased precipitation, but volume did not increase with more rainfall: *D. barbeyi* is the only species whose volume went up with higher precipitation rate (Figure 17). One possible explanation is due to flower morphology. In the presence of rain, water falls into the nectaries and simultaneously dilutes the concentration, but a large accumulation of water would lead it to drop out of the flower, thus no increase in volume is seen for *Castilleja* spp., *Ipomopsis aggregata* and *Mertensia ciliata*. The reason why *D. barbeyi*'s volume increased with precipitation is due to its two-chambered nectary, for which each chamber is smaller than the other three species' singular-chambered nectary, allowing for more capillary action to retain water (Novikoff and Jabbour 2014).

If this hypothesis is incorrect, perhaps the flowers have a mechanism to regulate nectar volume and prevent nectar concentration from overdiluting, which may be energetically unfavorable for pollinators. In this case, *D. barbeyi* is an exception due to its naturally high concentration.

2. Temperature vs. Nectar Quality

“Typical” and “atypical” hummingbird flowers show different changes in nectar quality in response to daily temperature fluctuations. As shown in Figure 19, the two typical hummingbird flower species' concentrations remained stable despite fluctuating average daily temperature. On the contrary, the atypical species' concentrations increased with higher temperatures.

For nectar volume, the opposite trend emerged: *Castilleja* spp. and *I. aggregata*'s exhibited a positive correlation with temperature while *D. barbeyi* and *M. ciliata* showed a slight

negative correlation. My hypothesis that concentration increases with higher temperatures and volume decreases is supported by data of *D. barbeyi* and *M. ciliata*, but not by data from *Castilleja spp.* and *I. aggregata*.

These differential responses suggest a potential evolutionary advantage for typical flowers. On a hot day, not only do the concentrations of the typical flowers remain at an optimum for the birds' capillary nectar extraction, higher volume is beneficial to the bird's osmotic homeostasis and alleviating water loss on such days (Baker 1975; Calder 1979). This further supports the findings for visitation by hourly temperature, which suggested hummingbirds' foraging patterns are influenced by temperature-mediated water balance (Figure 4, Supplemental Figures 2-20). Apart from their red color catered to the birds' color vision and long corolla suited for the birds' long beak (Cronk and Ojeda 2008), these typical flowers' flexibility in nectar quality depending on environmental conditions may suggest a stronger coevolution than previously known, effectively maximizing the plant-pollinator dynamic across varying conditions.

Broad-tailed hummingbird visitation rate was inversely correlated to average daily temperature for typical hummingbird flowers only in some years. Based on nectar quality against temperature trends, I predict more visitation to *I. aggregata* and *Castilleja spp.* on hotter days, and less to *D. barbeyi* and *M. ciliata*. Similarly, Calder 1979 predicted an inverse relationship between temperature and optimal nectar concentration when we consider osmotic homeostasis, meaning they would reach for typical flowers with lower concentrations as temperature increases.

However, the data revealed more complexity. In 2024, visitation rates to typical flowers were inversely correlated with average daily temperature: hummingbirds visited these flowers

more frequently on cooler days (Figure 20; Figure 21). A similar trend was observed in 2020, while 2018 displayed the opposite pattern, with higher visitation rate on hotter days. This incongruence can be due to the nature of calculating visitation rate, which looks at the *number of visits* over an amount of time. For 2020 and 2024, it is possible that while the birds visit less typical flowers on a hot day, they may spend longer feeding on those flowers, consistent with the finding of positive correlation between typical flower volume and temperature (Figure 19).

Another explanation for interannual variation in species visitation against temperature trend considers other environmental factors. Considering how much snowmelt timing, precipitation and floral abundance vary across years, this emphasizes the complexity of how these factors interact to influence Broad-tailed hummingbirds' feeding behavior, whether by affecting their resource abundance or energetic constraints. Further analyses examining nectar quality changes across different breeding seasons may help clarify the observed year-to-year differences in Figure 21.

Limitations

It is important to acknowledge the short-comings of this study. First, analyses are purely correlational using linear regression models, which can imply little to no causal relationships between the variables despite revealing patterns. To further determine the relationship between these variables, it is necessary to conduct manipulated field experiments, such as using controlled temperature treatments, or utilize more complicated statistical approaches.

Second, there were logistical constraints limiting the number of data points for nectar quality. Due to the invasive nature of nectar extraction and the project's ethical guidelines, I was only able to collect at most three flowers of a species per day (Table 3). Additionally, since I opted for flowers located near HFW's transects, there were many species not considered in my

dataset. For example, nectar characteristics of highly visited species like *Lonicera spp.* may offer important insight and support for current results. Moreover, nectar data collection started later in the season, leaving out early species like *E. grandiflorum* and *M. fusiformis* that can help determine how energetically beneficial they are for newly migrated birds.

There were some technical challenges, one of which was flower morphology. Certain species in our transects like *Chamerion angustifolium* and *Salix spp.* were difficult to sample with microcapillary tubes due to complex or small floral structures. As a result, potentially important nectar sources for Broad-tailed hummingbirds were omitted from nectar quality analyses as *Chamerion angustifolium* resembles a typical hummingbird flower with high visitation rate (Figure 3), and *Salix spp.* bushes are a common territory for male birds (personal observation). Other technical challenges involved not bringing enough tools, bringing the right tools and collecting more data points as a one person effort.

Lastly, there is some bias to address surrounding our data. The trails where we set up camera traps and their transects have high traffic as popular tourist hiking trails (Figure 2). Human disturbances have been shown to have a wide effect on wildlife. For example, an experiment creating a phantom road effect by playing traffic noises has been shown to drive off bird species in the vicinity (Ware et al. 2015). A study on hummingbirds in Guatemala shows remarkable resilience to anthropogenic disturbances, though it is unclear whether the same trend applies to specifically Broad-tailed hummingbirds in a subalpine environment (Bustamante-Castillo et al. 2018). From personal and other scientists' observations, the birds exhibit little fear for human presence, often flying up to mere feet away from a person, and even nestling on top of personal belongings (pers. comm. Audrey Miller and Dr. Benedict Hogan). However, this can signify that even if the birds are not driven away by human presence

compared to a remote area, the presence of humans and our activities may alter their behavior. Therefore, our camera trap data may not reflect a representative behavioral image of the typical hummingbird population.

Apart from human disturbance, there is bias inherent in our flower selection process for the camera traps. Despite attempts to randomize flower selection and minimize proximity to human trails, the cameras are sometimes placed on a convenience basis due to logistical reasons, such as terrain accessibility or interference with other researchers' plot. Such decisions can influence visitation pattern as seen in *Lonicera spp.*, for which we saw a huge spike in visitation in 06/2024 due to bushes near feeder areas (Supplemental Figure 24).

Future directions

Apart from addressing the caveats above, I would like to address some factors that may confound with the ones examined in this study.

First, the population dynamics between plant and pollinator may have a crucial role as plants can produce less nectar when there are more pollinators present and vice versa (Ratnieks and Balfour 2021). This study only analyzed floral abundance, but incorporating hummingbird population numbers may shed light on the variation visitation between years (Figure 21).

Second, confounding resources may influence visitation rate in ways not examined in the study, such as artificial feeders. Inouye et al. 1991 found a significant negative correlation between the number of birds captured *at feeders* and peak number of *Erythronium grandiflorum*, *Delphinium nuttallianum*, *Ipomopsis aggregata* and *Delphinium barbeyi* flowers from 1979-1989, suggesting they feed more on the flowers as their abundance increases. However, our results show a mismatch in floral abundance and visitation rate (Figure 9). Combining feeder visitation, hummingbird population number and floral density in future analyses can shed light

on these contradictory findings. Other confounders with floral abundance include competition with insects and Rufous hummingbirds (Brown et al. 1981; Camfield 2006). Rufous hummingbirds are known to be more territorial, often displacing Broad-tailed hummingbirds in their territories and feeders, potentially altering the visitation rate seen in our data (Camfield 2006).

Third, incorporating soil moisture can enhance understanding of how abiotic factors influence nectar quality. Although this study analyzed nectar variation on the basis of air temperature and precipitation, soil moisture more directly affects nectar quality, thus revealing clearer patterns in nectar fluctuations (Powers et al. 2022; Waser and Price 2016).

Fourth, analyzing environmental factors apart from temperature on an hourly scale may reveal finer patterns. Nectar quality has been shown to vary at different hours of the day (Pleasant 1983), and perhaps nectar quality more directly correlates with *hourly* temperature as opposed to average *daily* temperature (Figure 18, Figure 19).

Lastly, I would like to collect nectar quality data for multiple years to compare differences between seasons in terms of temperature, snowmelt date, precipitation. Long-term nectar data can reveal interannual differences in nectar quality's relationship with visitation rate across different breeding seasons.

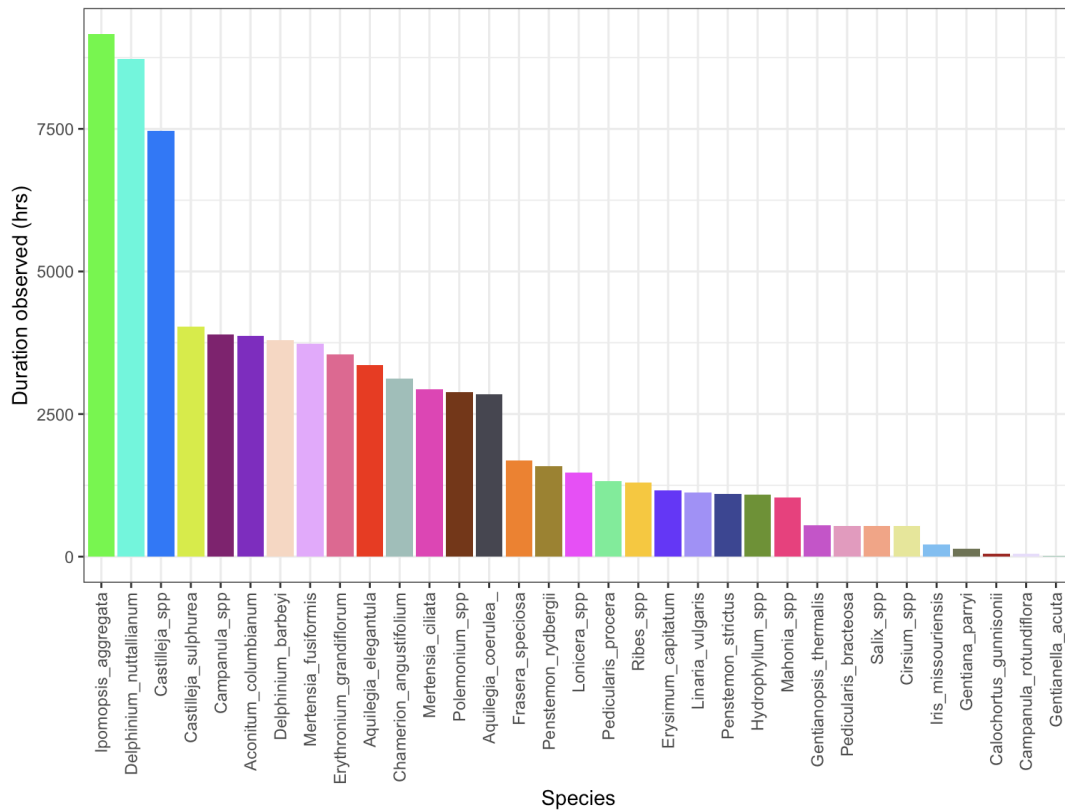
Conclusion

This study is the first to systematically examine the relationship between five environmental factors and hummingbird visitation rate. Although many individual regression analyses did not reveal statistical significance, many ecological patterns emerged that may shed light on Broad-tailed hummingbirds' foraging behavior in subalpine ecosystems, and potentially other hummingbird species in similar environments, with similar feeding habits. First, results

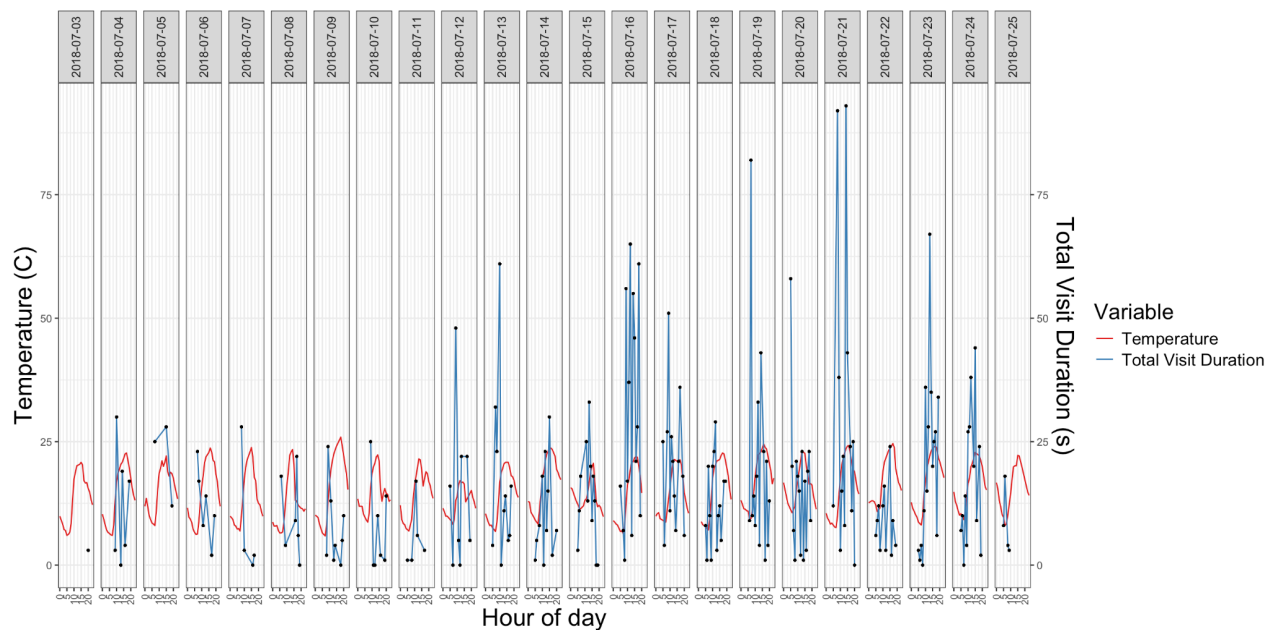
show how hummingbird daily foraging patterns may be influenced by temperature, likely prioritizing water balance rather than strictly maximizing energy intake. Second, the study reinforces how snowmelt timing is tied with plant phenology, and how shifts in resource availability can or may not synchronize with peak hummingbird activity. Most importantly, it highlights the role of nectar quality, hummingbirds' main source of energy, and shows how typical hummingbird flowers not only cater to the birds' sensory and morphological preference, but also maintain favorable nectar traits in response to environmental fluctuations.

Overall, these results highlight how a complex network of environmental factors shape Broad-tailed hummingbird foraging decisions. As climate change is causing more pronounced extremes and variations in temperature, precipitation and snowmelt patterns around the world, hummingbirds and their ecosystem are being more affected everyday. Therefore, studies integrating biotic and abiotic factors across multiple temporal scales may help predict and mitigate climate change impacts on plant-pollinator dynamics and other systems sensitive to environmental fluctuations.

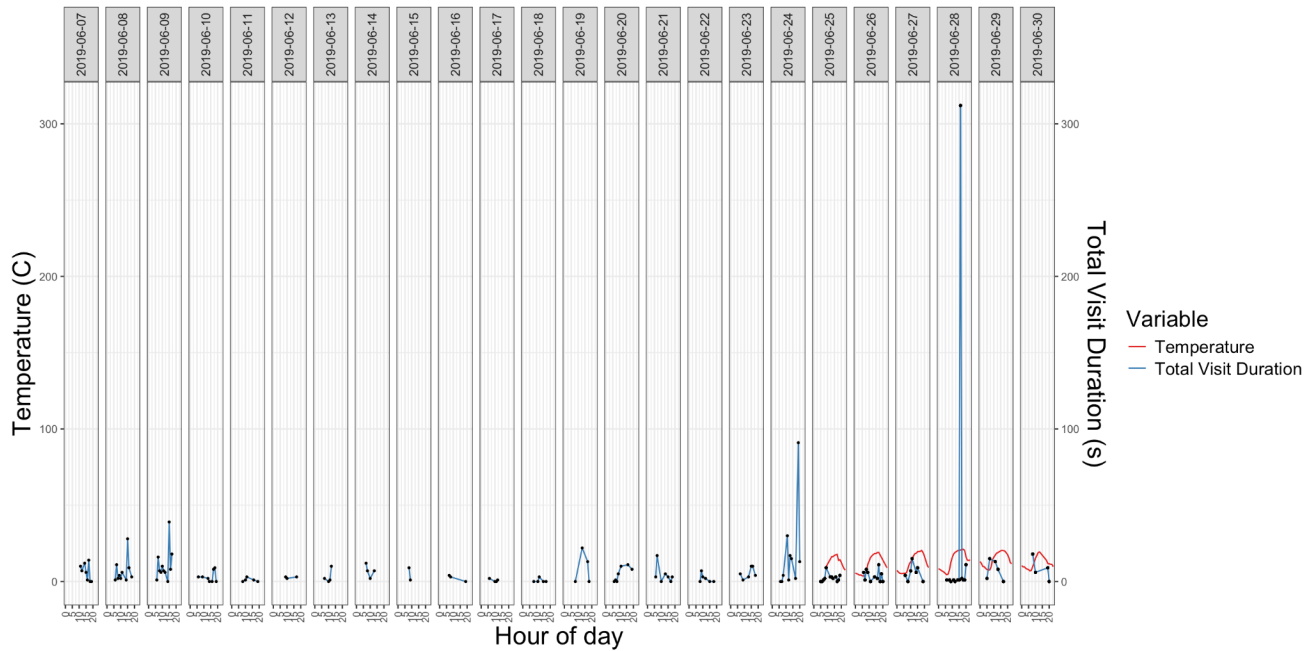
APPENDIX



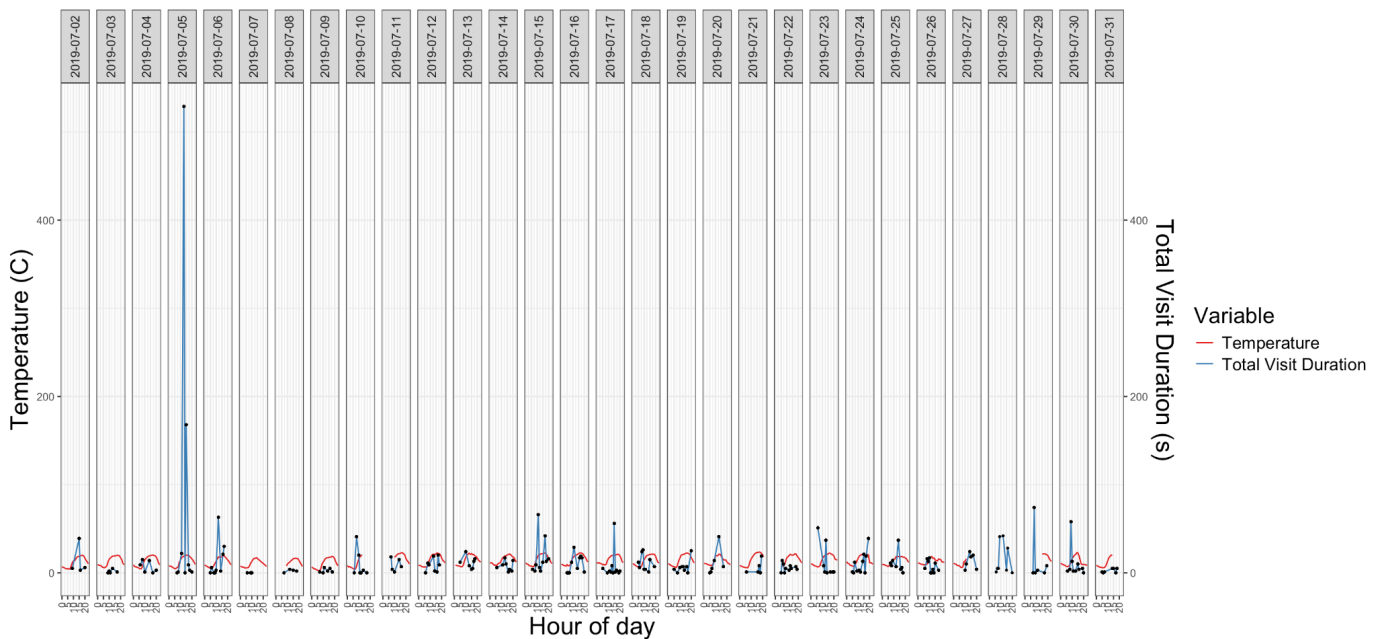
Supplemental Figure 1. Total observation duration for each flower species.



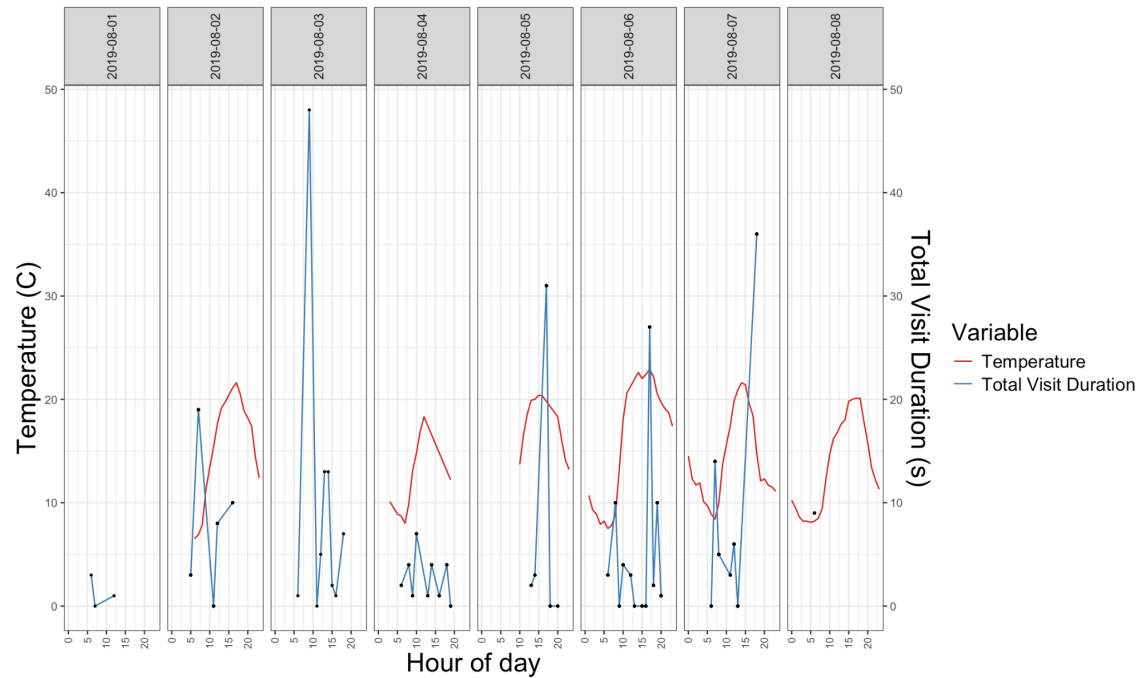
Supplemental Figure 2. Time series graph for July 2018 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs. *There is no visitation data for August 2018.



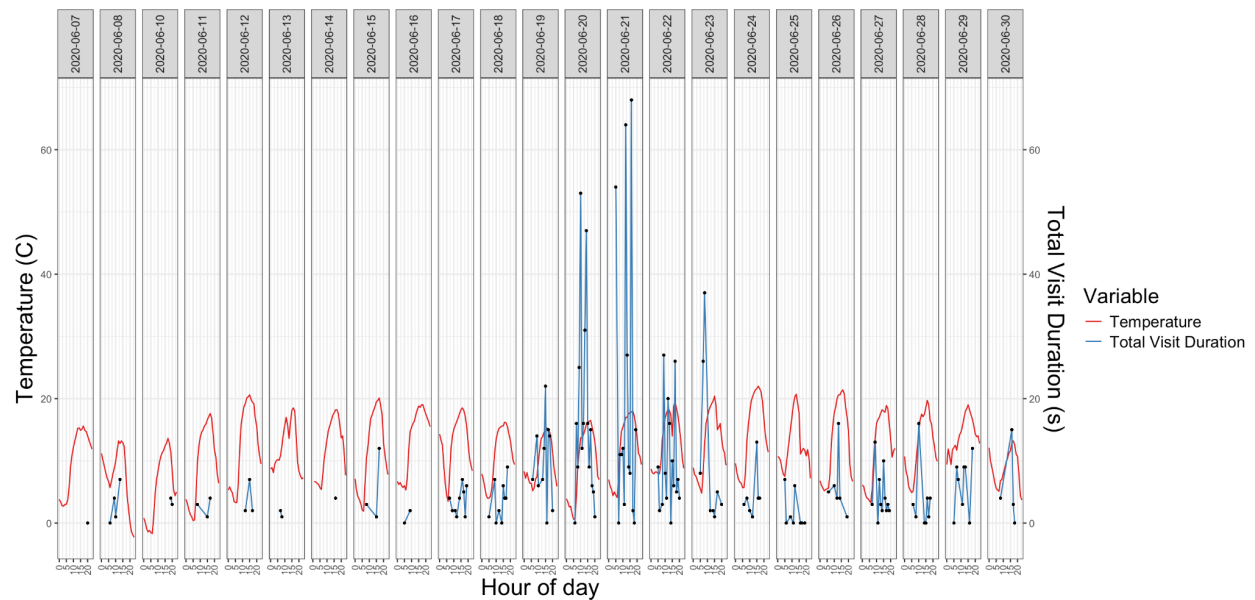
Supplemental Figure 3. Time series graph for June 2019 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs. *There was no Temperature data from 06/07-06/25.



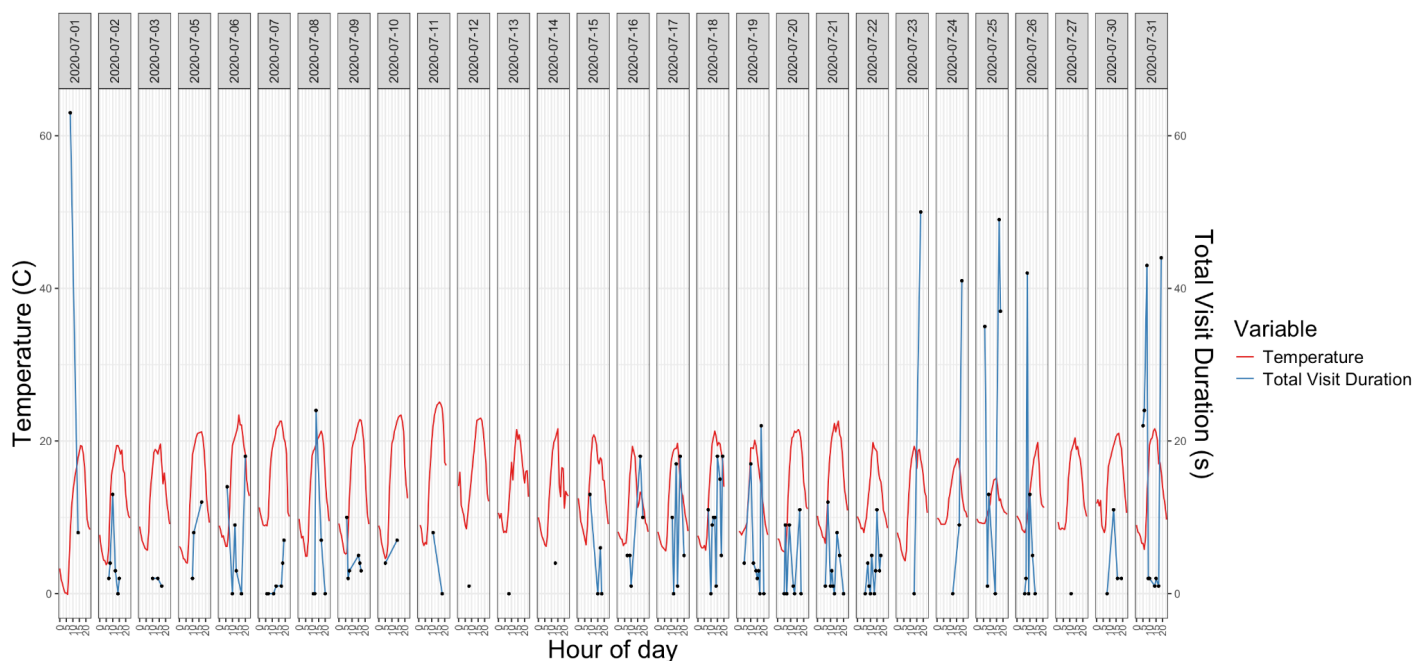
Supplemental Figure 4. Time series graph for July 2019 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



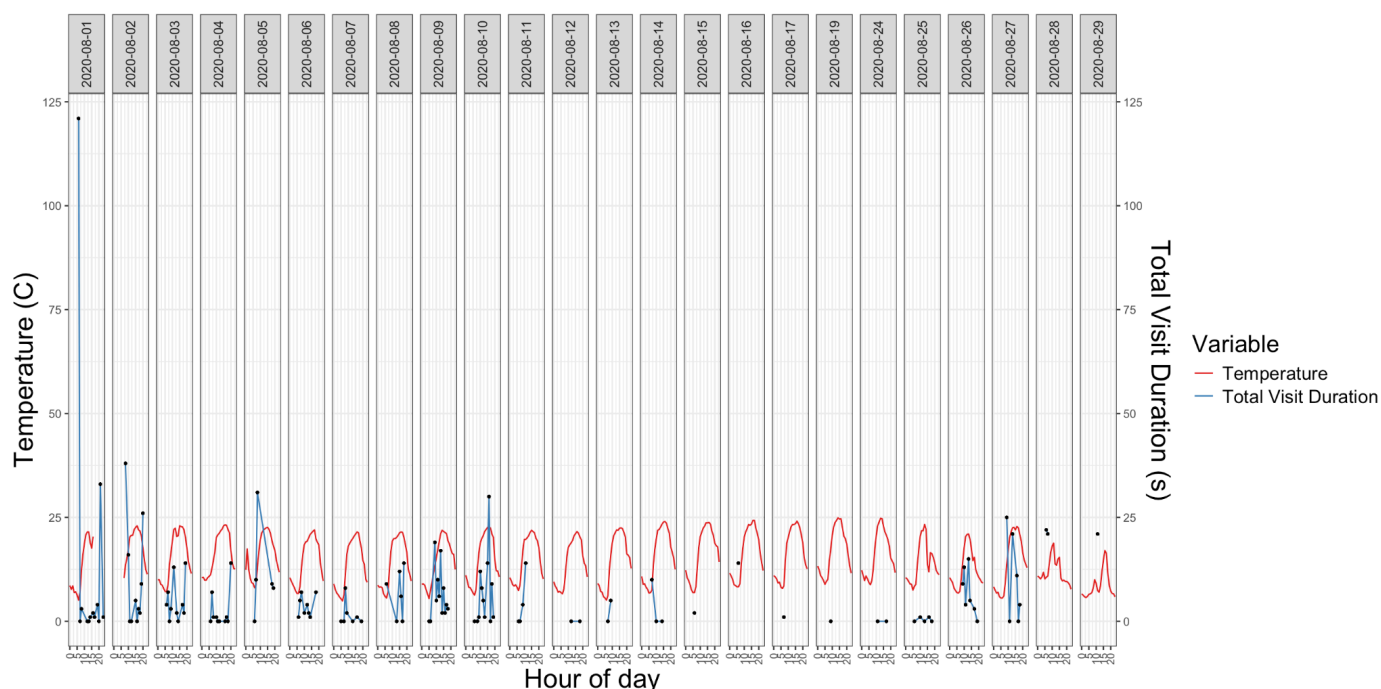
Supplemental Figure 5. Time series graph for August 2019 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour; separated by day. Only days with visitation(s) recorded are included in the graphs.



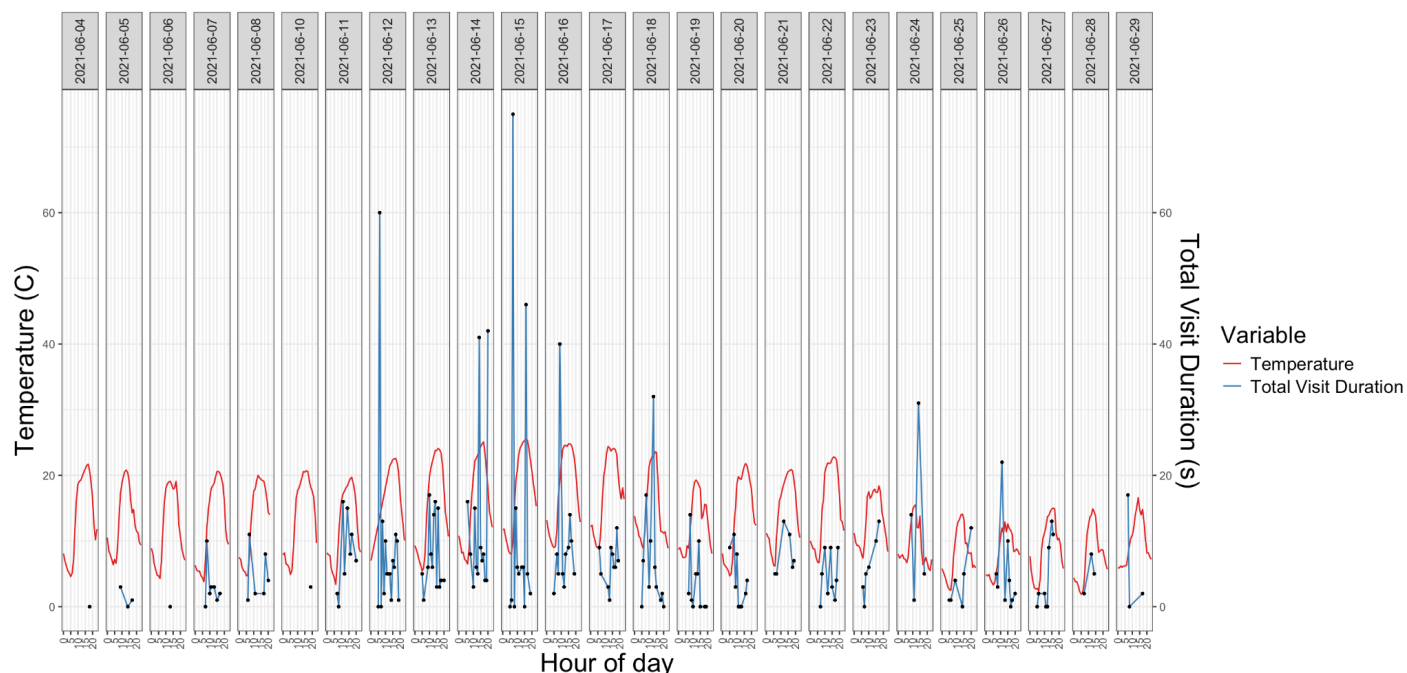
Supplemental Figure 6. Time series graph for June 2020 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour; separated by day. Only days with visitation(s) recorded are included in the graphs.



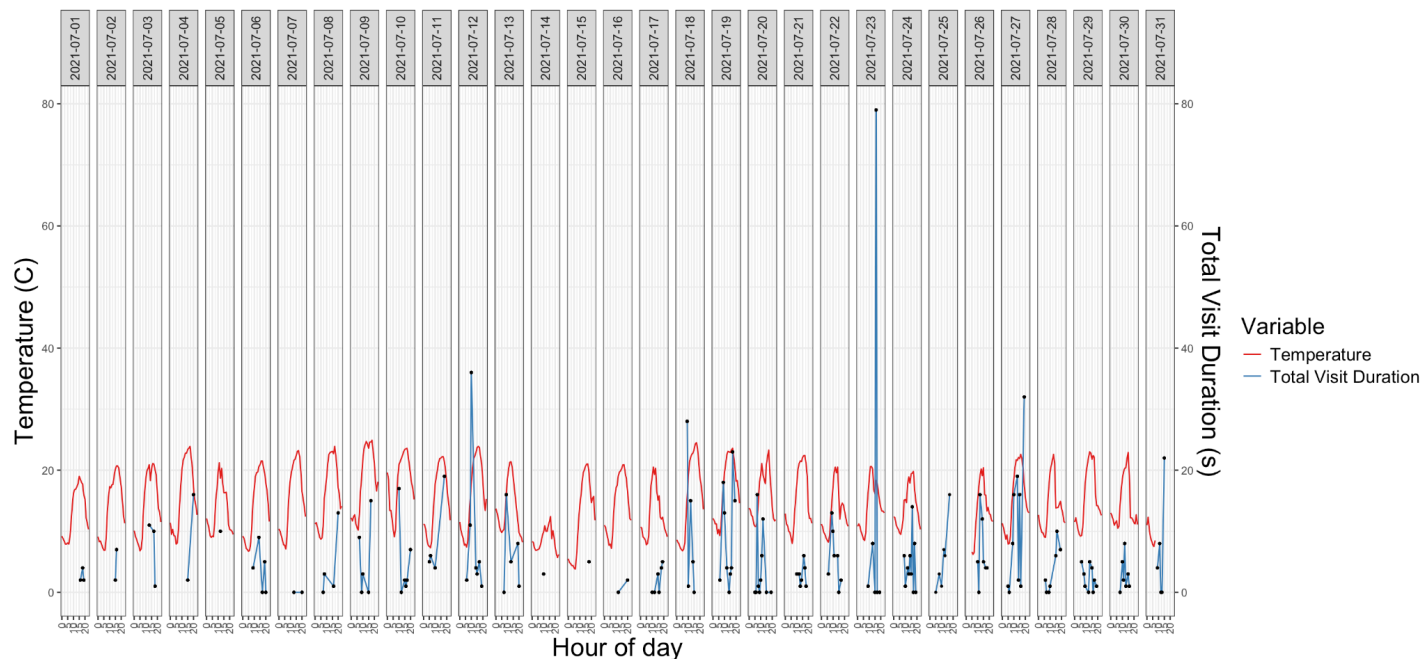
Supplemental Figure 7. Time series graph for July 2020 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



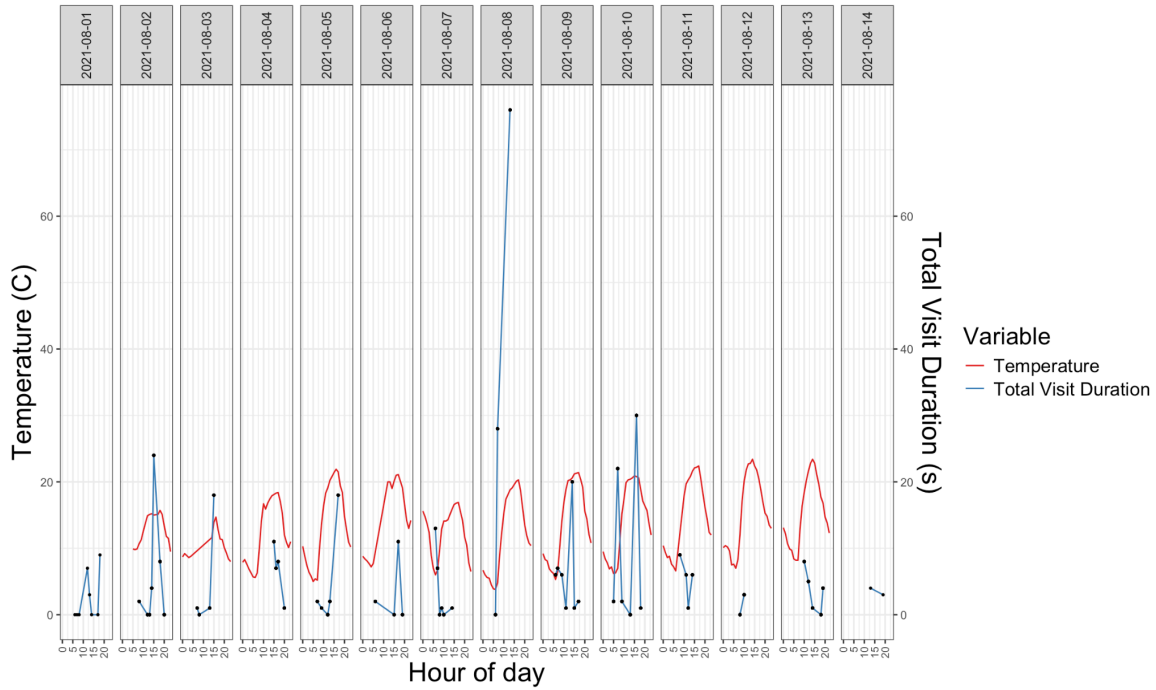
Supplemental Figure 8. Time series graph for August 2020 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



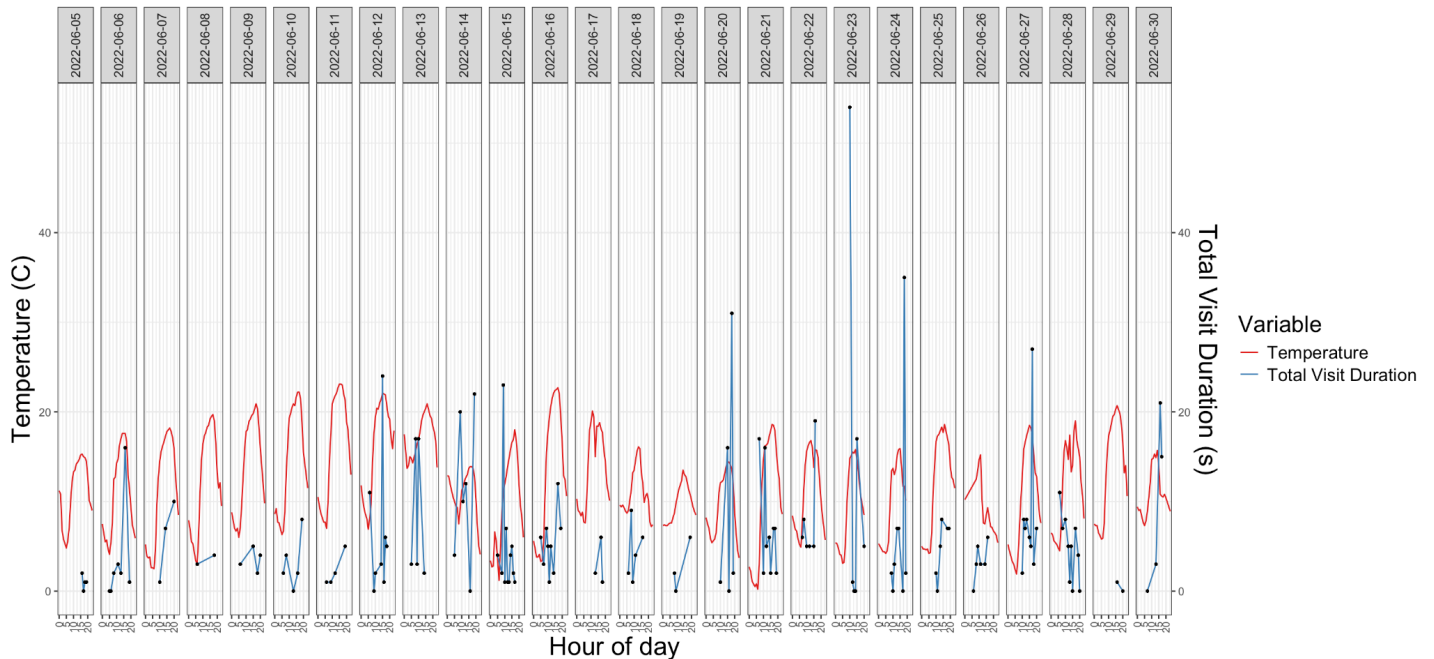
Supplemental Figure 9. Time series graph for June 2021 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



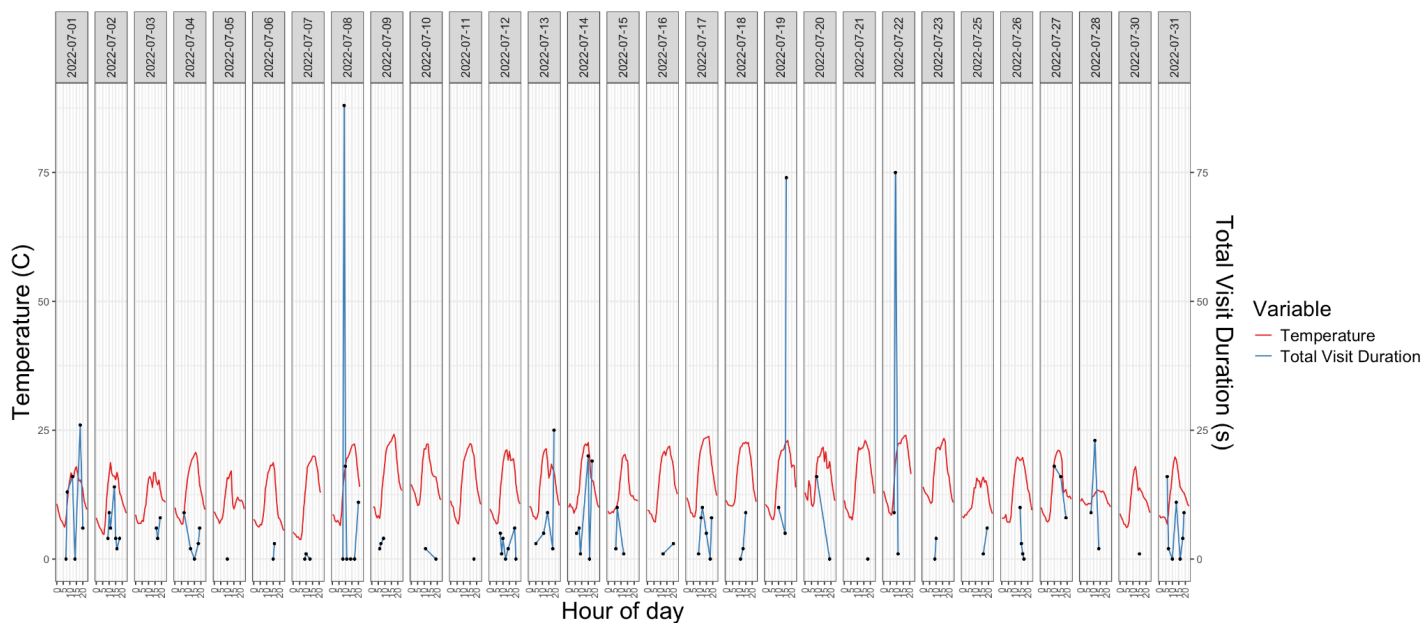
Supplemental Figure 10. Time series graph for July 2021 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



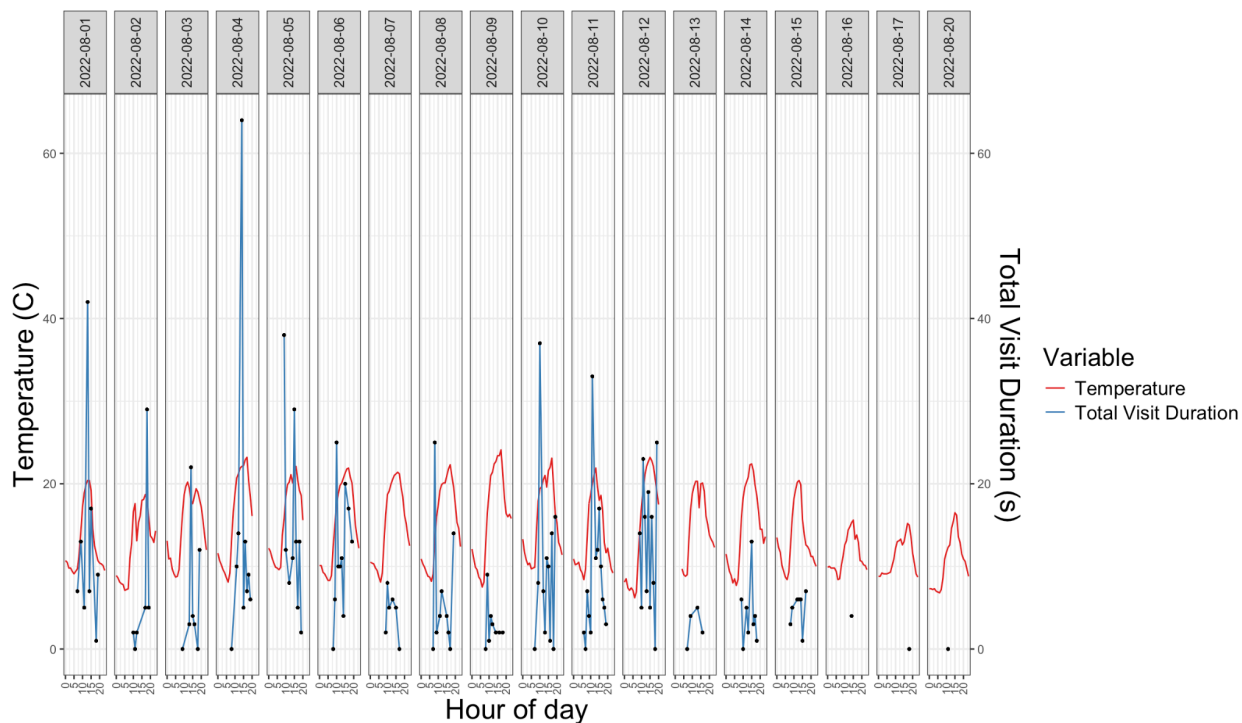
Supplemental Figure 11. Time series graph for August 2021 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour; separated by day. Only days with visitation(s) recorded are included in the graphs.



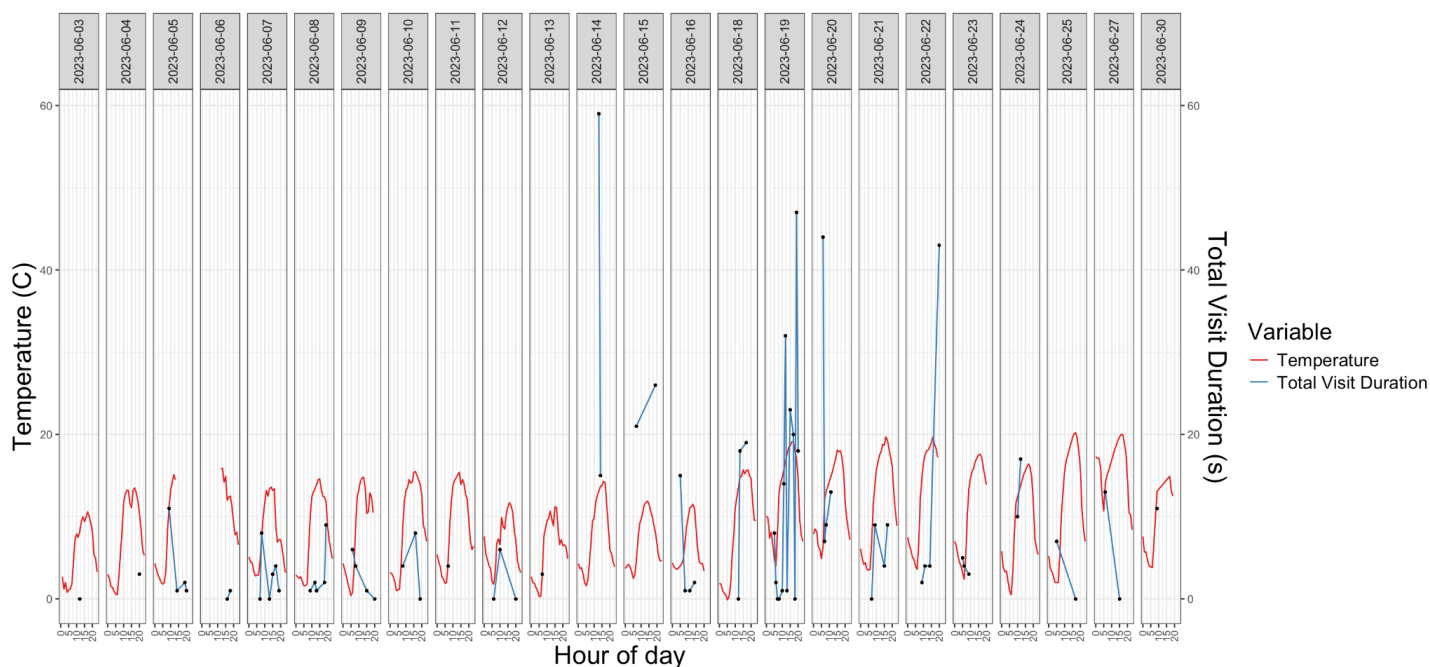
Supplemental Figure 12. Time series graph for June 2022 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour; separated by day. Only days with visitation(s) recorded are included in the graphs.



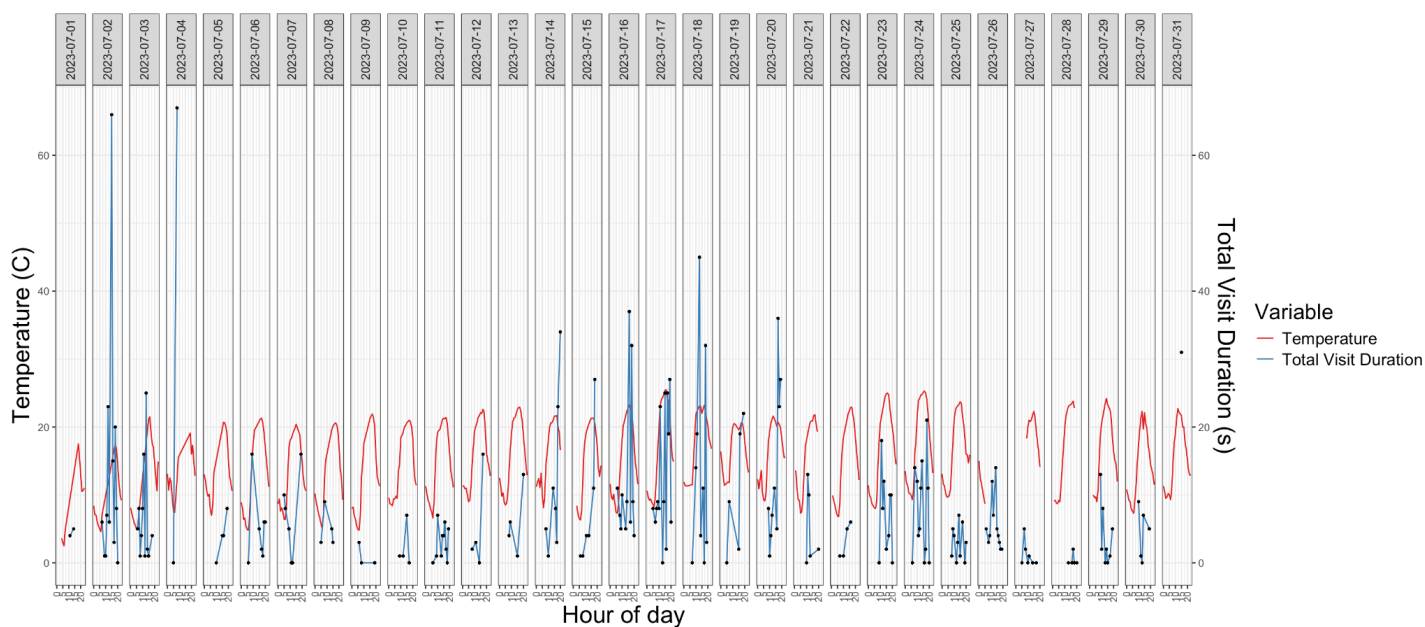
Supplemental Figure 13. Time series graph for July 2022 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



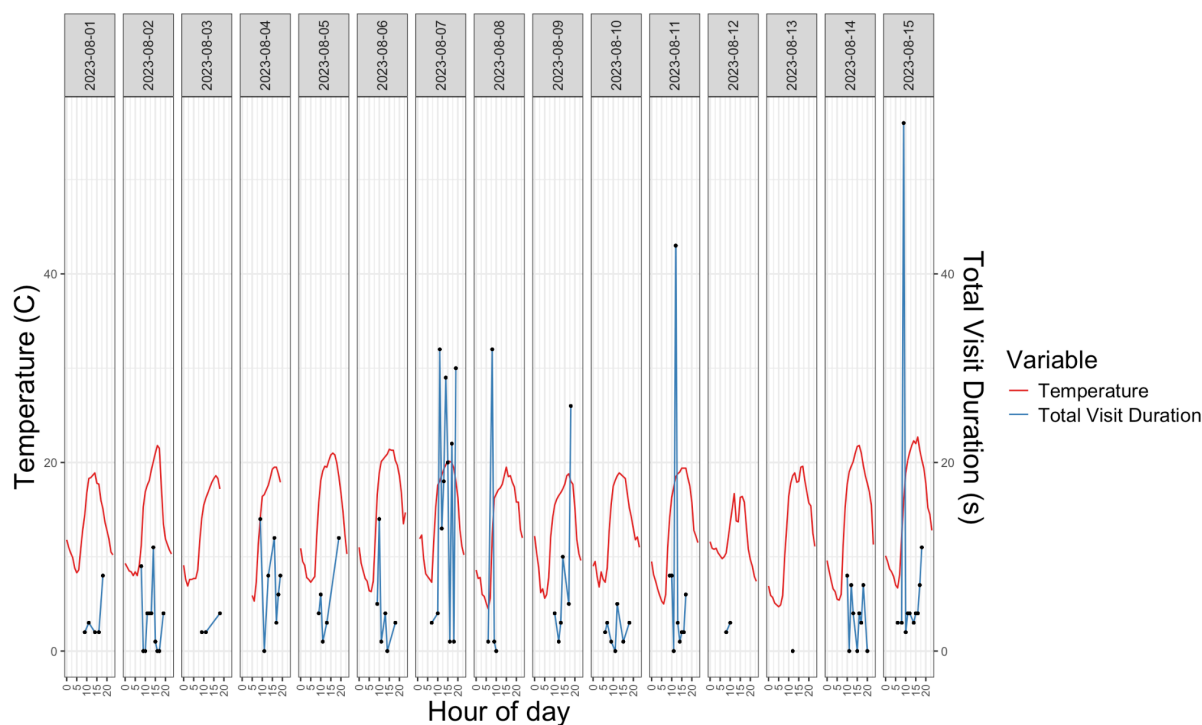
Supplemental Figure 14. Time series graph for August 2022 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



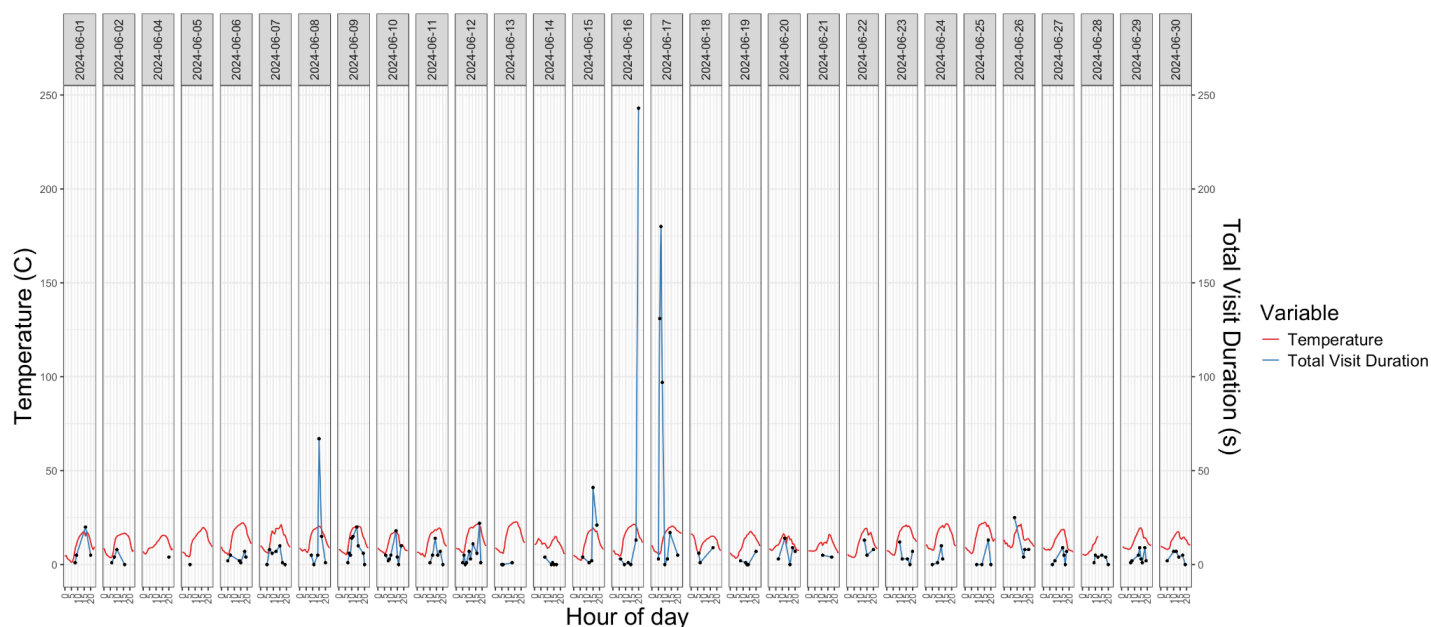
Supplemental Figure 15. Time series graph for June 2023 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour; separated by day. Only days with visitation(s) recorded are included in the graphs.



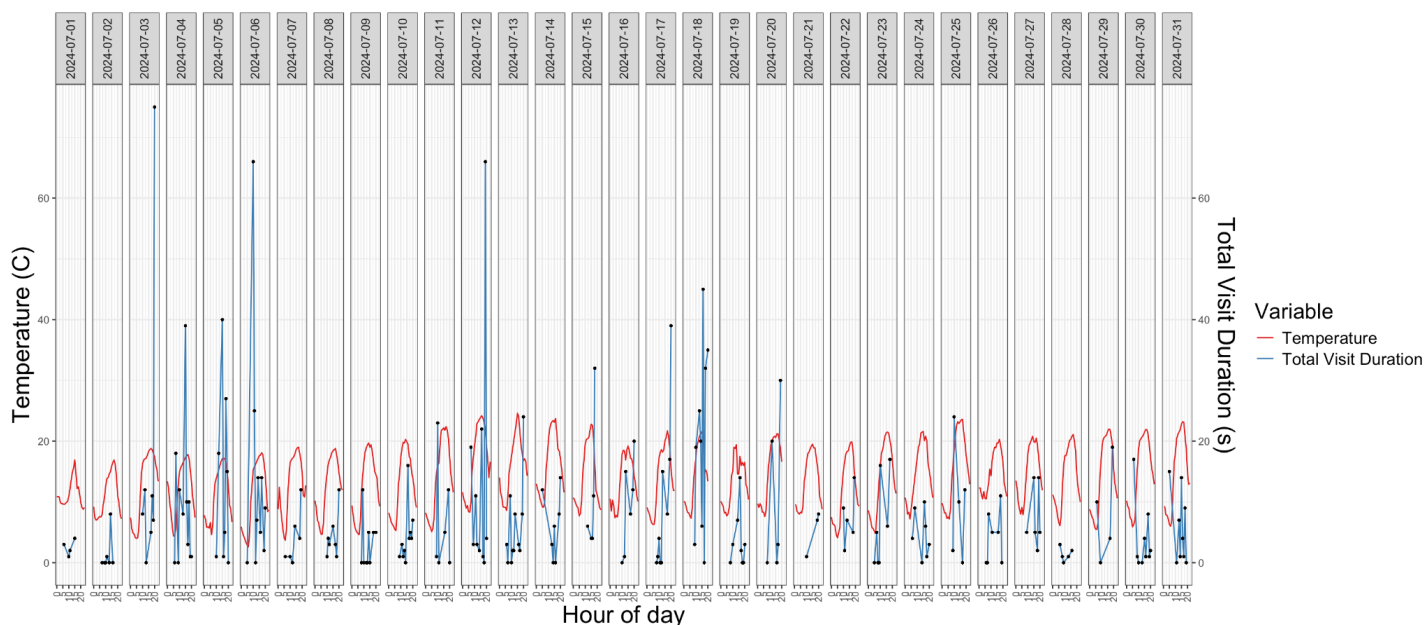
Supplemental Figure 16. Time series graph for July 2023 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour; separated by day. Only days with visitation(s) recorded are included in the graphs.



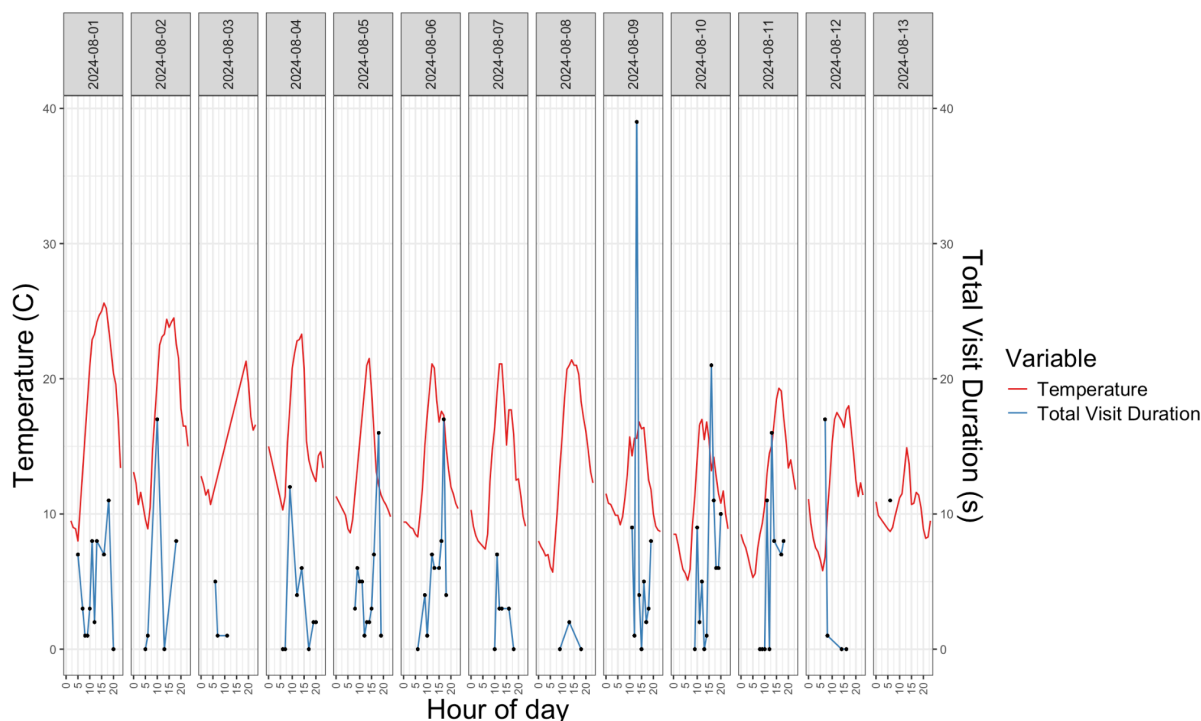
Supplemental Figure 17. Time series graph for August 2023 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



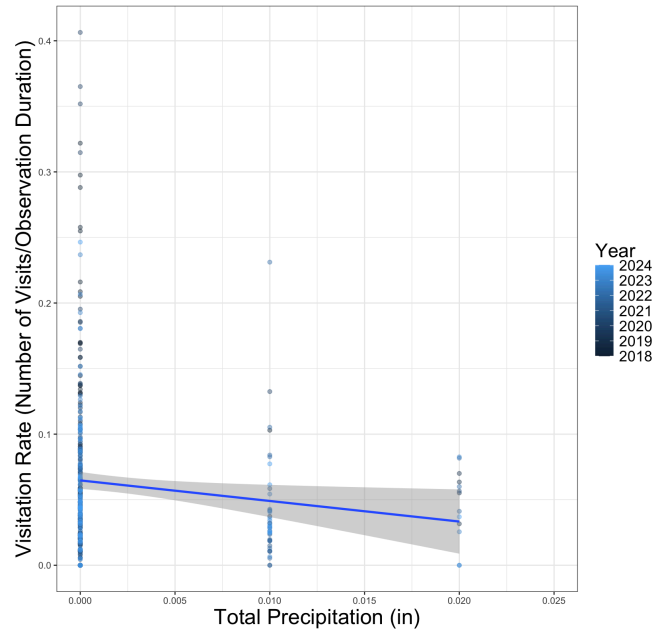
Supplemental Figure 18. Time series graph for June 2024 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



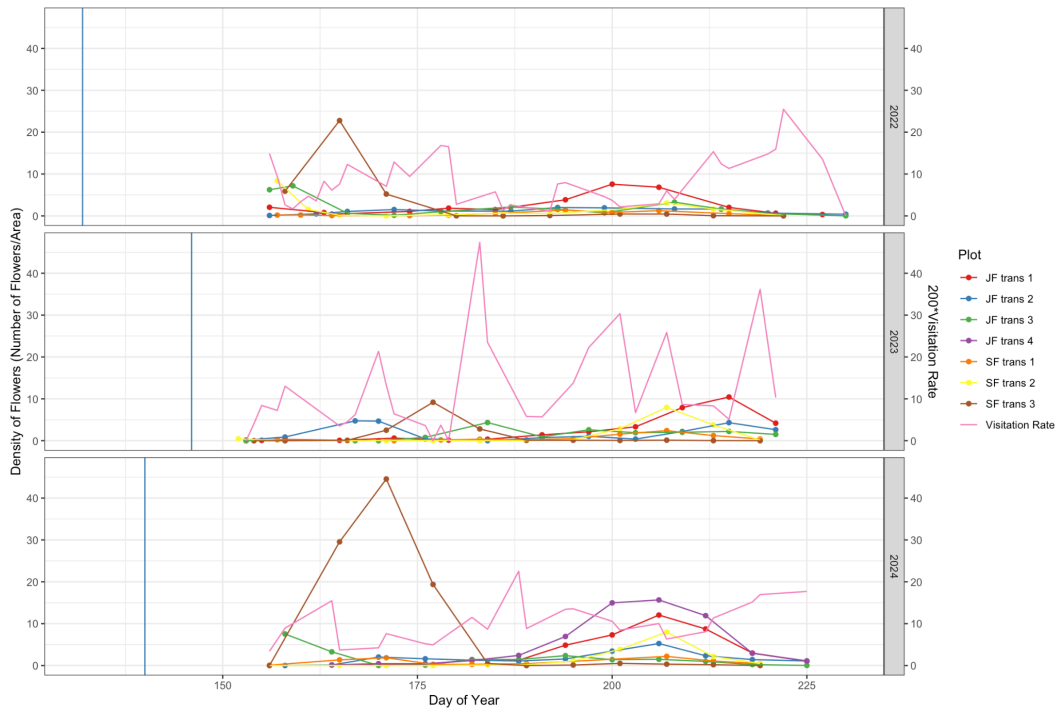
Supplemental Figure 19. Time series graph for July 2024 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



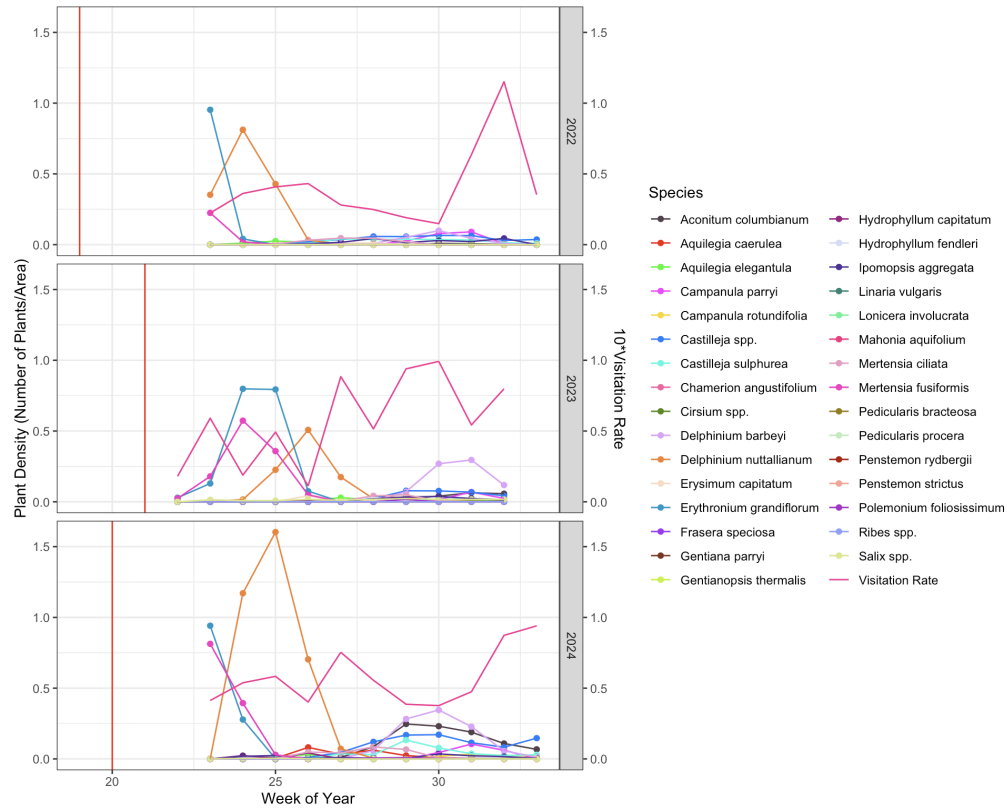
Supplemental Figure 20. Time series graph for August 2024 of hourly temperature data (in Celcius, red line) against the total visit duration (in seconds, blue line and black dots) within the corresponding hour, separated by day. Only days with visitation(s) recorded are included in the graphs.



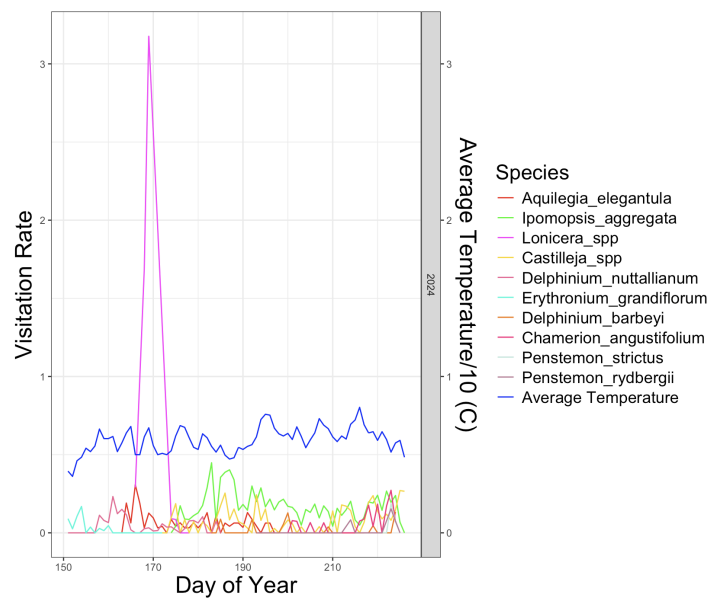
Supplemental Figure 21. Linear regression (without outliers) for visitation rate against daily precipitation rate reveals negative correlation. Statistics: $p=0.020$, $R^2=0.014$, and adjusted $R^2=0.012$.



Supplemental Figure 23. Flower density by plot for each DOY. Snowmelt date is the blue line, and weekly visitation rate is the magenta line. SF Transect 3 shows most density early in the season across all three years, and JF Transect 1 later in the season except for 2024 due to the new JF Transect 4. *Visitation rate is multiplied by 200 for scaling purposes.



Supplemental Figure 22. Plant density by species for each week of year. Snowmelt date is the red line, and weekly visitation rate is the magenta line. Unlike Figure 9, this plot shows a higher number of *E. grandiflorum* than *D. nuttallianum* early in the 2023 season. Other trends are similar to Figure 9's. *Visitation rate is multiplied by 10 for scaling purposes.



Supplemental Figure 24. Top 10 species' visitation rate in the 2024 breeding season against average daily temperature (blue line). *Lonicera spp.* showed a huge increase in visitation rate on DOY 169. *Average temperature was divided by 10 for scaling purposes.

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