

EFFECTS OF DAILY TEMPERATURE CHANGES ON BROAD-TAILED HUMMINGBIRD FORAGING PATTERNS

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ABSTRACT

Climate change threatens the close relationship between wildflowers and the hummingbirds that pollinate them, both through gradual warming that shifts and misaligns their phenologies, and also potentially through increasingly erratic day-to-day temperature changes, a phenomenon especially apparent at high altitudes. We investigate how these temperature changes affect the flower visitation rate of broad-tailed hummingbirds (*Selasphorus platycercus*) in high-elevation Gothic, Colorado, where a significant portion of the birds' marginal energy budget is spent on thermoregulation. We hypothesize that on days much colder than average, hummingbird visitation will increase as the birds have higher energy demands to thermoregulate. Using hummingbird visitation data collected on cameras around Gothic from 2018-2022 and temperature highs and lows recorded in Gothic weather data from 2016-2022, we calculate visitation deviation from the average on a given day, plotting it against temperature deviation from the average on the same day to explore the relationship between the two variables. We found that there was no evidence of a relationship between short-term temperature changes and hummingbird visitation rate. Temperature did not seem to have an effect on foraging patterns for male or female Broad-tailed hummingbirds in Gothic from 2018 to 2022.

INTRODUCTION AND GENERAL PLAN OF STUDY

There is a close mutualistic relationship between plants and pollinators. Flowers provide nectar, which is a major energy source for the pollinators. In turn, the pollinators, as their name suggests, help with flower reproduction by transporting pollen between flowers. One of these pollinators is the hummingbird. Studies have shown that flower phenology aligns with the breeding season of hummingbirds and closely corresponds with their migration patterns (McKinney 2012). However, climate change has disrupted this mutualistic relationship. Climate change influences plant phenology, with warmer temperatures causing flowers to bloom earlier than in the past. For example, McKinney's study in 2012 highlighted the effects of climate change on flower phenology and broad-tailed hummingbirds (*Selasphorus platycercus*), an important pollinator in Gothic, Colorado. Major early nectar sources for hummingbirds at Gothic such as *Erythronium grandiflorum* or *Delphinium nuttallianum* are blooming 4.6 ± 1.6 days and 4.3 ± 1.5 days earlier, respectively, on average. Consequently, the birds are arriving closer to the first and peak blooming times, compared to the past where their arrival precedes flower appearance by a few days, effectively shrinking their breeding season (McKinney 2012).

In addition to seasonal effects, climate change also causes day-to-day temperature changes to be more erratic, especially at higher altitudes (Ohmura 2012). Hummingbirds are especially susceptible to daily changes in temperature because they already operate on a tight budget of daily energy expenditure (DEE). Hummingbirds are diurnal and fast during the

nighttime, but their small body size means they have a high metabolism and a very limited fasting endurance (Calder 1975a). These factors, combined with hummingbirds' lack of insulation and high surface area for heat dissipation means they must budget their energy carefully to maintain homeostasis throughout the night (Calder and Booser 1973).

Hummingbirds may enter a state of hypothermic torpor at night, in which they do not expend energy on thermoregulation, if they do not have sufficient energy (Calder and Booser 1973). Hypothermic torpor is a state of inactivity, where hummingbirds reduce their metabolism and body temperature, and they can remain in this state for a few hours or for an entire night.

A study on broad-billed hummingbirds (*Cynanthus latirostris*) in Arizona investigated whether daily temperature changes affected their activity and found it was not as significant as flower and nectar availability (Shankar et al., 2019). The researchers found that hummingbirds' DEE are flexible and adaptable to current changes in temperature and resource availability. However, the environment of this study had average daytime temperatures that were 34.9°C (10–57°C) and average night-time temperatures that were 19.8°C (range 0–37°C), and the study was conducted at Harshaw Creek with an altitude of 1,370–1,635m, and Sonoita Creek with an altitude of 1,100–1,180m, which differs greatly from the subalpine environment of broad-tailed hummingbirds. The Rocky Mountain Biological Laboratory in Gothic, Colorado, where many broad-tailed hummingbirds migrate during the summer months, sits at an altitude of 2,900m. At this altitude, hummingbirds must maintain their tight energy budget in overall lower temperatures, increasing the need for thermoregulation. For example, in the summer of 2022, the daily temperatures at Gothic ranged from a high of 14.5–26°C to a low of -3.5–7°C (Gothic Weather 2022). Therefore, a climate change-induced increase in temperature variation may upset this delicate energy balance and affect hummingbird foraging patterns. Hummingbird foraging patterns changing could decrease plant pollination rate, with cascading effects on the subalpine environment. Additionally, significant changes in foraging behavior could hurt hummingbird populations due to their tight energy budget. Furthermore, energy budgets may differ between males and females, so sex is another factor to consider when examining whether temperature affects hummingbird visitation rate.

We investigated the following questions:

1. How does hummingbird visitation rate respond to temperature?
2. How does hummingbird response to temperature differ with respect to sex?

Our main hypothesis is: **If temperature has an effect on hummingbird visitation rate, then on days that are colder than average, visitation rate should increase.** We think this result is possible because we believe the broad-tailed hummingbirds would need to make up for the metabolic demands of staying warm in colder temperatures and maintaining thermoregulation by increasing their energy intake. Though some previous findings (Shankar et al., 2019) have not found that daily temperature significantly influences hummingbird activity, no studies have been conducted on broad-tailed hummingbirds, which experience much colder temperatures. We hypothesize that these colder temperatures could more significantly affect broad-tailed hummingbird visitation rate.

Our null hypothesis is that there is no relationship between temperature and visitation rate. This could potentially be explained by physiological constraints which limit a hummingbird's maximum energy intake (McWhorter 1997). Even if hummingbirds have higher energy demands in cold weather, their physiological constraints may prevent them from simply consuming more nectar. Hummingbirds might instead go into torpor in unusually cold temperatures, rather than upping their energy intake.

Our first alternative hypothesis is as follows: **If temperature has an effect on hummingbird visitation rate, then on days that are colder than average, visitation rate should decrease.** Perhaps it takes more energy to go out and forage instead of staying in one place and huddling, or perhaps if hummingbirds are more likely to go into torpor, their flower visitation rate would decrease.

Our second alternate hypothesis predicts what might happen on days that are warmer than average: **If temperature has an effect on hummingbird visitation rate, then on days that are warmer than average, visitation rate should decrease.** Additionally, some flowers, such as *Ipomopsis aggregata*, have been shown to produce more nectar when it's warmer. Hummingbirds may then visit fewer flowers if they can consume more nectar in a single visit. It could be more costly to forage on hot days if hummingbirds experience more water loss on hotter days.

On the contrary, our third alternate hypothesis is: **If temperature has an effect on hummingbird visitation rate, then on days that are warmer than average, visitation rate should increase.** Perhaps if it's warmer, there is less of a need to expend energy on thermoregulation, so the birds can afford to be more exploratory and spend more time foraging.

Our second question addresses the fact that the DEE of broad-tailed hummingbirds can also be sex-specific. While nesting, broad-tailed hummingbird females must incubate eggs and rarely resort to torpor, which could damage the development of eggs (Calder and Booser, 1973). Incubating females also have a shorter feeding window than males, likely because they must spend more time brooding in the nest (Calder 1975b). In some instances, lack of energetic resources may force females to abandon their chicks altogether, further illustrating the inflexibility of their energy budget (Calder 1975a). While males have more flexibility with torpor and thus may have lesser thermoregulation needs, they also expend significant energy defending their territory, and must balance the energetic benefits of the territory with its costs (Camfield 2006).

Thus, we also explored how hummingbird response to temperature changes differs between males and females. Because of the distinct energy expenditures of males and females over the course of the season, climate change-induced temperatures could have a more pronounced effect on the visitation rate of one sex versus the other. Uneven consequences of daily temperature changes could upset hummingbird sex ratios, impacting hummingbird behavior and population dynamics.

SPECIFIC METHODOLOGIES

To study the effects of temperature on daily hummingbird visitation rate, we analyzed data from a longer-term project at RMBL, referred to as HummerFlowerWatch, collected by the Stoddard Lab and based out of the Princeton University Ecology and Evolutionary Biology department. This dataset consists of five years of image data collected by the Stoddard Lab from 2018 to 2022 at the Rocky Mountain Biological Laboratory in Gothic, Colorado. Each summer from 2018 to 2022, the Stoddard Lab placed stop motion camera traps at various locations in Gothic on flowers (representing approximately 30 different species) most frequently visited by hummingbirds. After collecting image data from early June to late August, we analyzed the images and record for each hummingbird visit the following: time of day, duration of the visit, whether or not the hummingbird has a gorget (which is present in adult males), and flower species. We are currently in the process of collecting data for the 2023 field season to add to this long-term dataset; however, data from 2023 will not be included in this analysis.

Data collection

To collect data out in the field, we used Brinno TLC200 cameras and placed them securely within a waterproof case. These cameras were set up on tripods and took photos every second from 5 A.M. to 9 P.M., meaning these cameras took 57,600 photos per day per flower, and the result is a time-lapse video of these images. We placed these cameras in view of flower species that hummingbirds have been known to visit, such as *Delphinium nuttallianum* and *Ipomopsis aggregata*, which are two of the most frequently visited species. There are 31 flower species that we place cameras on in Gothic. We subdivide our research sites into three general locations: Stupid Falls, Judd Falls, and townsite (meaning near residential areas in Gothic). We visited each of these locations on a different day, working on a three-day cycle. We removed these cameras after leaving them out for three consecutive days. When we visited a site, we removed the camera, swapped out the batteries and SD card, and placed it near a different flower, being sure that no two cameras are on the same species within 100 meters of one another.

The 2018-2022 HummerFlowerWatch data was collected using the same procedure, with the exception that up until the summer of 2022, PlotWatcher cameras were used instead of Brinnos. The time-lapse videos are processed by the Stoddard Lab at the end of each field season using the DeepMeerkat software, which can detect movement. DeepMeerkat has been trained to accurately identify not only animal movement, but hummingbird visitations specifically. As a precautionary measure, the Stoddard Lab reviews all videos flagged by DeepMeerkat as having a hummingbird order to ensure the accuracy of the identification. Because there are many false positives from movement such as flowers blowing in the wind, this final step is important to filter out the videos that actually contain hummingbirds.

The data collected and processed via this procedure, based on five years of camera footage, consists of over 3,000 recorded hummingbird visits to our cameras. For each visit, and for each frame within a recorded visit, we have the time and date of the visit, the flower species visited, and whether the visiting hummingbird had a visible gorget (with a visible gorget indicating that a hummingbird is male).

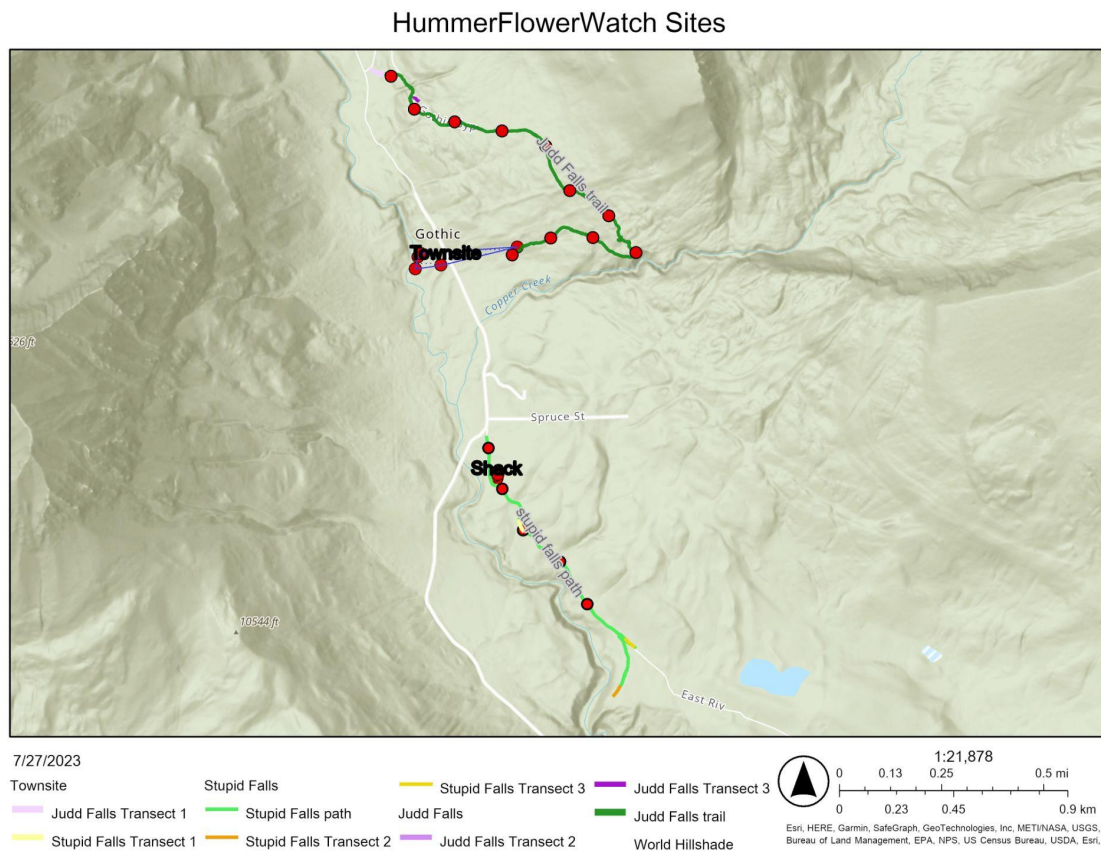


Figure 1. GPS mappings of trails and transects used for data collection.

Weather data

In order to determine the effects of temperature on hummingbird visitation rates, we used 5 years of daily Gothic weather data, from 2018 to 2022 (Gothic Weather website), which matched up with the years that visitation data has been collected.

Analysis

We used R Studio to download and combine the Gothic weather data and HummerFlowerWatch visitation data. We used the 5 years of weather data to calculate the average high and low for every day from June 1 to August 31st. Using these average highs and lows, we also calculated the average daily temperature range. We then compared the average highs and average lows to the daily highs and daily lows of each year from 2018-2022 to calculate temperature deviations from the average. We also calculated the daily temperature range across these years. With the HummerFlowerWatch data, we grouped together the top 6 visited flowers and calculated the daily visitation rate to these flowers by dividing the total hours the flowers were watched each day by the number of recorded visits.

We then created two types of graphs: time series and linear regressions. To visualize general patterns between weather and visitation, we created five time series graphs for each year with both temperature and visitation rate on the y axis. On one graph, we plotted average high, daily high, and daily visitation rate together, and on another we plotted daily deviation from the average high and daily visitation rate. We recreated the same two graphs for the lows and daily deviation from the low. On our fifth graph, we plotted average range, daily range, and visitation together.

To visualize and quantify the relationship between the two datasets, we also created a series of linear regressions. We evaluated these linear regressions using R^2 values and Pearson correlation p-values. We first created a graph of average daily highs and lows versus visitation rate to test if there was a relationship between temperature and visitation rate. We also plotted average daily highs and lows versus the visitation rate of the following day to see if the birds' daily activities reacted more strongly to the weather of the previous day. However, not seeing a significant difference between the two graphs, we did not create any further linear regressions using visitation rate of the following day.

We then plotted daily deviation from the average high temperature and the average low temperature for each year, color coding our points by the month in which they were recorded to see how temporal and seasonal factors influenced the graphs.

We also suspected that the absolute daily temperatures played a role unaccounted for by simple deviation. For example, a two degree deviation from a 6°C day might affect visitation rate very differently as compared to a two degree deviation from a 16°C day. To account for the absolute daily temperature, we created linear regressions in which we combined all five years of daily deviations from the average high into one dataset. We then separated these data points into four absolute daily temperature bins: daily highs of 9.5 - 16°C, >16 - 22.5°C, >22.5 - 29°C, and >29 - 35°C. We used these bins to create four separate graphs comparing deviation rate to visitation rate. We repeated this process with daily deviations from the average low, using the ranges -3.5 - -0.25°C, >-0.25 - 3°C, 3 - 6.25°C, and 6.25 to 9.5°C.

Finally, we subsetting our visitation rate into visitation rates by the males, which were marked by their gorgets, and visitation rates by females, which we assumed to be all visits without a gorget. We disregarded visits in which it was unclear if the individual had a gorget. We recreated our yearly linear regressions of deviation from the average high and low versus visitation rate for both subsets.

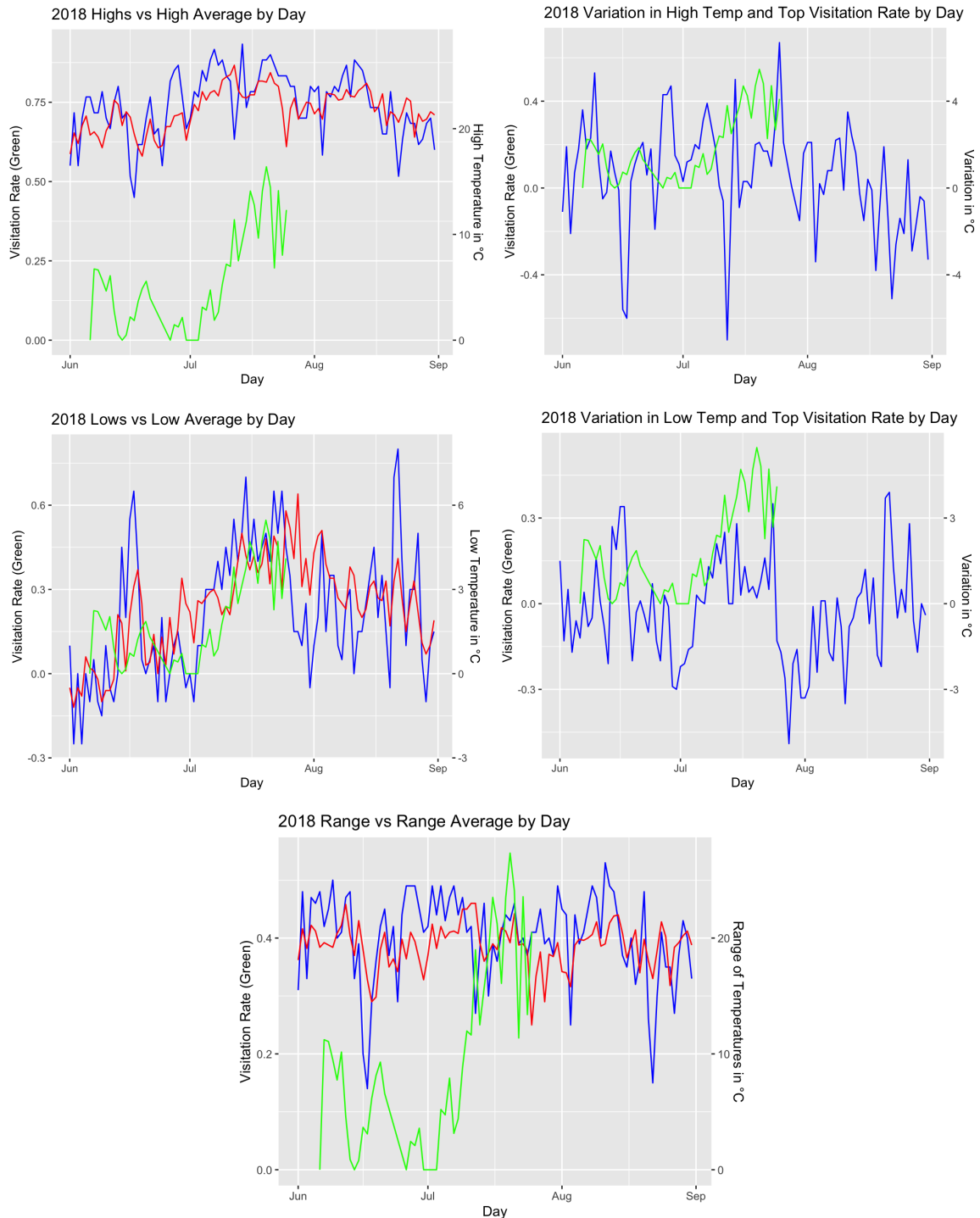
RESULTS

1: Temperature variation by day and hummingbird visitation rate

Our overall question is: how does hummingbird visitation rate respond to temperature? The purpose of our time series graph is to see whether there are any distinguished visual relationships between temperature and hummingbird visitation rate over time. If the shape of the visitation rate graph (green) seemed to track closely with the high or low temperatures over the

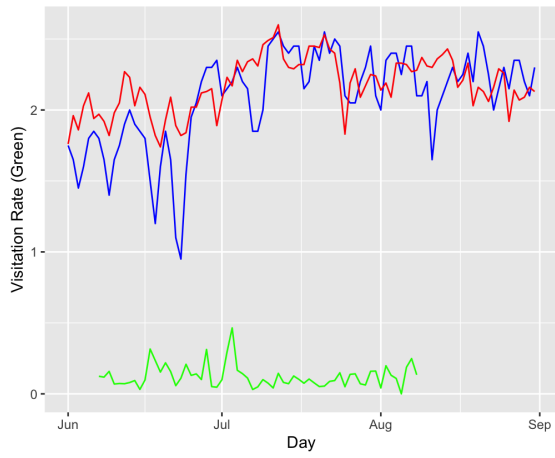
course of a year, this might suggest that hummingbird visitation rate and temperature are somehow related. However, none of the years' weather and visitation data seem to show a strong correlation visually (Figure 2), neither high nor low temperature nor temperature range variations.

2018

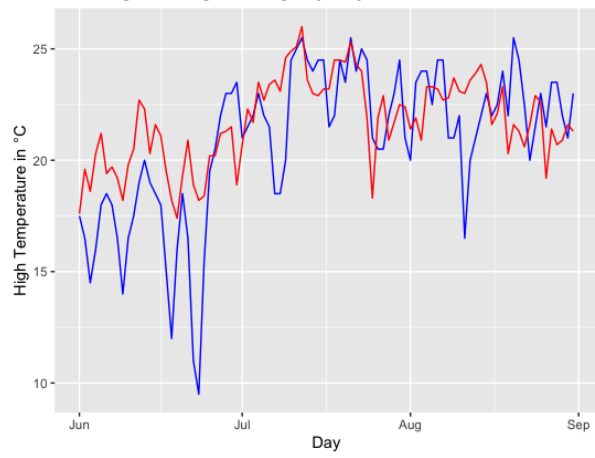


2019

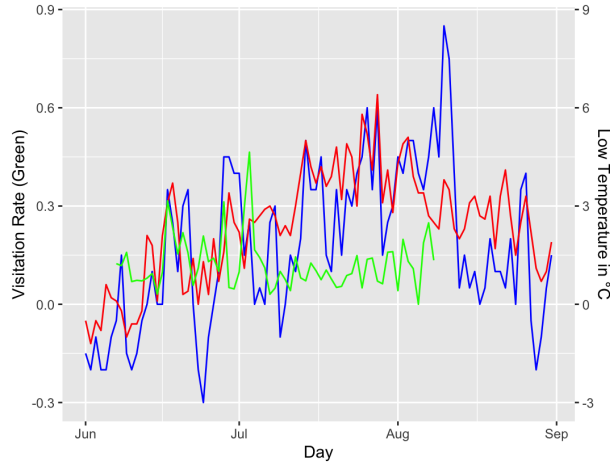
2019 Highs vs High Average by Day



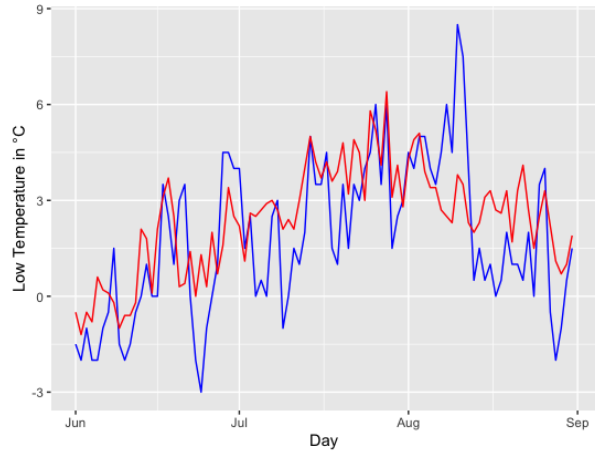
2019 Highs vs High Average by Day



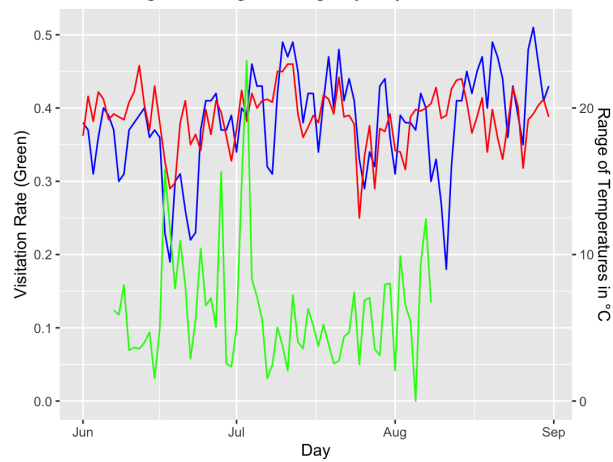
2019 Lows vs Low Average by Day



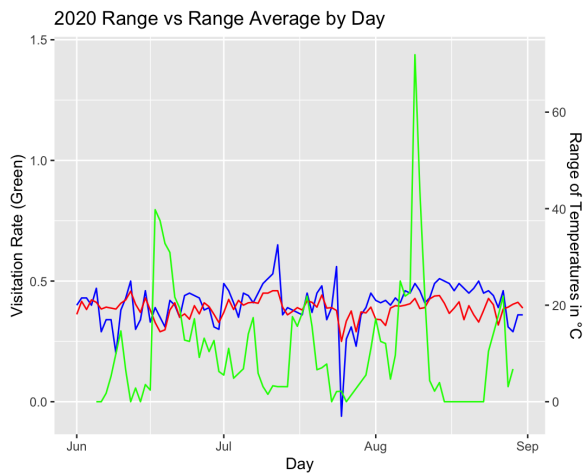
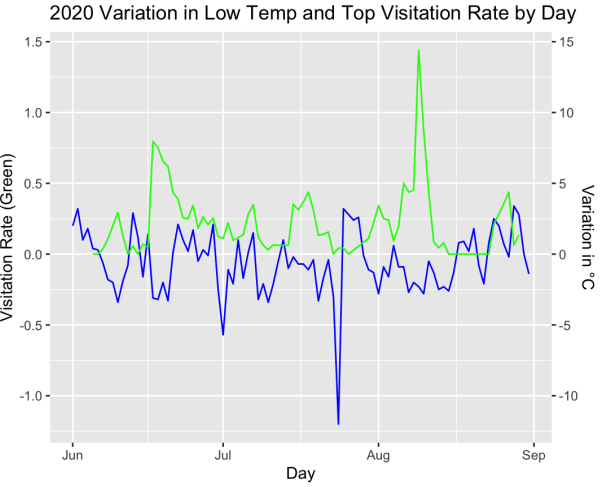
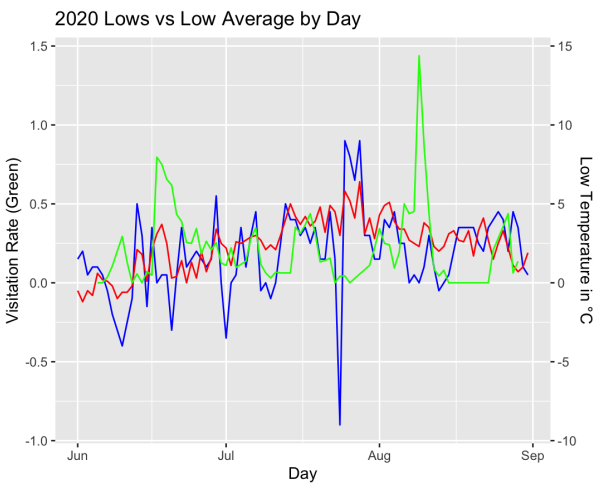
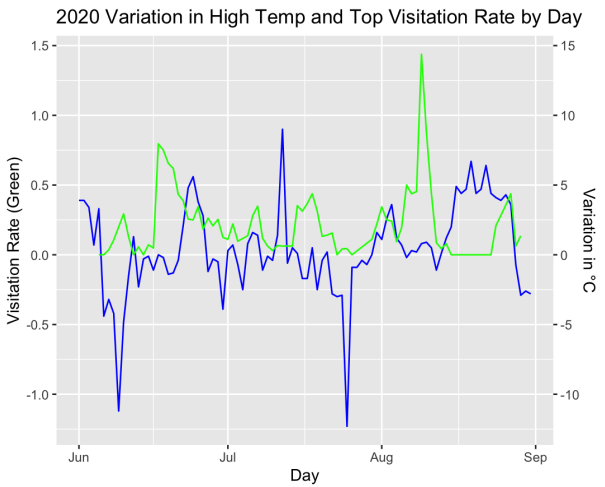
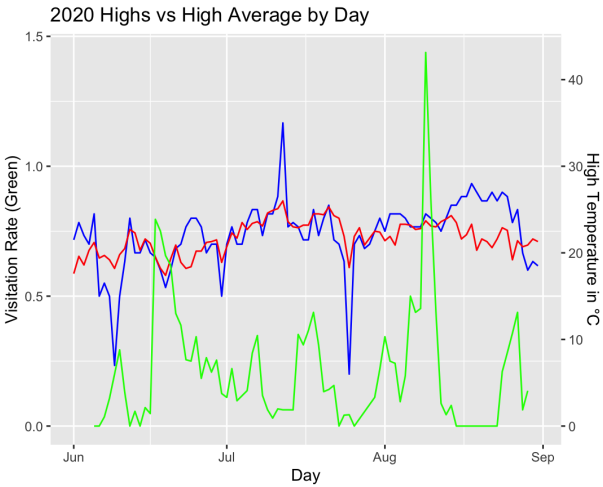
2019 Lows vs Low Average by Day



2019 Range vs Range Average by Day

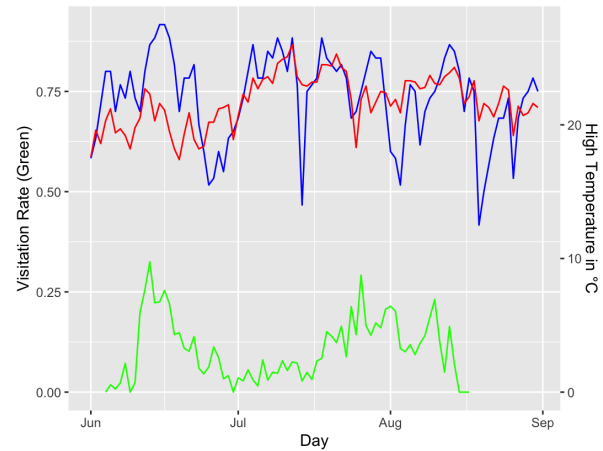


2020

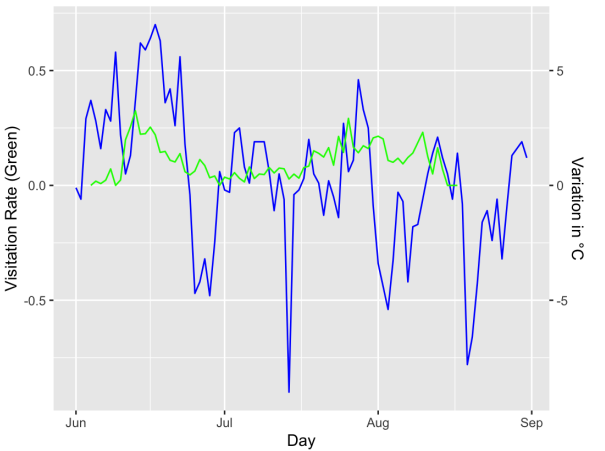


2021

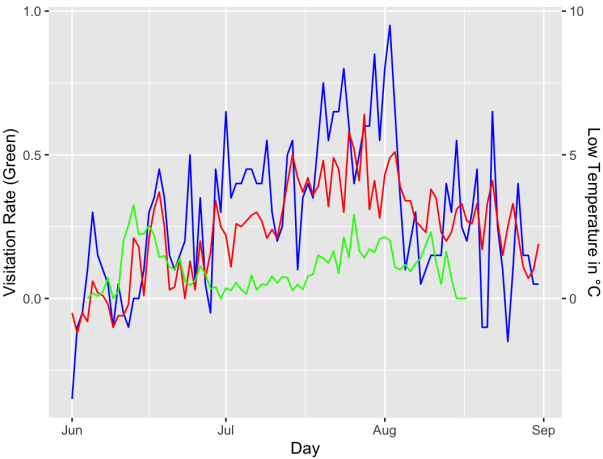
2021 Highs vs High Average by Day



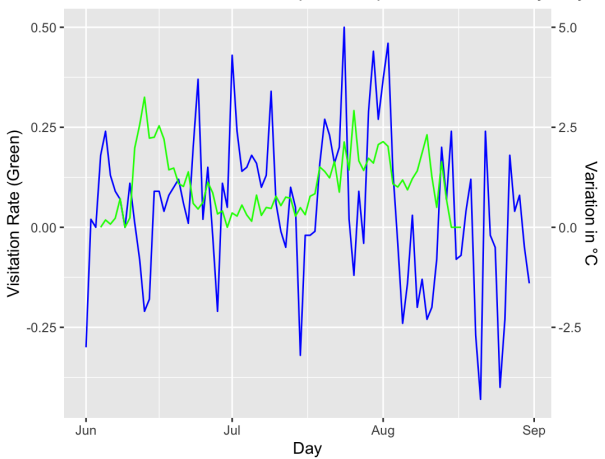
2021 Variation in High Temp and Top Visitation Rate by Day



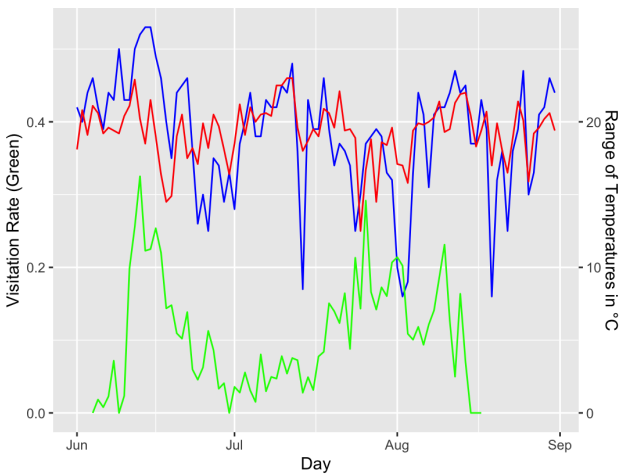
2021 Lows vs Low Average by Day



2021 Variation in Low Temp and Top Visitation Rate by Day



2021 Range vs Range Average by Day



2022

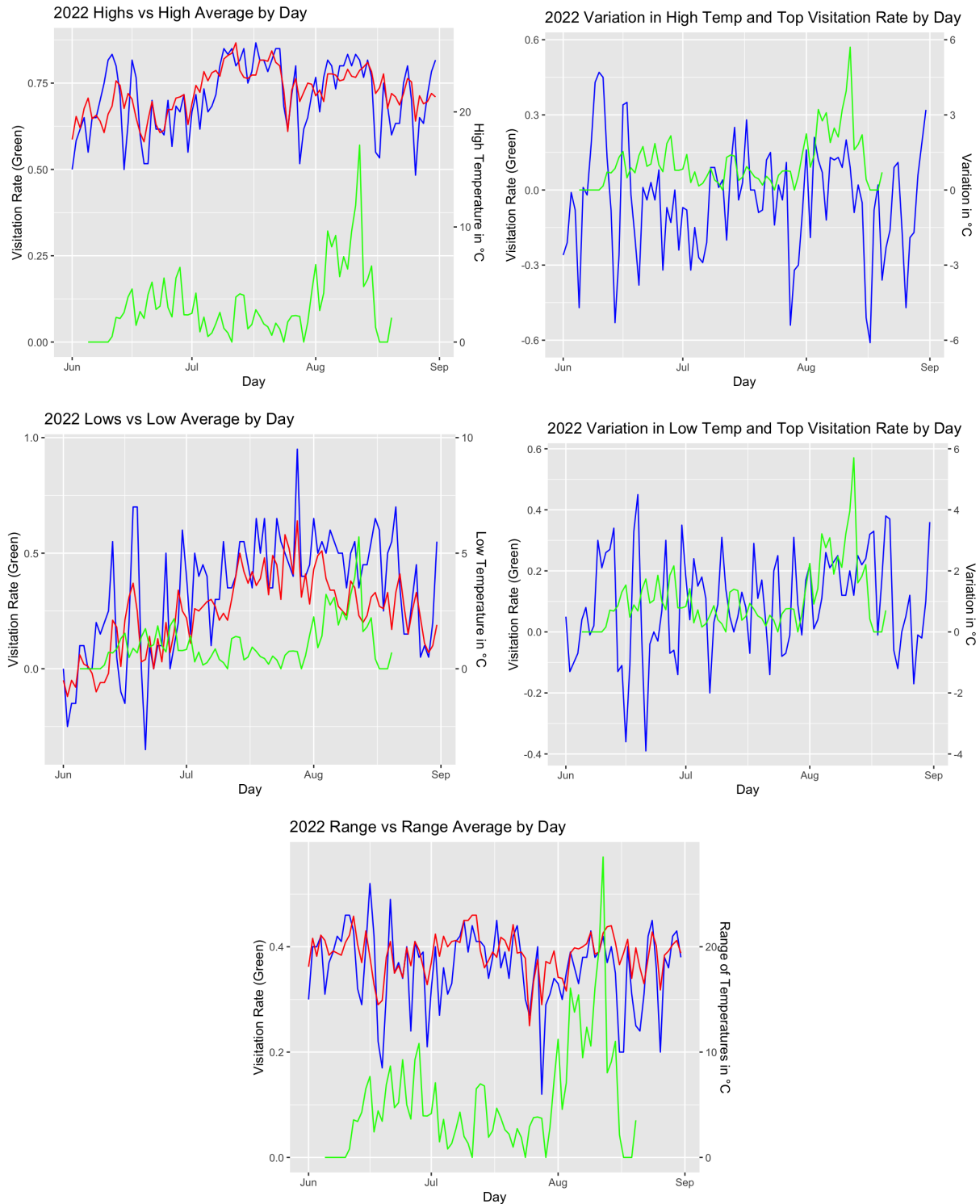


Figure 2. Time series graph separated by year: Temperature highs and high average (top left), variation in high temperature (top right), temperature lows and low average (bottom left), variation in low temperature (bottom right) and temperature range versus range average by day (bottom) plotted with hummingbird visitation rate (green).

1a: Average high and low temperatures versus hummingbird visitation rate

To address the question of whether temperature affects hummingbird visitation rate from another angle, we created some simple linear regressions. These four linear regressions (Figures 3 and 4) attempt to demonstrate the basic relationship between temperature and visitation rate. The first two (Figure 3) plot average highs and average lows against average visitation rate across all 5 years, with points color coded by month. Visually, June and August have a more variable visitation rate, and July and August tend to have higher average high and low temperatures than June. The R^2 values are 0.01 for the high temperature graph and less than 0.01 for the low temperature graph, and the p-values of the correlation are 0.05 and 0.68 respectively. This does not suggest that there is a linear relationship between average high temperatures or average low temperatures and average visitation rate, and that in the case of the high temperature graph, the lack of relationship between temperature and visitation rate is statistically significant.

The next two linear regressions (Figure 4) plot average highs and average lows against average visitation rate of the following day (labeled “Delayed visitation rate”), with points again color coded by month. The points display similar monthly patterns to Figure 3, and both R^2 values are less than 0.01. The p-values are 0.11 for the average highs and 0.80 for the average lows. Again, these low R^2 values and high p-values suggest that there is no relationship between temperature and hummingbird visitation rate.

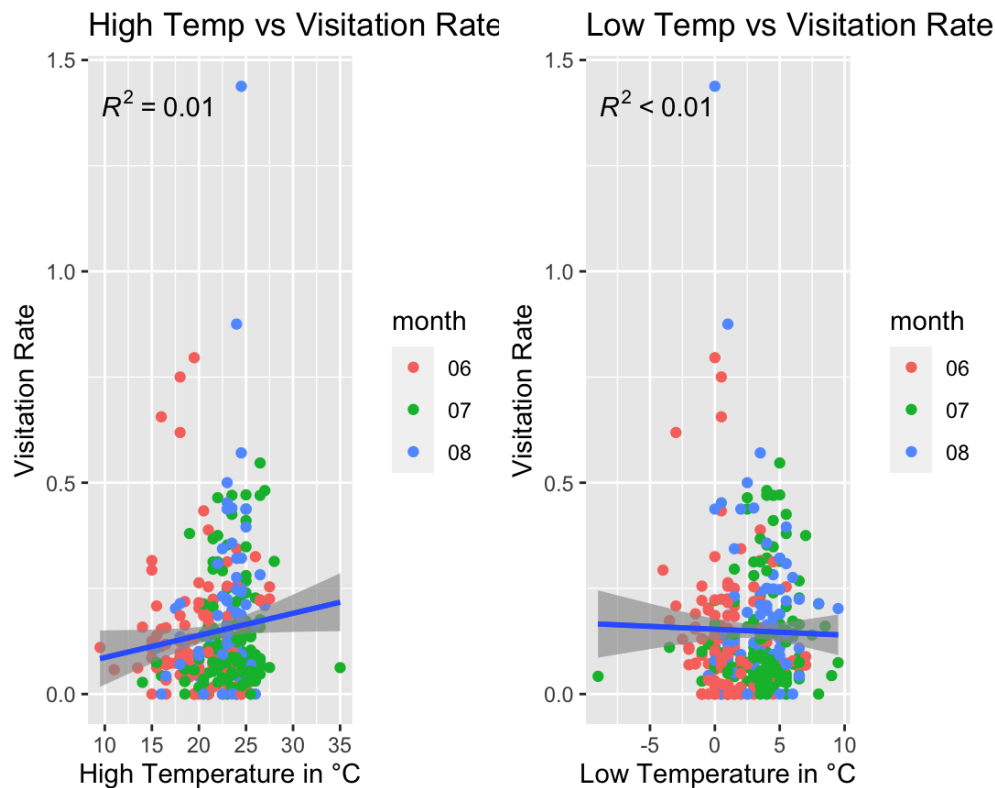


Figure 3. Linear regressions of average low and high temperature versus average visitation rate

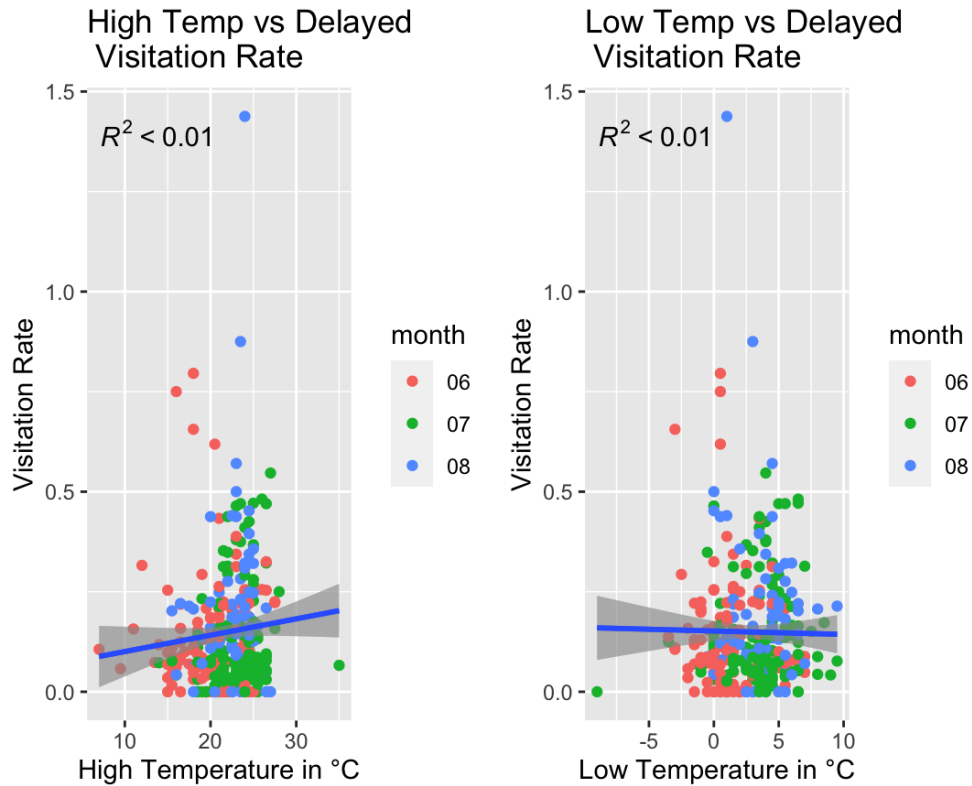


Figure 4. Linear regressions of average low and high temperature versus average visitation rate of the following day

Daily deviations from average high and low versus visitation rate by year

For each year, we graphed deviation from the average high temperature (labeled “high deviation”) and deviation from the average low temperature against visitation rate (“low deviation”), color coding points by month.

In 2018, the linear regressions (Figure 5) have R^2 values of less than 0.01 for high temperature deviation and 0.06 for low temperature deviation, as well as p-values of 0.77 and 0.72 respectively. July seems to have much higher visitation rates than June but not much difference in temperature deviation. The highest visitation rates are centered around 0 degrees in deviation for both graphs. There is no data for August.

The 2019 linear regressions (Figure 6) show R^2 values of 0.01 for high temperature deviation and 0.04 for low temperature deviation. The p-values of these associations are 0.31 for high temperature deviation and 0.24 for low temperature deviation. The months seem generally evenly distributed with no clear patterns, and the highest visitation rates fall around 0 degrees of deviation.

The R^2 values of the 2020 linear regressions (Figure 7) are less than 0.01 for high temperature deviation, which has a p-value of 0.89, and 0.02 for low temperature deviation, with a p-value of 0.61. June and August have the highest visitation rates, and they closely follow the

line of 0 degrees of deviation from the average high. For the low temperature deviation graph, the highest visitation rates are centered around 2.5 degrees below the average low.

The 2021 linear regressions (Figure 8) have R^2 values of 0.02 for high temperature deviation and less than 0.01 for low temperature deviation, and p-values of 0.04 and 0.12 respectively. This demonstrates that the high temperature deviation and visitation rate in particular do not have a relationship. There are no significant patterns for months. The highest visitation rates have a range in temperature deviation but are generally centered around slightly above 0 degrees of deviation.

In 2022, the linear regressions (Figure 9) show R^2 values of 0.04 for high temperature deviation and less than 0.01 for low temperature deviation. The association between high temperature deviation and visitation has a p-value of 0.06, and that of low temperature deviation has a p-value of 0.62. August has the highest visitation rates. The highest visitation rates are between 0 and 2.5 degrees of deviation above the average high temperature and 0 to 2.5 degrees of deviation above the average low temperature.

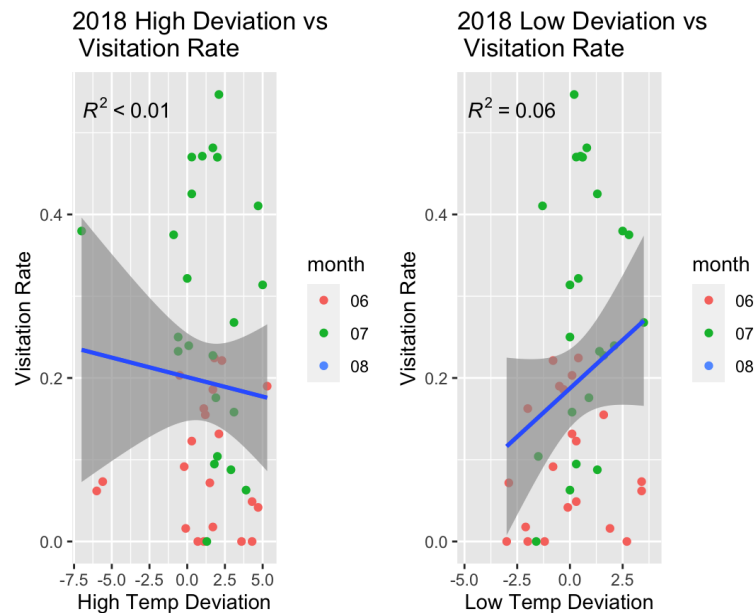


Figure 5. Linear regressions 2018 of high temperature deviation and low temperature deviation versus visitation rate

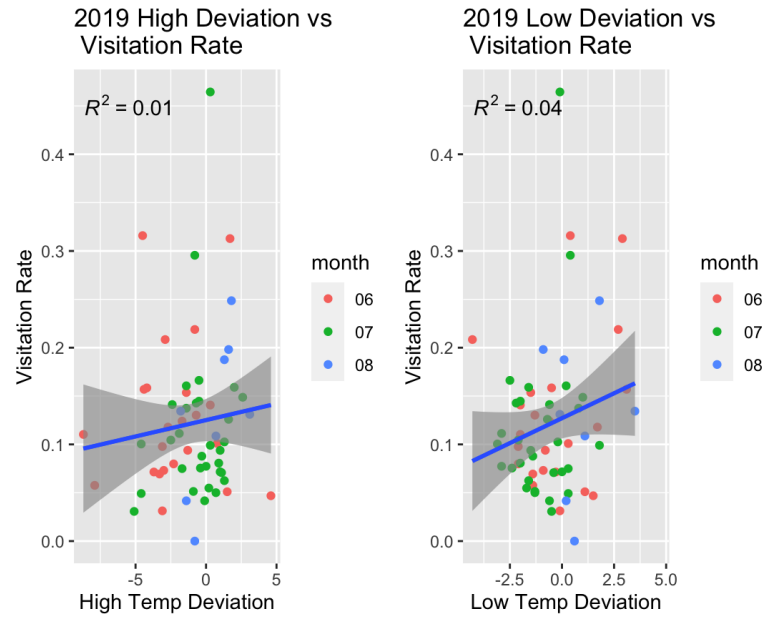


Figure 6. Linear regressions 2019 of high temperature deviation and low temperature deviation versus visitation rate

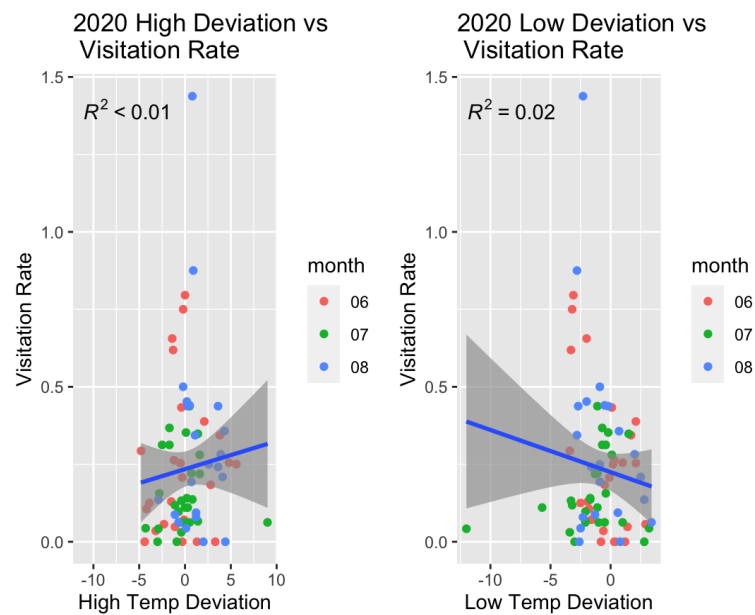


Figure 7. Linear regressions 2020 of high temperature deviation and low temperature deviation versus visitation rate

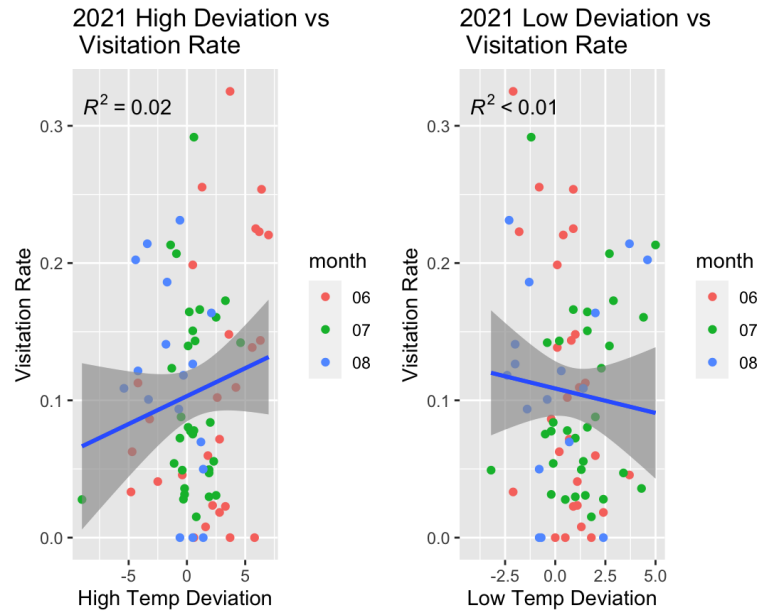


Figure 8. Linear regressions 2021 of high temperature deviation and low temperature deviation versus visitation rate

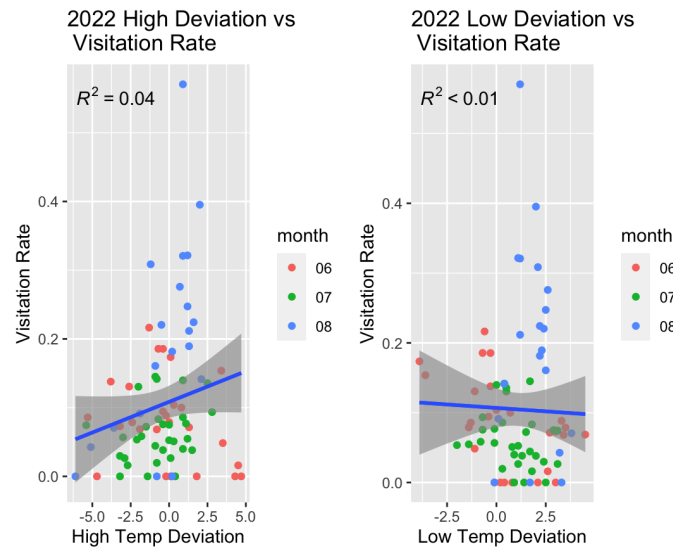


Figure 9. Linear regressions 2022 of high temperature deviation and low temperature deviation versus visitation rate

1b: Alienating potential effects of temperature variation

Because our temperature metric for some of our graphs is low and high temperature deviation, we wondered whether deviation from average high or low temperature might have different effects depending on what this average temperature is. For example, a high temperature that is 2 degrees Celsius higher than the expected temperature for a given day, based on the average of previous years' weather data for that day, might have more of an effect if the expected high temperature for that day is 27 degrees Celsius than if the expected high temperature is 20

degrees Celsius, if hummingbirds are more sensitive to extreme temperatures. For this reason, we created the eight graphs shown below—four linear regressions of high temperature deviation versus visitation rate (Figure 10), and four linear regressions of low temperature deviation versus visitation rate (Figure 11).

The R^2 values for the first three graphs looking at high temperature deviation versus visitation rate are 0.16, <0.01 , and <0.01 respectively. The p-values are 0.58, 0.93, and 0.81 (the fourth temperature subset only contains a single data point and therefore does not have an R^2 value nor a p-value.) The R^2 values for the second four graphs looking at low temperature deviation versus visitation rate are 0.02, 0.07, 0.01, and <0.01 . The p-values of these relationships are 0.29, 0.44, 0.19, and 0.07.

While the R^2 values for all eight graphs are too small to suggest that there is any strong relationship between temperature deviation, it is interesting to note that the highest R^2 value is seen in the graph of visitation rate versus high temperature deviation in the temperature bin of 9.5 to 16 degrees Celsius. This graph hints at a positive relationship between high temperature deviation and visitation rate in the 9.5 to 16 degree Celsius temperature range, meaning if the high temperature is significantly lower than average, we might expect the visitation rate to be lower as well. However, since the R^2 value is still only 0.16, only 16% of the variation in visitation rate can be explained by high temperature deviation, and this is not a high enough value to argue conclusively that there is a relationship between high temperature deviation and visitation rate in the 9.5-16 degree Celsius temperature range.

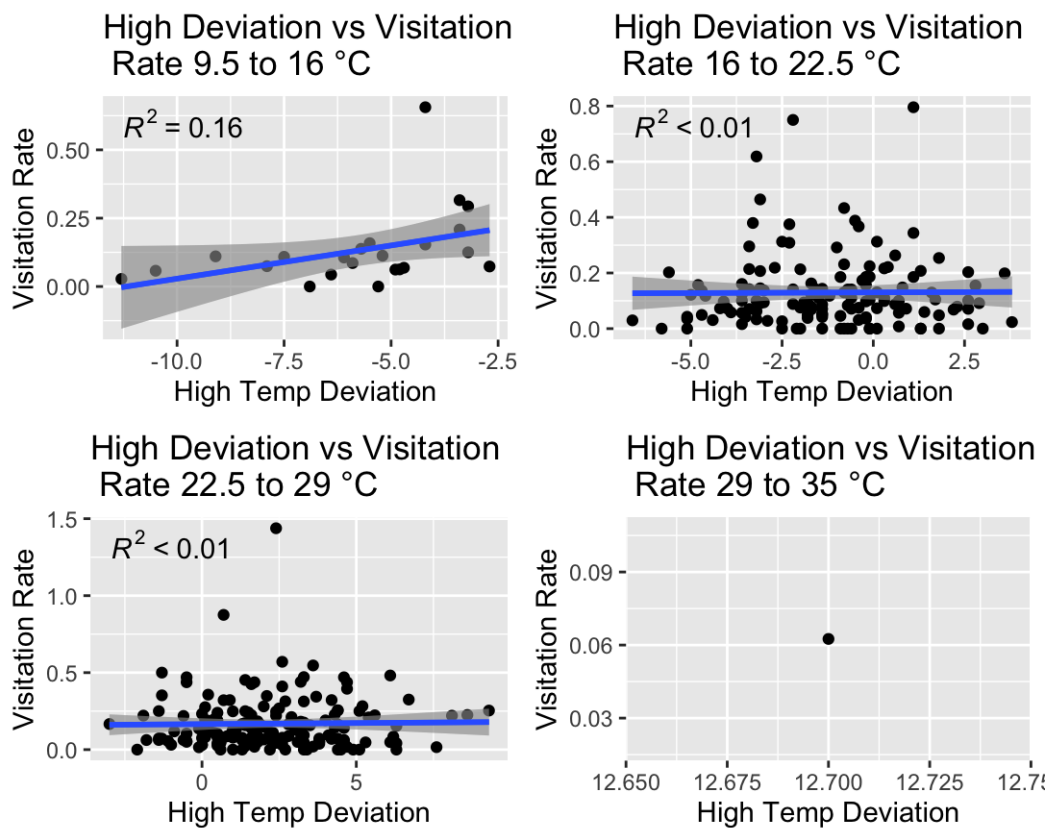


Figure 10. Linear regressions of visitation rate versus high temperature deviation, binned by temperature.

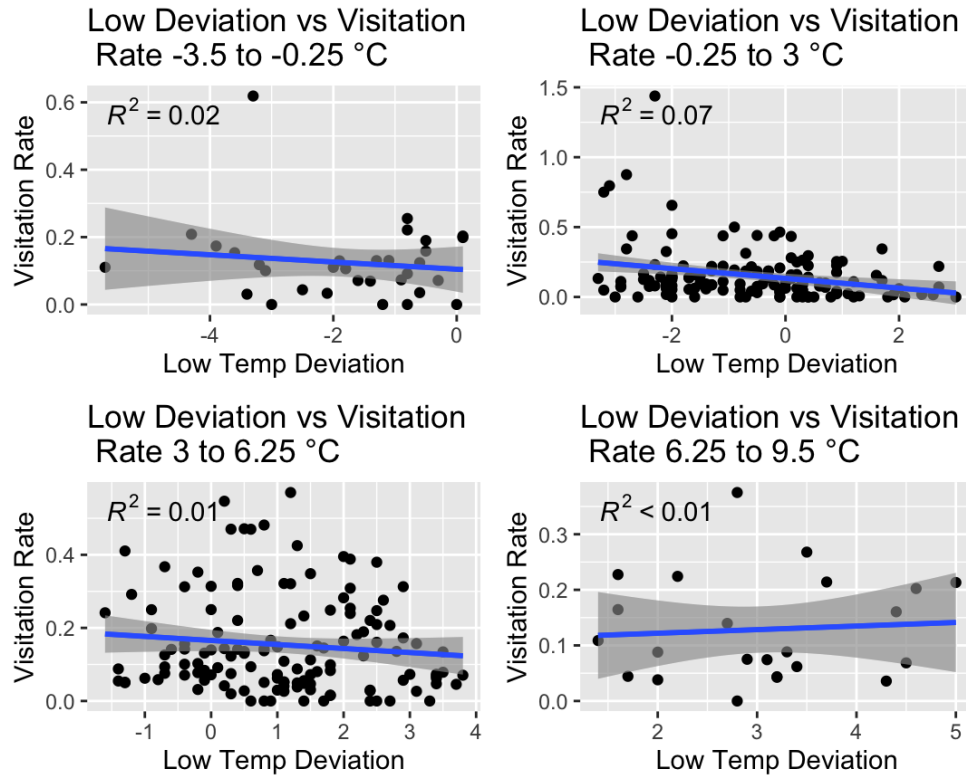


Figure 11. Linear regressions of visitation rate versus high temperature deviation, binned by temperature.

2: Differences by sex

Our second question was: how does hummingbird response to temperature differ with respect to sex? While our previous graphs do not suggest a relationship between daily temperature change and hummingbird visitation rate at all, we still decided to investigate whether there seems to be a difference in visitation rate according to sex, on the off chance that the lack of visible relationship between temperature and visitation rate was due to the fact that sex played a role in whether or not there was a relationship. Sex is determined by whether or not the hummingbird has a gorget, which introduces the caveat that birds we assume to be female could potentially be juvenile males.

We created four graphs: male visitation rate versus high temperature deviation, male visitation rate versus low temperature deviation, female visitation rate versus high temperature deviation, and female visitation rate versus low temperature deviation. None of our graphs produced statistically significant results, with the highest R^2 value being 0.06 for the female visitation rate versus high temperature deviation graph. This means only 6% of the variation in female visitation rate is explained by daily high temperature deviation from the expected high temperature. All of the other R^2 values are less than 0.01. The p-values were 0.88 for male visitation vs high temperature deviation, 0.60 for male visitation vs low temperature deviation,

0.03 for female visitation (suggesting a statistically significant lack of relationship) vs high temperature deviation, and 0.81 for female visitation vs low temperature deviation.

We therefore do not have any evidence to suggest that male and female broad-tailed hummingbirds are differently affected by temperature variation, if affected at all. We can conclude that our overall results are not being driven by differences in how and whether temperature affects visitation rate by sex.

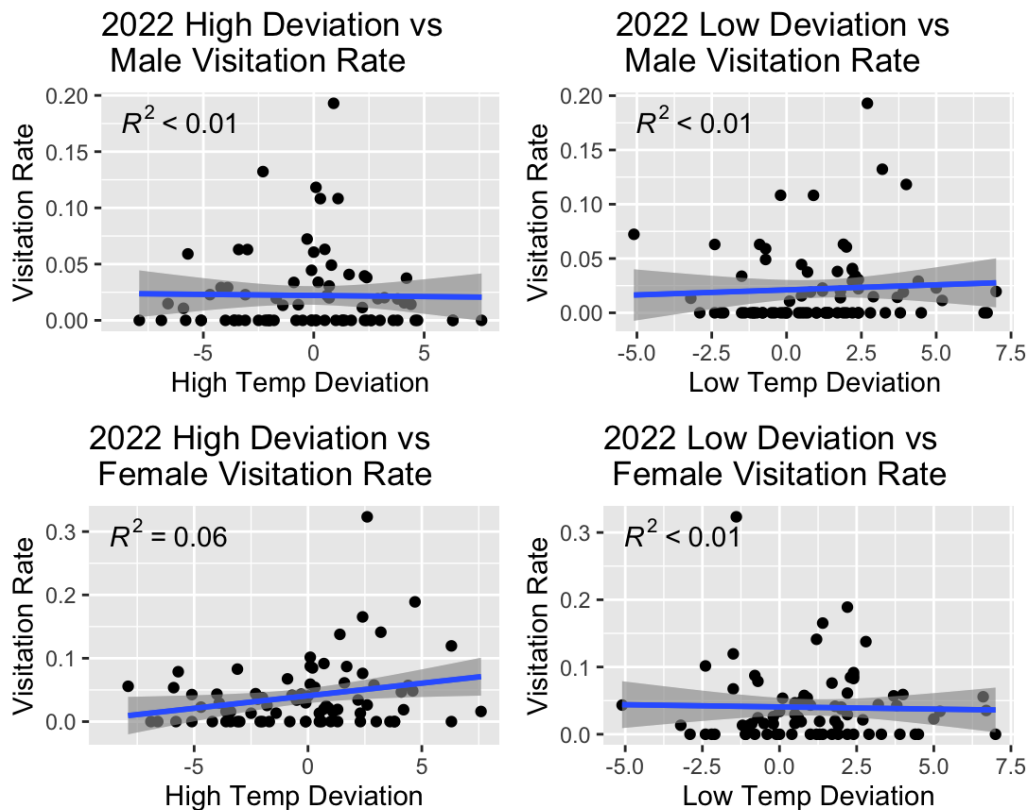


Figure 12. Linear regressions of hummingbird visitation rate versus high and low temperature deviation, separated by sex.

DISCUSSION

The main purpose of our project was to investigate whether temperature affects hummingbird visitation rate to wildflowers for Broad-tailed Hummingbirds in Gothic, Colorado. Our results lead us to conclude that there is no relationship between temperature and hummingbird visitation rate for the Broad-tailed Hummingbirds included in our study. Our time series graphs (Figure 2) show no clear visual patterns indicating that for a given year, temperature and hummingbird visitation rate correspond to each other. Our linear regressions of our calculated average visitation rate versus our calculated average high or low temperature for each day (Figures 3 and 4) have R^2 values of 0.01 and below, meaning there is no relationship between average visitation rate and average temperature. Our linear regressions of visitation rate

versus deviation from average high or low temperature, separated by year, also have low R^2 values, once again indicating that there is no relationship between temperature and visitation rate for these hummingbirds. Even when we created linear regressions with temperature binnings (Figures 10 and 11), we did not find any relationship between temperature and visitation rate. Furthermore, we did not find any evidence of a relationship between temperature and visitation rate when we created additional linear regressions of temperature and visitation rate, separated by sex (Figure 12).

However, we did note in our yearly linear regressions (Figures 5-9) that the highest visitation rates seemed to fall on days that did not deviate from average temperatures, or deviated very little. High visitation rates on days with “normal” or expected weather conditions for a given day might occur because of maximum resource availability. The wildflowers might be better suited for these weather conditions, while stress from unusually high or low temperatures could damage wildflower tissue, decrease the amount of flowers produced, and decrease nectar output (Forrest and Thomson, 2010; Hedhly 2011; Went 1953). Our hypotheses all took the form of predictions that visitation rate would uniformly increase or decrease as temperature increased or decreased. Based on this observation that highest visitation rates tended to fall on days with less temperature deviation from average, we see that another kind of relationship could be the case. Perhaps, as temperature deviates more from the expected temperature for that day in either direction, visitation rate decreases as well. Another potential explanation for higher visitation rates on dates with less temperature deviation could be that days with more “normal” temperatures are more likely to be sunny, predictable weather. Days with significant temperature deviation might be less likely to be stormy, and hummingbirds might be less likely to forage on stormy days. However, there is very little literature exploring this possibility directly. Future studies could more closely examine this potential relationship and its significance.

Overall, the lack of direct relationship between temperature deviation and visitation rate echo the findings of the Shankar et al. (2019) study on broad-billed hummingbird visitation and daily temperatures in Arizona. The researchers found that the DEE of daytime activity, such as feeding and defending territory, was much more significant than the DEE of thermoregulation at night. Thus, factors that directly influence daytime activity, such as flower availability and rain, affect visitation rate much more strongly than temperature. While they suggested that thermoregulation might demand more significant changes in visitation at high altitudes where temperatures are more variable, our research suggests no significant difference.

Thus, the paper suggests a number of factors indirectly informed by temperature variation and erratic weather that could more significantly influence visitation rate. A more comprehensive approach to understanding hummingbird visitation rates could account for how erratic temperature changes affect floral and nectar availability, harsh weather conditions, and where hummingbirds tend to forage (Shankar et al. note that hummingbirds could adapt their activity by foraging in the shade on hotter days). Additionally, we could examine how erratic temperatures interact with other phenologically important events, such as snowmelt timing, which can affect flower phenology and thus resource availability (Kudo and Ida, 2013). We could also adopt a

more physiological approach to understand how the many variables of DEE (such as energy expended during feeding and energy expended during thermoregulation) interact with each other, and how they may respond variably to tight energy budgets.

It is important to note the shortcomings of this study that may affect the accuracy of our results. Firstly, there may be a bias of camera placement on a convenience basis, as HummerFlowerWatch researchers tend to place cameras near the paths of our sites (see Figure 1 for site locations), in places that are more accessible but more heavily trafficked. While we try to vary flower locations and spread cameras evenly along the trails as detailed under Methods, there is no strong method for randomization. More research is needed to see whether location and disturbances affect hummingbird visitation rate. Secondly, we were unable to use any floral abundance data to understand the resources available and how well we represented flower populations with camera data. The HummerFlowerWatch team started collecting transect data in 2022, but it was not sufficient enough to be included in our study.

The finding that foraging patterns of Broad-tailed Hummingbirds in Gothic do not seem to be affected by day-to-day temperature changes or temperature patterns over the course of a summer may suggest that these hummingbirds can withstand erratic temperatures in the short-term. While they have tight energy budgets, they do not seem to be significantly harmed by temperatures being much warmer or cooler than expected relative to previous days. Our findings indicate that in a given summer, after hummingbirds have arrived, temperature variability does not seem to affect their ability to sustain themselves on local wildflower nectar. Furthermore, both male and female hummingbirds are able to survive even if temperatures change erratically daily or over the course of a season. However, as other research has suggested, this does not mean that hummingbirds are not being affected by climate change. It may be that larger-scale, longer-term temperature changes impact Broad-tailed hummingbirds more significantly than short-term changes in temperature (McKinney 2012). Thus, it seems that issues of phenological mismatch between wildflower blooming and hummingbird arrival must be addressed on a broader, more global scale (over decades rather than years, perhaps) in order to more fully understand how warming affects earlier wildflower blooming and hummingbird arrival dates. Only by unraveling these complex relationships can we help to ensure the stability and survival of hummingbird populations for the indefinite future.

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