# The Relationship between Color, Nectar Concentration, and Broad-Tailed Hummingbird Visitation of Typical and Atypical Hummingbird Flowers

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## Author Note

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## Abstract

Some wildflowers have evolved characteristics such as color and nectar concentration to target specific pollinators, creating pollination syndromes. We focus on hummingbirds and bees—with an emphasis on hummingbirds—as well as plants of their respective syndromes. Despite wildflowers' apparent evolution to cater to specific pollinators, researchers have observed bird and bee visitations to atypical plants, calling into question the effectiveness of pollination syndromes in distinguishing the bird and bee niches. This investigation uses Broad-tailed hummingbird visitation, flower color spectra, and floral nectar concentration datasets from the Rocky Mountain Biological Laboratory (RMBL) to answer the questions: How is hummingbird visitation influenced by flower color and nectar concentration? How are flower color and nectar concentration related to each other? We visualized flower spectra in tetrahedral and triangular color spaces for bird and bee vision, respectively. Our results reveal that hummingbirds prefer red-colored flowers. Color perception greatly influences hummingbird visitation, even more than nectar concentration does. In addition, we found that UV coloration and high nectar concentration successfully distinguish the bee pollination syndrome. Our results align with the previous finding that hummingbirds can effectively pollinate a wider variety of flowers than bees. We conclude that the pollination syndromes are generally effective in separating the pollinators' niches, avoiding competition. Finally, when separating our visitation data into two year ranges (2018-2021 and 2022-2024), we noted changes in visitation frequency to certain flower species, revealing that a changing climate may alter which plants are most energetically profitable to hummingbirds.

## Introduction

Both hummingbirds and bees are important pollinators in many ecosystems, and floral nectar is an essential component of both of their diets (Calder and Hiebert 1983; Haydak 1970). In this close relationship between pollinators and plants, flower color is especially important—for example, it has long been known that typical "hummingbird flowers," including *Ipomopsis aggregata*, often reflect red wavelengths (Cronk & Ojeda 2008; Pickens 1930). Hummingbirds and bees perceive color differently, owing to several key differences in their visual systems. Hummingbirds have four single cones, rendering them tetrachromats; in contrast, bees have three, rendering them trichromats (Peitsch et al. 1992; Stoddard et al. 2020). Bees have cones sensitive to ultraviolet, short (blue), and medium (green) wavelengths; peaking at 340 nm, 430 nm, and 535 nm, respectively (Peitsch et al. 1992). Birds have a similar set of three—peaking at 370 nm, 440 nm, and 508 nm—with the addition of a cone sensitive to long (red) wavelengths, peaking at 560 nm (Herrera et al. 2008). Therefore, hummingbirds are sensitive to a greater range of wavelengths (reviewed by Stiles 1976; Whitney et al. 2020). While both pollinators can see UV wavelengths, bees' visual systems are not as sensitive to wavelengths longer than 550 nm, which humans perceive as the red end of the visual spectrum (Chittka & Waser 1997; Peitsch et al. 1992; Stoddard et al. 2020).

Due to the differences in these two pollinators' visual systems, certain plants have evolved suites of traits—pollination syndromes—to cater to one or the other (Brown et al. 1981; Cronk & Ojeda 2008; León-Osper et al. 2025; Lunau et al. 2011). For example, a plant may experience selective pressure to make itself less attractive to bees because many bees rob

nectar—taking nectar without pollinating—which decreases the plant's fitness (Bolten & Feinsinger 1978; Chen et al. 2020b). It is hypothesized that plants in the bird pollination syndrome have evolved red flowers in order to avoid being conspicuous to bees (Chen et al. 2020b; Cronk & Ojeda 2008; León-Osper et al. 2025; Lunau et al. 2011). On the other hand, plants in the bee pollination syndrome have evolved flowers which include UV peaks in their spectra, corresponding to bees' innate preference for UV-containing flowers (Chen et al. 2020a; Lunau et al. 2011). Bird-syndrome and bee-syndrome plants have also evolved different nectar characteristics. Bird-syndrome flowers tend to produce nectar of lower concentration, while bee-syndrome flowers tend to produce nectar of higher concentration (Bolten & Feinsinger 1978; Cronk & Ojeda 2008; Nicolson & Thornburg 2007; Pyke & Waser 1981). Hummingbirds, like bees, prefer more concentrated nectar; however, bird-syndrome flowers likely evolved to produce less concentrated nectar in order to avoid nectar-robbing bees (Bolten & Feinsinger 1978).

While some flowers may have evolved to cater to hummingbirds, hummingbirds do not exclusively visit bird-syndrome flowers. Atypical hummingbird flowers—less-preferred flowers that are not red or pink in color, and not tubular in morphology—are still visited by hummingbirds and could provide energetic profit (Waser et al. 2018). Bees also have been recorded visiting bird-syndrome flowers, robbing the nectar of species such as *Ipomopsis aggregata* regardless of its bee-deterrent traits (Chittka & Waser 1997). Thus, despite plants exhibiting traits that target certain pollinators, hummingbirds and bees do not limit themselves to the plants of their own syndrome. These unexpected visitation behaviors reflect the non-exclusivity of plant evolution and establish a competitive relationship between hummingbirds and bees. More research is needed on pollinators' choice of plant species, especially in an era of a quickly-changing climate, which impacts flower availability throughout each breeding season (McKinney et al. 2012). Specifically, because hummingbirds visit a variety of flowers, it is unclear how their visitation rate per wildflower species is influenced by color perception and nectar composition. Additionally, given the competition between hummingbirds and bees for the same plant species, it is uncertain how effective the pollination syndromes truly are in separating their niches.

In this investigation, we examined the relationships between flower color, nectar concentration, and visitation frequency of Broad-tailed hummingbirds (*Selasphorus platycercus*) at the Rocky Mountain Biological Laboratory (RMBL). RMBL is situated in an alpine ecosystem where Broad-tailed hummingbirds breed every summer. In our analysis, we utilized our long-term dataset of hummingbird flower visitation at RMBL, separating the data into earlier and later year ranges (2018-2021 and 2022-2024) to discover how visitation patterns have changed recently. Firstly, we examined the spectral reflectance (Chang 2023) of our most and least hummingbird-visited plants, in order to develop an understanding of hummingbird flower color preference at RMBL. We then plotted these flower spectra as points within the color spaces of birds and bees—graphs in which a point's position corresponds to its photoreceptor stimulation. To clarify, the only instance of bees in our quantitative analysis was the color space—we did not focus on bee visitation to our selected flowers. These color spaces additionally encoded hummingbird visitation data for both year ranges, revealing how the pollinators' different color perceptions relate to hummingbird foraging behavior over time. Finally, we analyzed data on nectar concentration (Ngo 2025) to understand its relationship with flower color perception and

hummingbird visitation. By connecting these variables, we examined the factors influencing hummingbird visitation through a novel lens.

Using the most- and least-visited flowers from our hummingbird visitation data, we sought to answer these questions: How is hummingbird visitation influenced by flower color and nectar concentration? How are flower color and nectar concentration related to each other? Our investigation aims to refine current hypotheses on pollinator-specific evolution of flower color and nectar concentration, as well as reveal insights on hummingbird-bee competition for particular flower species. Future research can use our results in combination with phenology and yearly nectar concentration data to explore how changes in flower timing may affect nutrient availability throughout the breeding season, thereby affecting hummingbirds' flower choice and populations. These findings may also inform us about how the changing climate influences pollination within alpine communities.

## Methods

### Data Collection

#### *HummerFlowerWatch*

In order to quantify hummingbird visitation, we used data from HummerFlowerWatch, a long-term dataset collected from 2018-2024. The HummerFlowerWatch methodology includes instrument installations of Brinno 200TLC cameras at field sites, previously approved by RMBL. The cameras took one photo per second from 5am to 9pm to make a time-lapse video.

The data collection procedure was as follows: Firstly, cameras were positioned on flowers in good condition out of 33 possible species which hummingbirds could visit. Cameras were placed at 3 possible sites at or near RMBL: Stupid Falls, Judd Falls, and RMBL Townsite. Each camera was trained on a focal flower for ~3 days before it was moved to a different focal flower, and its batteries and SD card replaced. Flowers were chosen opportunistically, but the researchers attempted to place cameras in a manner that was representative of the flower abundance at that time. When a camera was placed, metadata was recorded of its flower species, GPS location, and date. Videos retrieved from SD cards were transferred to a hard drive.

After each field season, videos were analyzed for hummingbird visits by the machine learning software DeepMeerkat (Weinstein 2018). The threshold for hummingbird detectance was set low, so researchers could look through detected visits to filter out the false positives. Next, using Matlab and R, the number of all true positive visits was compiled and disseminated to the research group. For each flower species, we quantified visitation rate as visits per hour of footage.

**Focal Species.** In our study, we focused on flower species with >1100 hours of footage in the HummerFlowerWatch database from 2018-2024, leaving us with 23 potential species. We chose 10 species which were among the most- and least-visited flowers for further analysis, under the assumption that they would most distinctly occupy the bird- and bee-syndromes.

Most Visited:
- *Ipomopsis aggregata*
- *Lonicera involucrata*
- *Castilleja spp.*
- *Aquilegia elegantula*
- *Delphinium barbeyi*

Least Visited:
- *Frasera speciosa*
- *Aconitum columbianum*
- *Campanula rotundifolia*
- *Aquilegia coerulea*
- *Polemonium foliosissimum*

***Reflectance Spectra***

To quantify flower color, we used reflectance spectrophotometry, which generates a graph of reflectance as a function of wavelengths ranging from UV to visible light. Because variation in spectral sensitivity among species causes different perceptions of color, these spectra provide an objective measure of what wavelengths are reflected by the flowers.

Most of the flower reflectance spectra used in this investigation were collected in 2022 by lab member Darcy Chang using an Ocean Optics (Orlando, FL, USA) USB400 UV-Vis spectrophotometer, a 1/4 inch (6350 micrometer) bifurcated fiber optic reflectance probe, and a PX-2 lamp. Spectra were normalized to a white Spectralon (Labsphere, Sutton, NH, USA) 99% reflectance standard, integration time was set to 100 ms, and both scans-to-average and boxcar width were set to 10 (Chang 2023).

We supplemented this dataset with two additional species of interest: *Lonicera involucrata* and *Frasera speciosa*. We collected spectra using an Ocean Optics Flame Miniature Spectrometer and a 400 micrometer bifurcated probe. Following the methods in Chang 2023, we picked approximately 3 flowers of each species a few centimeters from the flower head, placed them in a plastic container with a wet paper towel for transportation, and measured the reflectance of their petals on a sheet of black velvet paper with the spectrophotometer probe at a 90° angle from the surface. We took measurements of each distinct color patch—qualitatively characterized and named—on sepals and each side of the petals. We took 3 replicate spectra for each patch. If individual petals were transparent, we stacked multiple petals until the specimen was opaque enough to generate consistent spectral readings. The number of petals stacked was noted in the metadata.

***Nectar Concentration***

For nectar data, we used nectar concentration values from a 2024 database collected by lab member Trang Ngo. Nectar volume was also a major component of this database, but we decided not to include it in this investigation because previous work has shown that for each flower species, nectar concentration more strongly predicted hummingbird visitation than nectar volume, yielding a higher $R^2$ value (Ngo 2025).

The nectar concentrations were collected using the following method: Flowers in good condition were opportunistically chosen and bagged with white fine mesh netting 2 days before nectar collection. After 2 days, the netting was removed, and a Drummond (Broomall, PA, USA) microcapillary 5µl or 10µl glass tube was placed into nectaries. The exact nectar collection methodology varied by species, and was noted in the metadata. To measure concentration, nectar was gently blown onto a handheld refractometer (Fisher Scientific, Hampton, NH, USA), and concentration was read in degrees Brix. Altogether, 12 species from Stupid Falls and Judd Falls were measured. It should be noted that if nectar concentration exceeded 62%, Ngo signified this data as >62 in her dataset. In our calculations, we regarded these values as 62%.

**Data Analysis**

***Reflectance Spectra***

In order to analyze our data, we created figures using the pavo package (Maia et al. 2019) in R (R Core Team 2026). Firstly, we visualized the reflectance spectra of our 10 flower species of interest, and utilized the spec2rgb function to color the spectra with its human-perceived color. Because distinct patches on each flower may produce different spectra, we chose the spectrum of the color which occupies the qualitatively greatest externally-visible surface area to represent that flower. In these spectra, the independent variable is wavelength (nm), and the dependent variable is reflectance (%).

To investigate how bird and bee perceptions of these flower colors may differ, we plotted the 10 colors in two visual spaces: A tetrahedral space representative of tetrachromatic bird vision, first proposed by Burkhardt (1989) and Goldsmith (1990); and a triangular space representative of trichromatic bee vision, attributed to Maxwell (1860). We used the avg.v and apis phenotypes in pavo to model cone stimulation in birds and bees respectively. We then plotted points within the tetrahedral and triangular spaces. This is possible because the flower spectra are represented by the relative stimulation of each type of individual cone in bird and bee vision, allowing each flower to be plotted as a single point within these geometric spaces. We used pavo's vismodel and colspace functions to achieve this visualization, and points were colored with their human-perceived colors. In order to determine whether the most-visited and least-visited flowers occupy significantly different positions in either color space, we used each flower's achieved chroma: its distance from the center of the visual space (Stoddard & Prum 2008), where a value of 1 represents the space's vertex (Maia et al. 2019). A greater achieved chroma signifies that the flower occupies a more polar area of the color space (i.e. generates colors that are more saturated), and is more likely to contrast against a natural background, thereby being more detectable to the species (Cazetta et al. 2007; Endler 1992). We calculated the achieved chroma for both the bird and bee visual systems and then ran Welch's t-tests to conclude whether there was a significant difference between the achieved chromas of the most- and least-visited flowers in either color space. Overall, visualizing the 10 flower spectra and plotting them in bird and bee color spaces revealed quantitative insights into hummingbird color preference.

### *Reducing Color into Single Variables*

Because we were interested in analyzing the relationship between color and other variables such as visitation and nectar concentration, it was necessary to simplify our set of 10 spectra into 10 points, for ease of performing linear regression. To do this, we first used two single colorimetric variables—S1R and S1U—which are outlined by Montgomerie (2006) and pavo documentation (Maia et al. 2019). S1R is defined as the relative contribution of wavelengths >605 nm to the spectrum's total reflectance, analogous to its "redness;" S1U is the relative contribution of wavelengths <400 nm, analogous to its "UV-ness" (reviewed by Maia et al. 2019). When using linear regression to find the relationship between color and other variables, we utilized S1R and S1U as single-point representations of "redness" and "UV-ness," comparing them side-by-side.

Most of our analyses on chroma were done with the achieved chroma measurement and involved comparisons within each color space. However, we had a secondary interest in how the chroma differed across the color spaces. In order to make this comparison with a single variable, we calculated each flower's chroma ratio—its achieved chroma in bird color space divided by its achieved chroma in bee color space. If the value was >1, then that flower is visually more chromatic to a hummingbird than to a bee. If it was <1 , the opposite would be true. Overall, simplifying flower color into quantitative variables allows us to more easily perform statistical analyses with regards to visitation and nectar concentration.

### *Color vs Hummingbird Visitation*

To understand the relationship between color and hummingbird visitation, we first plotted each flower's color within the tetrahedral and triangular visual spaces, sizing each point proportionally to its visitation rate. Therefore, more-visited flowers appear as larger points. In order to learn how hummingbird visitation has recently changed, we created two sets of these plots: one using visitation data from 2018-2021 ("early"), and one for 2022-2024 ("late"), splitting our dataset into two separate year ranges for comparison. In these plots, our independent variables are flower color and year range, and our dependent variable is hummingbird visitation rate (visits/hour).

For a statistical analysis of visitation over time, we first ran a paired t-test between the early and late year ranges, to find out if hummingbird visitation to all 10 flowers had significantly changed with the years. For a more granular view of this change, we applied the same paired t-test to the most- and least-visited flowers separately, for a total of three t-tests. For a statistical analysis of the relationship between color and visitation, we ran a linear regression of visitation for either year range against S1R, S1U, and chroma ratio, creating six combinations of variables overall. Thus, our independent variables for the regression are S1R, S1U, chroma ratio, and year range; and our dependent variable is visitation rate (visits/hour).

The color space plots qualitatively reveal to us the relationship between flower color—as perceived by both birds and bees—and hummingbird visitation, and how this relationship may have shifted recently. Our t-tests definitively indicate whether visitation has changed significantly between the year ranges. Finally, our linear regressions quantify the extent of the

relationship between color and visitation, specifically with regards to how “red” or “UV” a flower is, as well as to the flower’s saturation disparity between birds and bees.

### *Nectar Concentration vs Hummingbird Visitation*

We first utilized our nectar concentration dataset by plotting hummingbird visitation against nectar concentration for both 2018-2021 and 2022-2024. Thus, the independent variables are nectar concentration (% w/w) and year range, and the dependent variable is visitation rate (visits/hour). We then ran a linear regression on these graphs to reveal the strength of the relationship for either year range. From these graphs, we learn how closely nectar concentration is related to hummingbird visitation, and whether this relationship has changed in recent years.

### *Color vs Nectar Concentration*

We explored the relationship between color and nectar concentration by creating the same bird- and bee-color space plots, except each point was sized according to its nectar concentration (%), meaning flowers with more concentrated nectar appear as larger points. We omitted the flowers with no nectar concentration data, leaving 7 points. Our independent variables are color and year range, and our dependent variable is nectar concentration (%).

To determine whether the most- and least-visited flowers differed significantly in nectar concentration, we ran a Welch’s t-test comparing the groups. To statistically analyze the relationship between color and nectar concentration, we performed a linear regression of nectar concentration against S1R, S1U, and chroma ratio. Therefore, for this analysis, our independent variables are S1R, S1U, and chroma ratio; and our dependent variable is nectar concentration (%).

Using the color space, we visually assessed the relationship between color—in both bird and bee vision—and nectar concentration. Our statistical analyses provided a more quantitative measure of whether the most- and least-visited groups were significantly different, as well as the extent to which red hues, UV hues, and saturation disparity were related to nectar concentration.

## Results

### *Reflectance Spectra*

We observed that the four most-visited plants had peak reflectances at long wavelengths (600-700 nm), appearing red to humans (Figure 1). *Delphinium barbeyi* was an exception, peaking at a short wavelength (431 nm). The four least-visited plants had similar bimodal spectra, with peaks at ~400-500 nm and ~700 nm (Figure 1). *Frasera speciosa* was unlike these plants, with a somewhat flat shape from 450 nm to 700 nm.

### *Color vs Hummingbird Visitation*

We qualitatively observed that the most- and least-visited flowers did not occupy distinct areas within the bird color space, though the most-visited flowers tended to exist near the red

vertex while the least-visited flowers tended to exist near the achromatic center (Figure 2; Supplemental Figure 2). A Welch's t-test revealed that the achieved chroma of the most- and least-visited flowers did not differ significantly within this color space ($t(5.28) = 0.58$, $p = .59$).

We found through a paired t-test that the overall frequency of hummingbird visitation is not significantly different between 2018-2021 and 2022-2024 ($t(9) = 0.09$, $p = .93$). Additionally, when we ran the t-test on the most- and least-visited flowers separately, there was no significant difference in visitation rate between the year ranges (most-visited: $t(4) = -0.10$, $p = .93$; least-visited: $t(4) = 2.23$, $p = .09$). That said, we noted differences in the visitation rates of some species between Figures 2A and 2B, such as *Ipomopsis aggregata* (18.95% increase) and *Lonicera involucrata* (81.30% increase).

Qualitatively, we did not observe the most- and least-visited flowers occupying distinct areas of the bee color space (Figure 3; Supplemental Figure 2). Through a Welch's t-test, we found a significant difference between the achieved chromas of the most-visited and least-visited flowers in the triangular color space ($t(6.74) = -2.61$, $p = .04$). To bees, the most hummingbird-visited flowers had a lower average achieved chroma ($M = .1761$, $SD = .07498$) than the least hummingbird-visited flowers ($M = .2794$, $SD = .04719$).

S1R ("redness") significantly predicted hummingbird visitation only in the early year range, with a p-value of .02 (Table 1). The R value was .72 and the $R^2$ value was .52, meaning 52% of variance was explained by S1R in 2018-2021. In contrast, S1R did not significantly predict hummingbird visitation in 2022-2024. S1U ("UV-ness") did not significantly predict hummingbird visitation in either year range, though it had a higher $R^2$ value in the late year range than the early one (Table 1).

Chroma ratio significantly predicted hummingbird visitation in both year ranges (Table 1). The R value was .77 for the early year range and .72 for the late year range—both values indicate a strong ability for our linear model to explain our data's variance. In addition, we observed all chroma ratio values to be >1 (Supplemental Table 2), signifying that our models predict all 10 floral colors to be more chromatic in the bird color space than the bee color space. In order to confirm a difference in chroma ratio between the most- and least-visited flowers, we performed an additional Welch's t-test, finding a significant difference in the groups ($t(5.17) = 2.84$, $p = .03$).

***Nectar Concentration vs Hummingbird Visitation***

After performing a linear regression, we found a p-value of .27 and a low $R^2$ value of .23 for 2018-2021, suggesting that nectar concentration cannot significantly predict early hummingbird visitation (Figure 4A). For 2022-2024, we found a p-value of .25 and a low $R^2$ value of .25, suggesting that nectar concentration also cannot significantly predict late visitation (Figure 4B). In sum, we observed no significant relationship between nectar concentration and hummingbird visitation for either year range.

### *Color vs Nectar Concentration*

We qualitatively observed that the flowers which clustered near the red vertex of the bird color space tended to have lower nectar concentrations, while the "purple" flowers near the center of the space tended to have higher nectar concentrations (Figure 5). A Welch's t-test between the most- and least-visited flowers revealed no significant difference in nectar concentration ($t(4.91) = -0.56$, $p = .60$). However, when we qualitatively grouped the flowers into "red" and "purple" groups, a Welch's t-test revealed a significant difference in nectar concentration ($t(3.59) = -3.08$, $p = .04$). "Red" flowers consisted of *Ipomopsis aggregata*, *Castilleja spp.*, and *Aquilegia elegantula*. "Purple" flowers consisted of *Delphinium barbeyi*, *Aconitum columbianum*, and *Campanula rotundifolia*. On average, the "red" flowers had lower nectar concentrations ($M = 24.20\%$ w/w, $SD = 6.642\%$ w/w) than the "purple" flowers ($M = 44.71\%$ w/w, $SD = 9.446\%$ w/w).

In Figure 6, we qualitatively observed "red" and "purple" flowers to occupy distinct areas of the bee color space, much like the bird color space in Figure 5. Likewise, the "red" flowers' lower nectar concentrations and "purple" flowers' higher concentrations were visually apparent in Figure 6.

S1R ("redness") could not significantly predict nectar concentration, though it had a moderate $R^2$ value of .53, suggesting that the linear model explained some of the variation for this parameter (Table 2). On the other hand, S1U ("UV-ness") significantly predicted nectar concentration ($p = .02$; Table 2). Its high R value of .84 and high $R^2$ value of .70 signaled that our model could explain much of the variation in our data.

Additionally, chroma ratio did not significantly predict nectar concentration, with a p-value of .13 (Table 2). The low $R^2$ value of .39 indicated that our model explains little of the variation in our data.

## Discussion

### *Reflectance Spectra*

First, we measured the reflectance spectra of our 10 selected flowers. The spectra reveal that the most hummingbird-visited plants exhibit greater reflectance at longer wavelengths (Figure 1), aligning with past studies that have concluded that typical "hummingbird flowers" are red (Cronk & Ojeda 2008; Pickens 1930). Correspondingly, cone-stimulation histograms for bird vision indicate that these flowers stimulate the long-wavelength cone the most and UV the least (Figure 1). None of the least-visited flowers stimulate the long-wavelength cone the most. Additionally, instead of the general shape skewing left like the typical hummingbird flowers, the least-visited spectra are bimodal (with exception to *Frasera speciosa*). The combination of maxima at 400-500 nm and 700 nm forms what we perceive as purple. These spectra visually convey how the colors of our most- and least-visited plants are distinct from each other, supporting the hypothesis that hummingbirds have a color preference for red.

***Color vs Hummingbird Visitation***

We investigated the relationship between flower color and hummingbird visitation using color spaces and linear regressions of visitation against color variables. We found that a plant's UV reflectance does not determine foraging frequency—S1U did not have a significant relationship with hummingbird visitation in both past and recent years. In contrast, our results supported the observation that more-favored flowers are "redder" (Cronk & Ojeda 2008; Pickens 1930), as S1R had a positive relationship with visitation in 2018-2021, albeit no significant relationship in 2022-2024. Even though there was no significant change in the overall visitation rate between the early and late year ranges, hummingbirds are foraging at *Ipomopsis aggregata* and *Lonicera involucrata* more frequently while the visitation rate at the other eight plants decreased. Hummingbird visitation to non-favored flowers in 2022-2024 was miniscule (Figure 2B; Figure 3B). Despite not finding a significant difference in visitation between the year ranges, it is interesting to note that hummingbirds can learn to associate color with reward, consequently changing flower preference (Meléndez-Ackerman et al. 1997). Therefore, this pattern of favoring specific plants may imply a beneficial component of *Ipomopsis aggregata* and *Lonicera involucrata* that has made them more favorable in recent years. *Ipomopsis aggregata*, specifically, produces less sugar on overcast, drizzly, and humid days (Pleasants 1983). Relevantly, precipitation variability is increasing in warmer climates which could lead to many dry periods (Pendergrass et al. 2017). The increasing temperature and decreasing humidity may cause specific plants to produce more concentrated nectar. In turn, these plants may become more appealing to hummingbirds, which prefer more concentrated nectar (Bolten & Feinsinger 1978).

We found that the differing visual perceptions between birds and bees do relate to hummingbird foraging behavior—as the achieved chroma ratio between the bird and bee color spaces increases, so does hummingbird visitation. The typical hummingbird flowers are more chromatic to birds than to bees, which aligns with our understanding. Fascinatingly, the least-visited flowers are also more chromatic to birds than to bees, despite bees theoretically being more attracted to them. This unexpected result adds nuance to the pollination syndrome concept of plants evolving to be more visually noticeable to a certain pollinator (Chen et al. 2020a; Chen et al. 2020b; Cronk & Ojeda 2008; León-Osper et al. 2025; Lunau et al. 2011), because the bee-syndrome plants are more chromatic to birds. However, hummingbirds still significantly see "red" plants as more chromatic than the "UV" ones, so they may be more attracted to the plants of their own syndrome. An explanation for our results is that birds can effectively pollinate bee-syndrome flowers, but bees are ineffective pollinators for bird-syndrome flowers (Castellanos et al. 2003). Therefore, to prevent completely discouraging visitation from one of their pollinators, the least-visited flowers are still comparably chromatic to hummingbirds. The most-visited flowers remain significantly more chromatic to hummingbirds than to bees, aligning with the claim that they evolved to avoid visual detection by bees, which may rob their nectar (Chen et al. 2020b; Cronk & Ojeda 2008; León-Osper et al. 2025; Lunau et al. 2011). Overall, color seems to have a great effect on hummingbird foraging behavior. The pollination syndromes appear effective in partitioning flowers by color, but there are nuances in which pollinators each flower species visually targets.

### *Nectar Concentration vs Hummingbird Visitation*

We examined the relationship between floral nectar concentration and hummingbird visitation using linear regressions of visitation against nectar concentration. We found no relationship between nectar concentration and hummingbird visitation in 2018-2021 or 2022-2024, which refutes our hypothesis that as nectar concentration decreases, hummingbird visitation increases. This means that the dilute nectar characteristic of bird-syndrome plants does not have a major influence on our observed hummingbird visitation.

Though hummingbirds have an innate preference for higher-concentration nectar, it is not the primary driving factor for floral selection, as bird-syndrome plants have evolved dilute nectar to avoid nectar-robbing bees (Bolten & Feinsinger 1978), meaning pollinator competition may have a strong effect on plant evolution. Birds forage to optimize their net energy per unit volume consumed, which minimizes the need to visit many flowers. Therefore, despite having an innate preference for concentrated nectar, they optimize energy intake by minimizing visits (Montgomerie et al. 1984). By avoiding flowers with concentrated nectar that bees may have depleted, they spend less energy foraging and minimize competition. This explanation corresponds to our results showing a lack of strong hummingbird preference for nectar concentration—they simultaneously may benefit from the energy content of concentrated nectar and minimized inter-pollinator competition from flowers with dilute nectar. That said, this lack of overall preference raises a tension in our previously-discussed reasoning that hummingbirds may be altering their flower choice due to shifts in nectar concentration from a changing climate, decreasing our confidence in that conclusion.

### *Color vs Nectar Concentration*

We investigated the relationship between flower color and nectar concentration using color spaces and linear regressions of nectar concentration against color variables. Our results agree with previous findings that bees have an innate preference for both UV color and highly concentrated nectar (Bolten & Feinsinger 1978; Chen et al. 2020a)—out of the color variables investigated, only S1U had a significant positive relationship with nectar concentration. This result suggests that the bee pollination syndrome is quite distinct, since plants tend to exhibit these two traits together. In contrast, the bird pollination syndrome does not appear as distinct with regards to color and nectar concentration, because we found no relationship between S1R and nectar concentration.

Additionally, our results correspond with previous findings that flower color has little or no association with nectar concentration (Streinzer et al. 2021), as our t-tests between the most- and least-visited flowers revealed no significant difference in nectar concentration. However, we observed significant differences in nectar concentration when qualitatively grouping the flowers into “red” and “purple” instead of most- and least-visited, with “red” flowers producing less concentrated nectar compared to “purple” flowers. We gather that the categorization of a flower’s color may play an important role in whether one finds a relationship with nectar concentration.

Why don’t hummingbirds forage at “purple” flowers more frequently if they have an innate preference for concentrated nectar? Despite hummingbirds potentially benefiting from

visiting flowers with highly concentrated nectar (Waser et al. 2018), our results show that color is more influential on hummingbird visitation. Therefore, a hummingbird would prefer a "red" flower over a flower with concentrated nectar, and "red" flowers tend to have less concentrated nectar (Cronk & Ojeda 2008; Nicolson & Thornburg 2007; Pyke & Waser 1981). Overall, our results align with the hypothesis that flower color and nectar concentration create distinct niches for the pollinators. More specifically, color is a greater determinant in hummingbird visitation than nectar concentration, thus exerting a greater influence on what is categorized as a bird-syndrome plant.

## Conclusion

We studied the relationships between flower color, nectar concentration, and Broad-tailed hummingbird visitation to 10 wildflower species in the alpine ecosystem of RMBL. The goals of our investigation were to refine current hypotheses on the evolution of pollination syndromes and explore the extent of hummingbird-bee competition for flowers.

First, our results support the hypothesis that hummingbirds have a color preference for red. We found color to have a great effect on hummingbird visitation, and additionally, we found a strong relationship between UV color and nectar concentration. These results suggest that the pollination syndromes are distinct with respect to flower color and nectar concentration, but more so to flower color. We note that all flowers investigated—even those less-preferred by hummingbirds—are more chromatic to hummingbirds than bees, aligning with the previous finding that hummingbirds can effectively pollinate a wider variety of flowers than bees can (Castellanos et al. 2003). Additionally, we found that in recent years, hummingbirds have increased visitation to certain plants such as *Ipomopsis aggregata* and *Lonicera involucrata*. We hypothesize that climate change is affecting nectar concentration, thus altering flower favorability to hummingbirds. Finally, we found no strong hummingbird preference for nectar concentration, likely due to the benefits of consuming both concentrated and dilute nectar. While hummingbirds have an innate preference for concentrated nectar (Bolten & Feinsinger 1978), visiting flowers with dilute nectar minimizes competition with bees (Montgomerie et al. 1984). Overall, our results suggest that the bird and bee pollination syndromes are sufficiently distinct, where flower color plays a greater role than nectar concentration in defining the bird syndrome.

During our investigation, it became apparent that the way one categorizes flower color may greatly impact whether they find a relationship with dependent variables. There were several limitations in our definition of flower color: First, we represented each flower with only one color from one part, when the entire flower contains multiple colors, influencing its visibility to pollinators. Second, we used chroma (saturation) as an approximation of detectability, when it is a different measurement—chromatic contrast against a background—that most directly relates to how noticeable a flower is. Future work can utilize different measures of color to expand on the relationships found in this investigation. Our conclusions would be further strengthened by the addition of nectar concentration data for three focal species (which we were missing), as well as bee visitation data. Finally, for a more general picture of how climate change is affecting our alpine ecosystem, future work can incorporate data on flower phenology and year-to-year shifts in nectar concentration to examine how Broad-tailed hummingbirds' flower choice and populations are responding.

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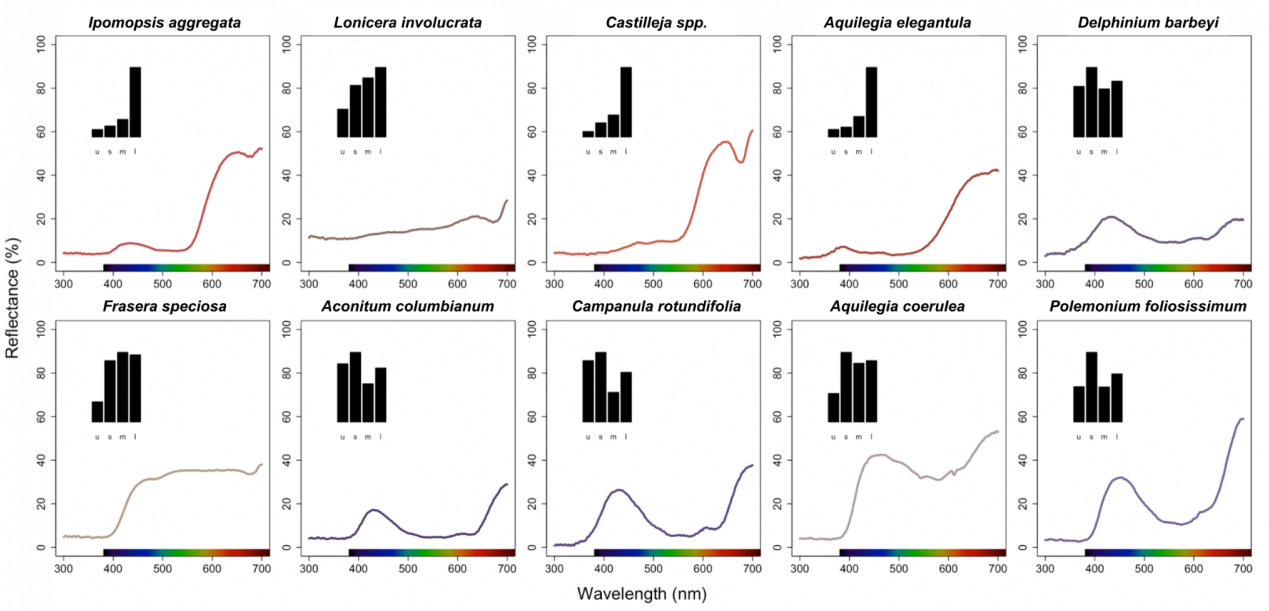
## Tables and Figures

### Figure 1

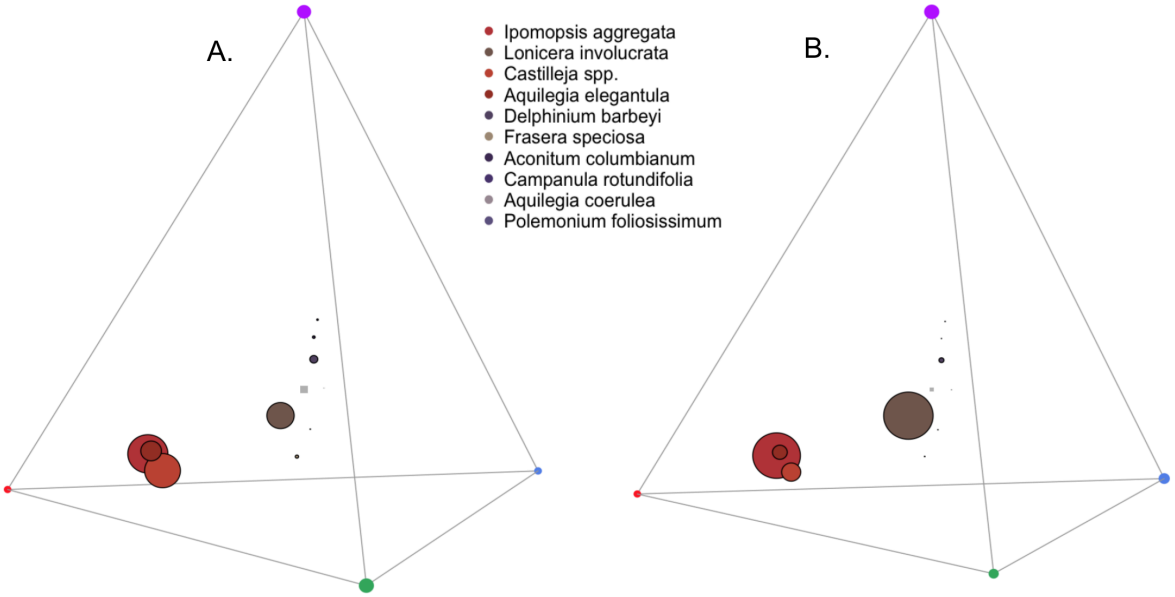
*UV-Vis Reflectance Spectra of 10 Selected Flowers*




*Note.* Flowers were selected based on Broad-tailed hummingbird visitation rate in our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). The top row contains the spectra of 5 most-visited flowers, and the bottom row contains the spectra of 5 least-visited flowers. Histograms represent cone stimulation using the avg.v phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). All spectra besides *Lonicera involucrata* and *Frasera speciosa* were collected by Chang (2023).

**Figure 2**

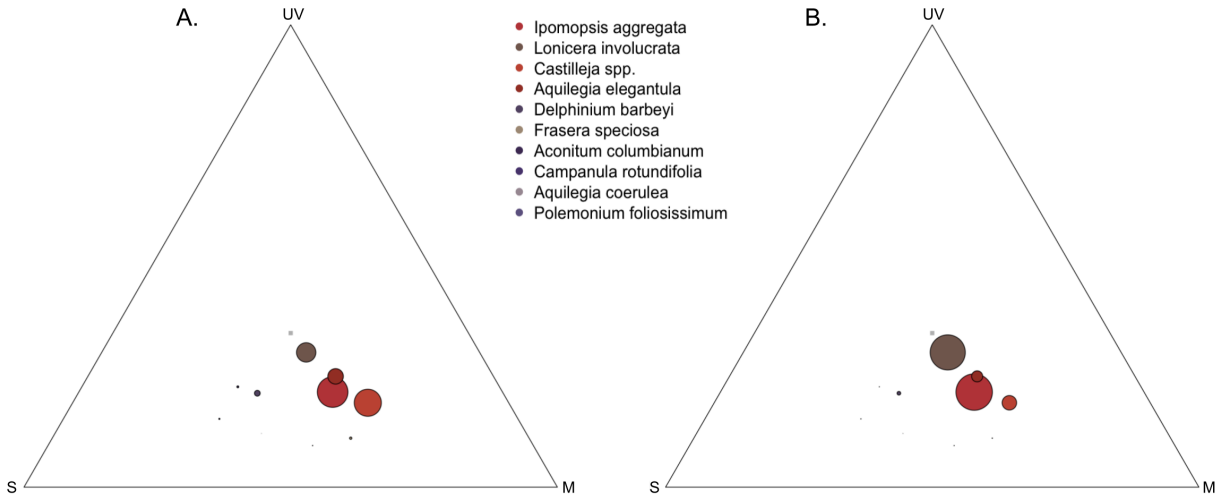
*Hummingbird Visitation in Bird Color Space*




*Note.* This figure depicts the color of 10 flowers, plotted within a tetrahedral color space—representative of bird vision—where cone stimulations determine each color's position. Cone stimulations were calculated using the avg.v phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were sized based on Broad-tailed hummingbird visitation rate (vis/hr) in our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). A. Points sized by visitation from 2018-2021. B. Same points sized by visitation from 2022-2024.

**Figure 3**

*Hummingbird Visitation in Bee Color Space*




*Note.* This figure depicts the color of 10 flowers, plotted within a triangular color space—representative of bee vision—where cone stimulations determine each color's position. Cone stimulations were calculated using the apis phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were sized based on Broad-tailed hummingbird visitation rate (vis/hr) in our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). A. Points sized by visitation from 2018-2021. B. Same points sized by visitation from 2022-2024.

**Table 1**

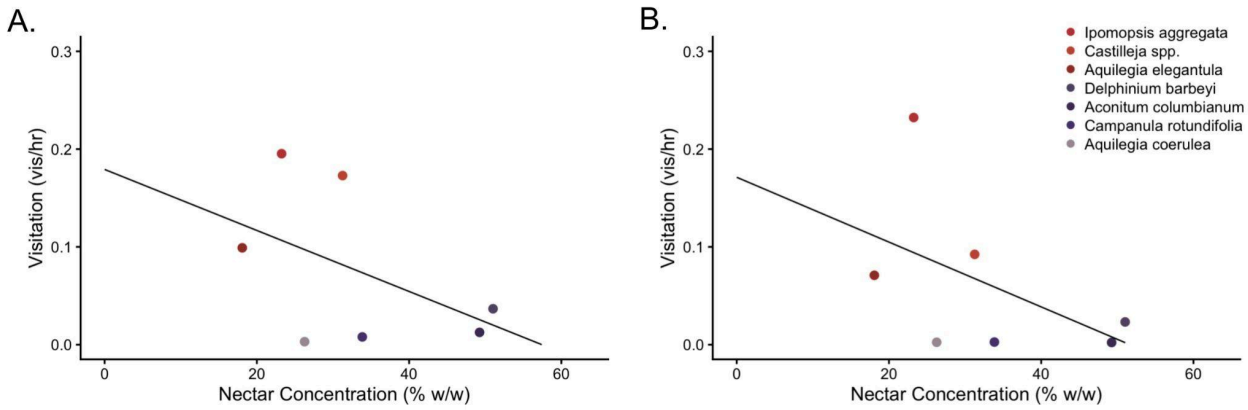
*Linear Regression Values of S1R, S1U, and Chroma Ratio vs. Hummingbird Visitation*

| | S1R | | S1U | | Chroma Ratio | |
|---|---|---|---|---|---|---|
| | Early | Late | Early | Late | Early | Late |
| R | .72 | .41 | .05 | .32 | .77 | .72 |
| $R^2$ | .52 | .17 | <.01 | .10 | .59 | .52 |
| P-value | .02 | .24 | .90 | .37 | .01 | .02 |

*Note.* This table contains the linear regression ($n$=10) values from Broad-tailed hummingbird visitation (vis/hr) as a function of 3 measures of color in 2 year ranges: 2018-2021 (Early) and 2022-2024 (Late). Visitation rates were taken from our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). S1R is the relative contribution of wavelengths >605 nm—representing "redness"—and S1U is the relative contribution of wavelengths <400 nm—representing "UV-ness." Chroma Ratio is the achieved chroma in bird color space divided by the achieved chroma in bee color space, representing the disparity in birds' and bees' saturation perceptions.

**Figure 4**

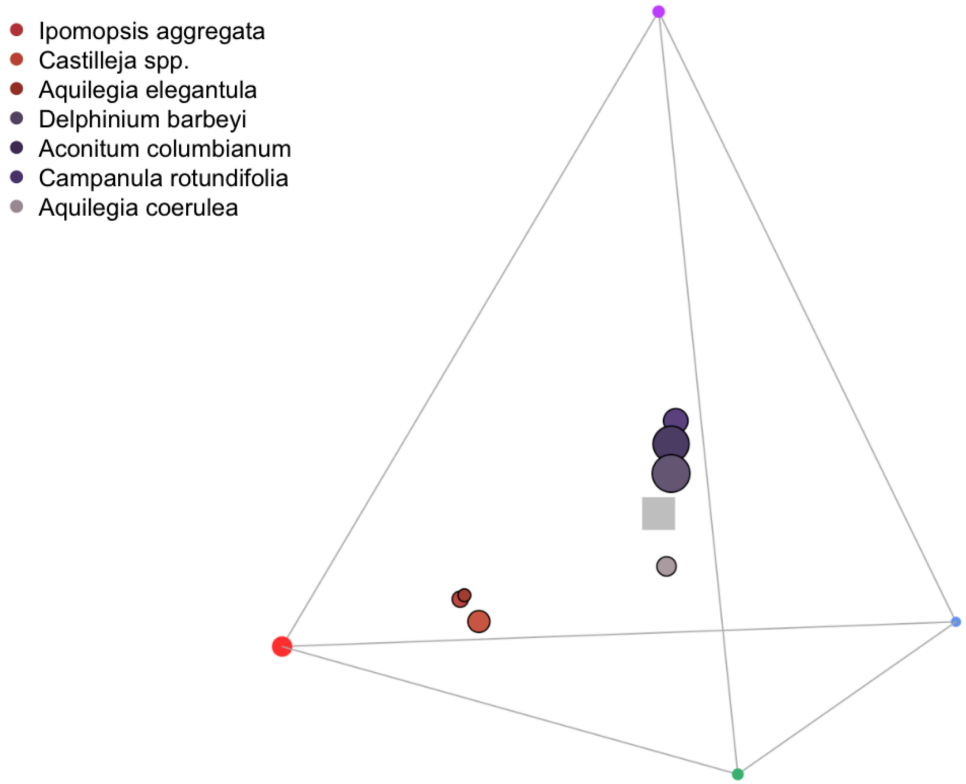
*Hummingbird Visitation as a Function of Nectar Concentration*




*Note.* This figure depicts hummingbird visitation rates (vis/hr) from 2 year ranges—2018-2021 and 2022-2024—as a function of nectar concentration (% w/w). Nectar concentrations were collected by Ngo (2025). Visitation rates were taken from our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). Black lines represent a linear fit for each plot. A. Portrays visitation from 2018-2021. B. Portrays visitation from 2022-2024.

**Figure 5**

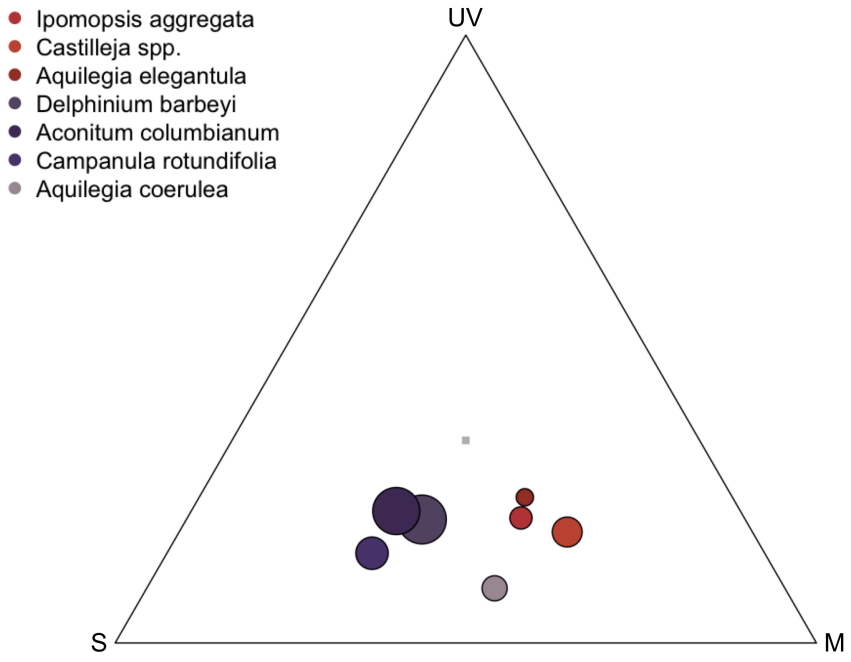
*Nectar Concentration in Bird Color Space*




*Note.* This figure depicts the color of 7 flowers, plotted within a tetrahedral color space—representative of bird vision—where cone stimulations determine each color's position. Cone stimulations were calculated using the avg.v phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were sized based on nectar concentrations (% w/w) collected by Ngo (2025).

**Figure 6**

*Nectar Concentration in Bee Color Space*




*Note.* This figure depicts the color of 7 flowers, plotted within a triangular color space—representative of bee vision—where cone stimulations determine each color's position. Cone stimulations were calculated using the apis phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were sized based on nectar concentrations (% w/w) collected by Ngo (2025).

**Table 2**

*Linear Regression Values of S1R, S1U, and Chroma Ratio vs. Nectar Concentration*

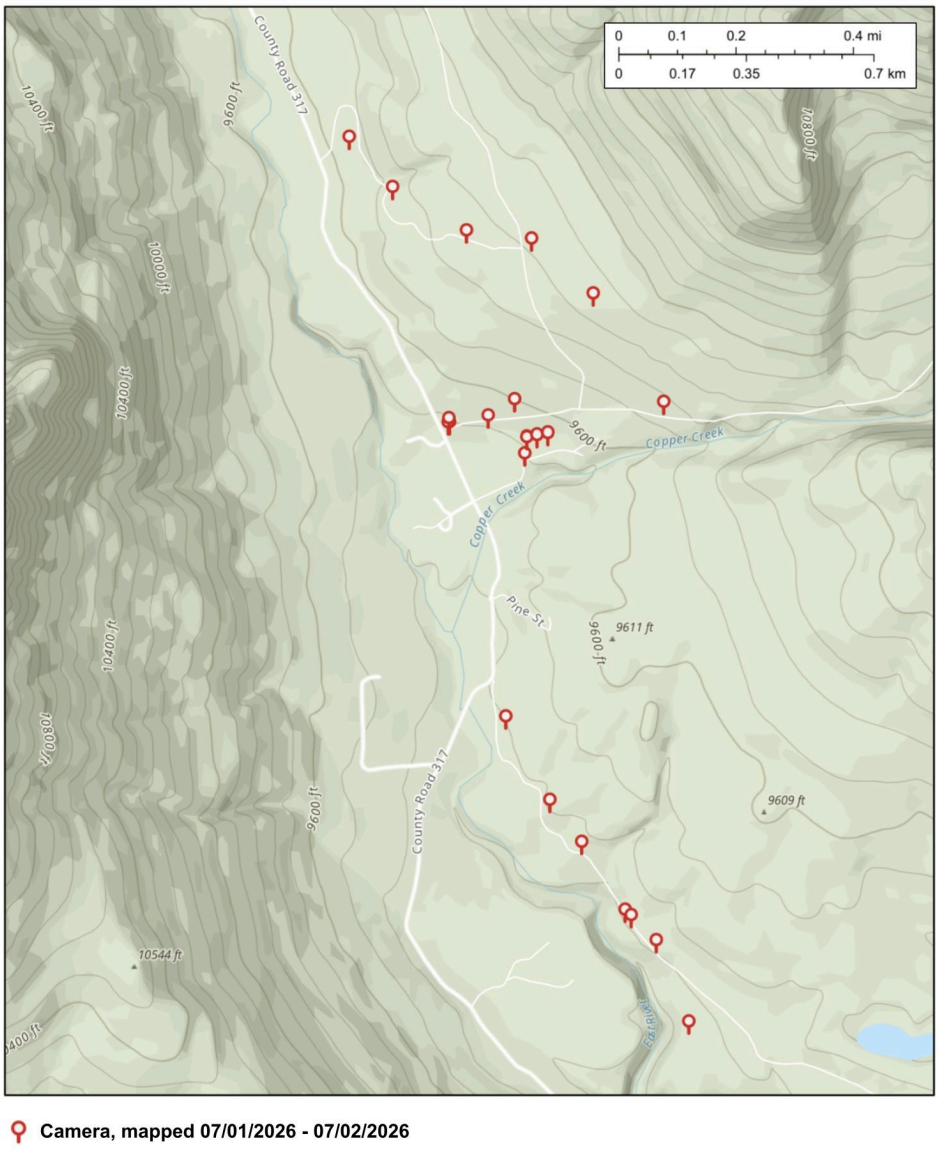
| | S1R | S1U | Chroma Ratio |
|---|---|---|---|
| R | -.73 | .84 | -.63 |
| $R^2$ | .53 | .70 | .39 |
| P-value | .06 | .02 | .13 |

*Note.* This table contains the linear regression ($n$=7) values from flower nectar concentration (% w/w) as a function of 3 measures of color. Nectar concentrations were collected by Ngo (2025). S1R is the relative contribution of wavelengths >605 nm—representing "redness"—and S1U is the relative contribution of wavelengths <400 nm—representing "UV-ness." Chroma Ratio is the achieved chroma in bird color space divided by the achieved chroma in bee color space, representing the disparity in birds' and bees' saturation perceptions.

## Supplemental Material

### Supplemental Figure 1

*Map of Typical HummerFlowerWatch Camera Locations in 2026*




*Note.* Map created in ArcGIS Online (https://rmbl.maps.arcgis.com/home/index.html). Copyright 2026 by OpenStreetMap contributors, and the GIS User Community.

**Supplemental Table 1**

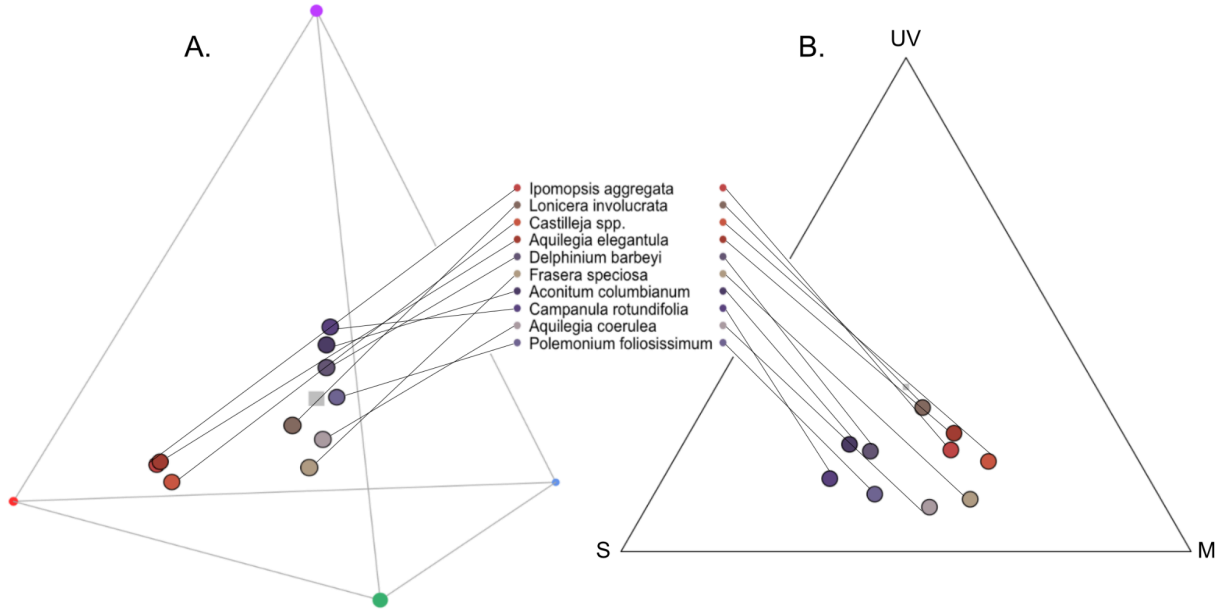
*Representative Flower Parts and their Human-Perceived Colors*

| Species | Flower Part | Human-Perceived Color |
|---|---|---|
| *Ipomopsis aggregata* | Side of corolla tube | Red |
| *Lonicera involucrata* | Outside of sepal | Red |
| *Castilleja spp.* | Middle of red part of bract, after it was removed from flower | Red |
| *Aquilegia elegantula* | Middle of spurred petal, from outside | Red |
| *Delphinium barbeyi* | Middle of purple petal, from front | Purple |
| *Frasera speciosa* | Inside of petal | White |
| *Aconitum columbianum* | Middle of hooded sepal, from outside | Purple |
| *Campanula rotundifolia* | Middle of petal, from outside | Purple |
| *Aquilegia coerulea* | Middle of sepal | Blue/Purple/White |
| *Polemonium foliosissimum* | Middle of petal | Blue/Purple |

*Note.* This table contains the flower parts selected to represent the color of each flower species used in our investigation. For each flower, the part occupying the qualitatively greatest externally-visible surface area was selected, and its reflectance spectrum was used to represent the entire flower's color.

**Supplemental Figure 2**

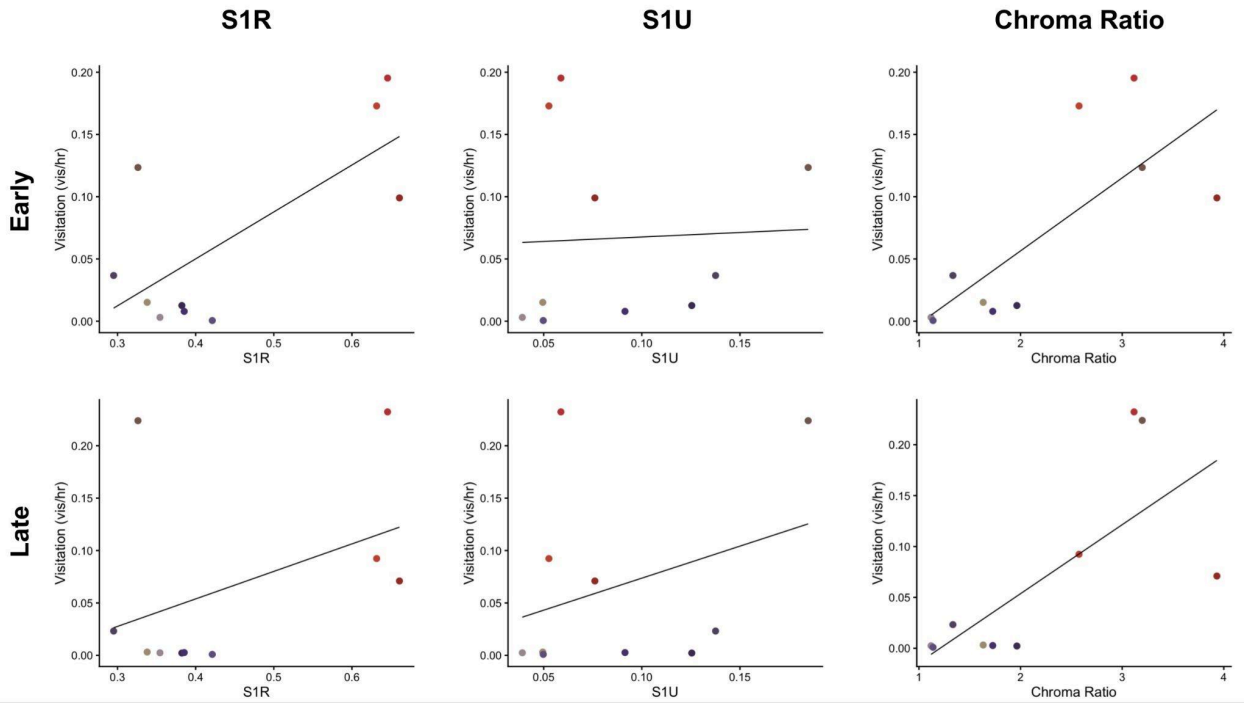
*Locations of Each Flower Point in Bird and Bee Color Spaces*




*Note.* This figure depicts the color of 10 flowers where cone stimulations determine each color's position within a color space. A. Plotted within a tetrahedral color space—representative of bird vision. B. Plotted within a triangular color space—representative of bee vision. Cone stimulations were calculated using the avg.v phenotype for the tetrahedral color space and apis phenotype for the triangular color space from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were plotted from flower spectra that were collected from the Rocky Mountain Biological Laboratory (RMBL). All spectra besides *Lonicera involucrata* and *Frasera speciosa* were collected by Chang (2023).

**Supplemental Figure 3**

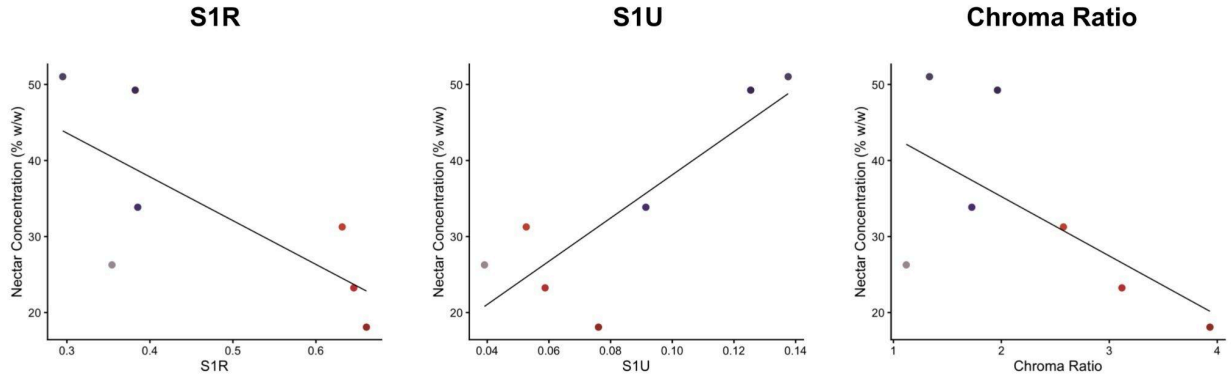
*Linear Regression Plots of S1R, S1U, and Chroma Ratio vs. Hummingbird Visitation*




*Note.* This figure corresponds to Table 1, and depicts the linear regression (*n*=10) plots from Broad-tailed hummingbird visitation (vis/hr) as a function of 3 measures of color in 2 year ranges: 2018-2021 (Early) and 2022-2024 (Late). Visitation rates were taken from our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). S1R is the relative contribution of wavelengths >605 nm—representing "redness"—and S1U is the relative contribution of wavelengths <400 nm—representing "UV-ness." Chroma Ratio is the achieved chroma in bird color space divided by the achieved chroma in bee color space, representing the disparity in birds' and bees' saturation perceptions. Black lines represent a linear fit for each plot.

**Supplemental Figure 4**

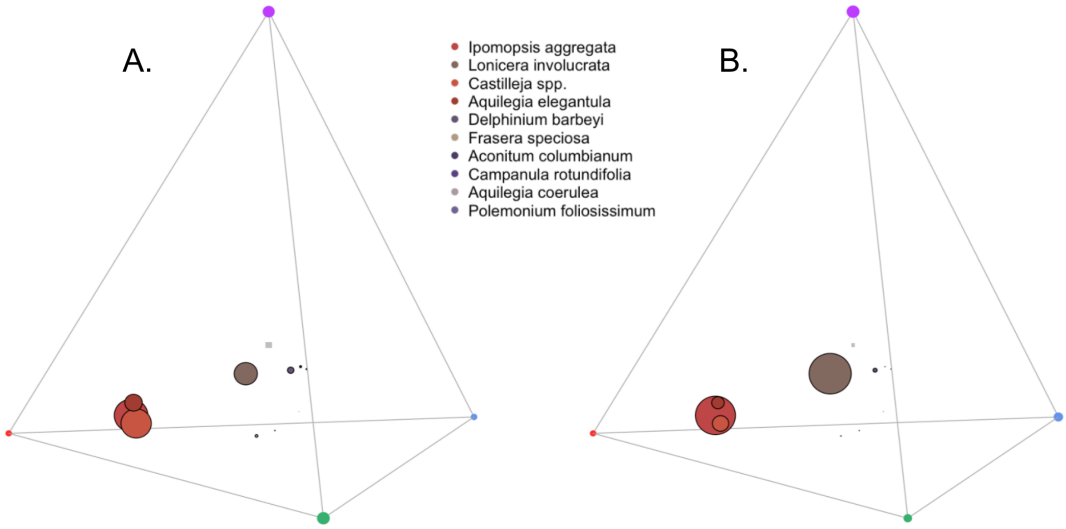
*Linear Regression Plots of S1R, S1U, and Chroma Ratio vs. Nectar Concentration*




*Note.* This figure corresponds to Table 2, and depicts the linear regression (*n*=7) plots from flower nectar concentration (% w/w) as a function of 3 measures of color. Nectar concentrations were collected by Ngo (2025). S1R is the relative contribution of wavelengths >605 nm—representing "redness"—and S1U is the relative contribution of wavelengths <400 nm—representing "UV-ness." Chroma Ratio is the achieved chroma in bird color space divided by the achieved chroma in bee color space, representing the disparity in birds' and bees' saturation perceptions. Black lines represent a linear fit for each plot.

**Supplemental Figure 5**

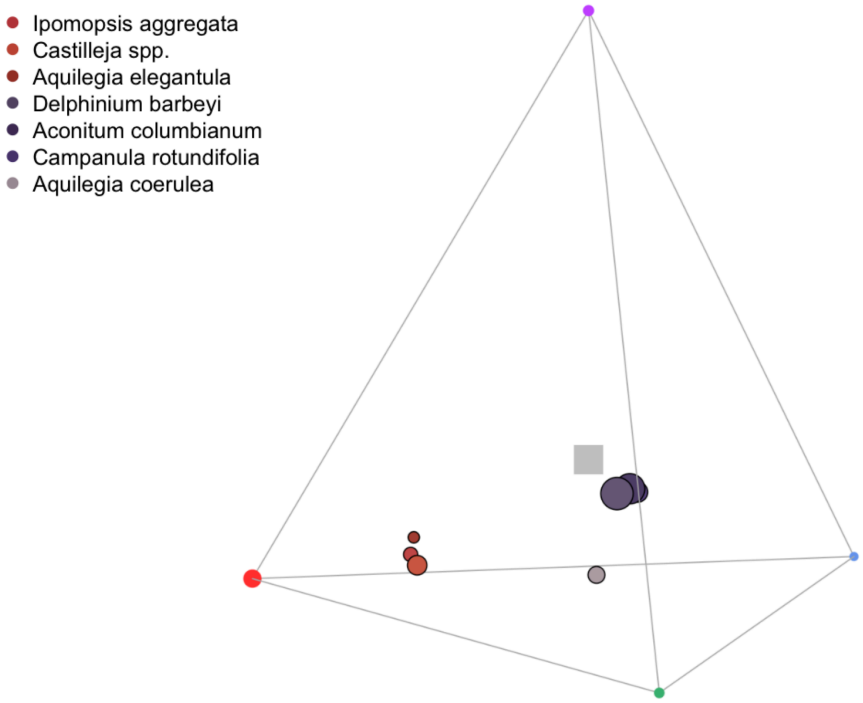
*Hummingbird Visitation in avg.uv Bird Color Space*




*Note.* This figure depicts the color of 10 flowers, plotted within a tetrahedral color space—representative of bird vision—where cone stimulations determine each color's position. Cone stimulations were calculated using the avg.uv phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were sized based on Broad-tailed hummingbird visitation rate (vis/hr) in our long-term dataset at the Rocky Mountain Biological Laboratory (RMBL). A. Points sized by visitation from 2018-2021. B. Same points sized by visitation from 2022-2024.

**Supplemental Figure 6**

*Nectar Concentration in avg.uv Bird Color Space*




*Note.* This figure depicts the color of 7 flowers, plotted within a tetrahedral color space—representative of bird vision—where cone stimulations determine each color's position. Cone stimulations were calculated using the avg.uv phenotype from the pavo package (Maia et al. 2019) in R (R Core Team 2026). Points were sized based on nectar concentrations collected by Ngo (2025).

**Supplemental Table 2**

*Raw Numerical Values for Observed Variables*

| Species | Visitation Rate from 2018-2021 (vis/hr) | Visitation Rate from 2022-2024 (vis/hr) | Nectar Concentration (% w/w) | S1R | S1U | Chroma Ratio (Bird:Bee) |
|---|---|---|---|---|---|---|
| *Ipomopsis aggregata* | 0.1953 | 0.2323 | 23.25 | 0.6456 | 0.05877 | 3.117 |
| *Lonicera involucrata* | 0.1235 | 0.2239 | NA | 0.3261 | 0.1848 | 3.197 |
| *Castilleja spp.* | 0.1729 | 0.09237 | 31.26 | 0.6316 | 0.05265 | 2.575 |
| *Aquilegia elegantula* | 0.09904 | 0.07097 | 18.08 | 0.6608 | 0.07607 | 3.932 |
| *Delphinium barbeyi* | 0.03673 | 0.02322 | 51.03 | 0.2950 | 0.1376 | 1.334 |
| *Frasera speciosa* | 0.01515 | 0.003174 | NA | 0.3379 | 0.04954 | 1.632 |
| *Aconitum columbianum* | 0.01260 | 0.002215 | 49.25 | 0.3823 | 0.1254 | 1.964 |
| *Campanula rotundifolia* | 0.007918 | 0.002677 | 33.85 | 0.3853 | 0.09143 | 1.726 |
| *Aquilegia coerulea* | 0.003074 | 0.002461 | 26.27 | 0.3543 | 0.03912 | 1.119 |
| *Polemonium foliosissimum* | 0.0005488 | 0.0009362 | NA | 0.4213 | 0.04978 | 1.138 |