

**Temperature and Relative Humidity Effects on Nectar Quantity, Nectar Quality, and
Plant-Pollinator Interactions**

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Abstract

Nectar plays a critical role in attracting pollinators, thereby facilitating pollination and the spread of pollen. Nectar traits like volume and sugar concentration are strongly influenced by environmental factors such as temperature and relative humidity. Yet, there is little understanding of how these environmental and biological variables combine to influence the ability for a plant to attract insect pollinators. This study examined how temperature and relative humidity influence nectar volume and sugar concentration, and how these factors, in turn, affect pollinator visitation rates. We conducted this research at three subalpine wildflower meadows in Gunnison County, Colorado, from July 2 to August 1, 2025. We surveyed plant-pollinator interactions, collected ambient temperature and relative humidity data, and examined nectar volume and sugar concentration. Using mixed effects models, we found that an increasing temperature significantly increased nectar volume but decreased sugar concentration. Similarly, higher relative humidity led to a significant increase in nectar volume and a significant decrease in concentration. Notably, higher relative humidity and nectar volume were associated with a statistically significant increase in pollinator visitation rates. In contrast, temperature and nectar concentration did not have a statistically significant effect on visitation. These findings highlight the importance of environmental conditions in shaping plant–pollinator interactions. Understanding how temperature and humidity influence nectar traits and pollinator behavior is essential for predicting the impacts of climate change on ecological relationships.

Key words

plant-pollinator interactions, nectar concentration, nectar volume, temperature, relative humidity

Introduction

Nectar is a crucial component of plant–pollinator interactions. It attracts pollinators, facilitating pollen transfer and increasing the likelihood of successful seed production. In addition to its attractive role, nectar also serves a defensive function by deterring or regulating unwanted visitors such as nectar robbers.¹ The specific type of nectar that draws pollinators is known as floral nectar (FN), which fosters mutualistic relationships between plants and a range of pollinating species.² These interactions enhance a plant's reproductive success by promoting cross-pollination, contributing to both offspring production and genetic diversity. Despite the high metabolic cost of nectar production—requiring assimilated carbon, photosynthetic energy, and water—plants continue to invest in it because of its essential role in reproductive success and competitive advantage in attracting pollinators.³

Nectar is composed primarily of sugars and water, nectar also contains proteins, amino acids, minerals, and other organic compounds.⁴ The rate and amount of daily nectar production can vary by plant species as well as under different environmental conditions.⁵ Plant species also have different compositions of nectar, which tend to attract different types of pollinators. For example, rufous hummingbirds (*Selasphorus rufus*) prefer higher sucrose concentrations within nectar⁶, while honeybees (*Apis mellifera*) typically prefer to forage on warmer nectar with lower viscosity. Honeybees liked more diluted nectar because higher viscosity makes it was harder for them to drink, and these preferences were independent of sugar concretions.⁷

Variations in nectar traits—such as sugar concentration, volume, and composition of amino acids or microbes—can be influenced by multiple environmental factors, including temperature, humidity, light, soil nutrients, and CO₂ levels.⁸ For instance in one experimental study, researchers found that *Balsamorhiza sagittata* and *Eriogonum umbellatum* had distinct optimal temperatures at which each species produced the highest amount of sugar and higher amount of volume of nectar.⁹ Another study discovered that a moderate increase in temperature would increase the amount of nectar produced by *Teucrium divaricatum*, but not *Ballota acetabulosa*. However, they acknowledged that water availability was not considered in their study, which could influence the future outcomes for these plants.¹⁰ In another study conducted in the Teton Range in Wyoming, researchers examined *Balsamorhiza sagittata* and *Eriogonum umbellatum*.¹¹ They applied a warming treatment and found that in both species, nectar volume decreased with artificial warming, while sugar concentration increased. These changes could affect the nectar-feeding community, which would need to adapt to the altered nectar composition.¹² A manipulation study on the collection of pollen loads from *Melipona rufiventris* Lepeletier in the coastal plain of Praia da Fazenda investigated the nectar found in those pollen loads. It was found that with an increase in relative humidity, there was a decrease in nectar sugar concentration.¹³ However, the quantity of nectar collected remained high regardless of relative humidity.¹³ Another study conducted by Robert Wyatt examined how the nectar of *Asclepias syriaca* and *A. exaltata* changed with different temperatures and levels of relative humidity. It was found that under more humid conditions, the flowers produced a higher volume of nectar, though the nectar was more diluted.⁸

Variations in nectar traits—such as sugar concentration, volume, and composition of amino acids or microbes—can be influenced by multiple environmental factors, including temperature, humidity, light, soil nutrients, and CO₂ levels.¹⁵ Most studies into the role of the environment in nectar production have focused primarily on variation in temperature and humidity, but have not found consistent trends in how either variable influence nectar volume or concentration across plant species. For instance, one study conducted in the Teton Range of Wyoming found that experimental warming caused a decrease in nectar volume and increase in nectar concentration in two focal plants¹¹, while another experiment in the Mediterranean found that plants tended to have an optimal temperature at which they produced the highest nectar volume and sugar concentration, with decreased values at both lower and higher temperatures.¹⁶ Increased humidity has often been associated with increased nectar volume and decreased nectar concentration¹⁴ and despite being the subject of fewer studies, may be more important, particularly in dry regions.

Despite these studies, our understanding of how changing environmental conditions may influence both nectar and the pollinators that eat that nectar is still incomplete. Few studies have examined natural variation in nectar quantity or quality or the effects of changing nectar traits on entire pollinator communities. Studies that have integrated pollinator visitation often do so through manipulation trials involving one or two focal plant species⁹ or through studies focusing on one or two pollinator species.⁶ Therefore in this study, we asked:

(1) *How do temperature and relative humidity affect the volume of nectar in natural plant communities?*

- (2) *How do temperature and relative humidity affect the concentration of nectar in natural plant communities?*
- (3) *How do temperature, relative humidity, volume of nectar, and concentration of nectar affect pollinator visitation to flowers in a natural community?*

I expect that increased temperature may result in lower volumes of more concentrated nectar due to the evaporation of water from that nectar. Additionally, I expect that increased relative humidity may result in higher volume and lower concentrations of nectar, as increased nectar volume may be made up of more water. Finally, I expect that lower volumes of nectar will be less attractive to pollinators as the expected amount of reward at each flower is lower. However, an increased sugar concentration in nectar may lead to greater pollinator visitation if the sugar content is high enough to be beneficial to the pollinators, or it may result in decreased visitation if the nutritional value is insufficient. Therefore, I examined how these four important variables — temperature, relative humidity, nectar volume, and nectar sucrose concentration — all contribute to the proportion of visitation events from pollinators to specific flowers. Nectar is essential for attracting pollinators, which in turn support plant reproduction across the landscape. Therefore, it is crucial to understand how nectar may be impacted by temperature and relative humidity and how this could alter those ecological relationships.

Methods

This work took place in three subalpine wildflower meadows surrounding the Rocky Mountain Biological Laboratory (Gunnison National Forest, Gunnison Co., Colorado, USA). . At each site, we set up four transects, each measuring 1x20-meters. Each transect was divided into 1x2-meter segments, resulting in 10 segments per transect and 40 segments per site. Each week, a team of 3–5 researchers recorded the identity and abundance of all flowers present in these transects and conducted surveys of plant-pollinator interactions within these transects. During these pollinator visitation surveys, researchers were randomly assigned segments to survey for 3 minutes of active sampling time, for a total of 120 minutes of visitation surveys per sampling round. During this time, researchers noted each insect that landed on the reproductive organs (anthers or stigmas) of a flower located within the transect and then, if possible, collected the insect for subsequent identification in the lab. At the beginning of each sampling round, we recorded temperature and relative humidity using a Fisherbrand™ Enviro-Meter™ (Cat. No. 02-401-5). Unless precluded by inclement weather, we conducted two sampling rounds on each survey day.

Once all plant-pollinator visitation surveys were completed, I identified the plant species that were visited more than five times by any type of pollinator. I placed mesh pollinator exclusion bags on five individuals of each of these focal species outside of the four transects to prevent further pollinator access and allow nectar to accumulate. After 24 hours, I collected nectar from each flower. For flowers that had accessible nectaries that produced visible drops of nectar (e.g., *Delphinium barbeyi*), I used a microcapillary tube (0.5 or 5 uL) to collect all nectar droplets. If a flower had multiple nectaries, I used the same tube to collect from all nectaries to obtain the total nectar volume.¹² For flowers with nectaries too small and/or numerous to directly insert a microcapillary tube, I collected entire flowers in 50-mL centrifuge tubes and transported them to the lab in a cooler. Then, I affixed the flower or umbel to the inside of a microcentrifuge tube lid and spun the tube in a microcentrifuge until the nectar collected at the bottom (approx. 2

minutes). I would then use microcapillary tubes to collect the nectar as above.¹² Once nectar was collected in microcapillary tubes, I measured the volume by calculating the portion of the tube filled with nectar (Eq. 1) and the sugar concentration using a handheld refractometer (Eq. 2).

$$\text{Equation 1: } v = (l * V)/L^{12}$$

where v = the total volume of nectar in the flower in μL , l = the length of microcapillary tube filled with nectar, V = the maximum volume of the microcapillary tube, and L = the total length of the microcapillary tube

$$\text{Equation 2: } C = ((0.0037921b + 0.0000178b^2 + 0.9988603) * b)/100^{13}$$

where C = nectar concentration in $\text{mg}/\mu\text{L}$ and b = the Brix value

To analyze our data, I used the packages *car*¹⁷, *lme4*¹⁸, and *lmerTest*¹⁹ to build three distinct statistical models. First, to understand the effects of temperature and relative humidity on nectar volume, I used a linear mixed effects model in which the volume of nectar measured was my response variable, the average recorded temperature and relative humidity on the day of the initial plant-pollinator survey were fixed effects, and plant species was a random intercept. I log-transformed the nectar volume following the results of a Box-Cox test on my data. Second, to understand the effects of temperature and relative humidity on nectar concentration, I used a linear mixed effects model in which the concentration of nectar measured was my response variable, the average recorded temperature and relative humidity on the day of the initial plant-pollinator survey were fixed effects, and plant species was a random intercept. Third, to understand the effects of temperature, relative humidity, concentration of nectar, and the volume of nectar on visitation, I used a generalized linear model in which the number of pollinators visiting the focal flower species compared to the number of visitation events to all other flowers was my response variable, the average recorded temperature and relative humidity and the measurements of the concentration of nectar and the volume of nectar on the day of the initial plant-pollinator survey were fixed effects, and plant species was a random intercept. For this model, I used a binomial error distribution.

Results

We collected data from July 2 to August 1, 2025, from 9 different focal flower species (Table 1). We were able to obtain nectar volume measurements from 126 individual flowers, and nectar concentration measurements from 56 individual flowers. We recorded a total of 991 interactions between plants and pollinators within the study. The maximum temperature was 25.5 °C and the minimum was 18.45 °C. The max relative humidity was 35.95 % and the minimum was 25.25 %.

I performed three sets of statistical tests to examine the relationship between environmental conditions and (1) nectar volume (Table 2), (2) nectar sugar concentration (Table 3), and (3) plant-pollinator visitation (Table 4). First, I found that temperature ($p = 0.007$; Figure 2) and relative humidity ($p < 0.001$; Figure 3) had significant positive effects on nectar volume. Second, I found that temperature ($p = 0.049$; Figure 4) and relative humidity ($p = 0.042$; Figure 5) had significant negative effects on the sugar concentration of nectar. Third, I found that

relative humidity had significant positive effects on plant-pollinator visitation ($p = 0.002$; Figure 7), while temperature had a non-significant effect ($p = 0.207$; Figure 6). Nectar volume was also significantly positively correlated with plant-pollinator visitation ($p < 0.001$; Figure 8), but nectar sugar concentration did not have a significant relationship ($p = 0.197$; Figure 9).

Discussion

How do temperature and relative humidity affect the volume of nectar?

I found that both temperature and relative humidity had significant positive effects on the volume of nectar produced by distinct floral species (Figures 2 and 3). This relationship between temperature and nectar volume contrasts with prior work that found no significant relationship between temperature and nectar volume in a single flowering plant, *Allium cepa*, and work showing that nectar secretion decreases at lower temperatures.³ While I had initially thought that higher temperatures would result in decreased nectar volume via evaporation, these results suggest that evaporation of water from nectar is not the primary process linking temperature and nectar volumes. Rather, nectar production may increase with temperature because the specific mechanisms used to produce nectar can be affected by cold stress. In other regions, heat can act as a stressor, but in this area, nighttime temperatures are very low. It may be that the temperature helps signal to the plant that it should begin secreting nectar.²⁰ My finding that higher relative humidity was correlated with increased nectar volume aligned with my expectations. While studies on specific plants may vary, nectar secretion is often linearly dependent on ambient humidity, with nectar-producing plants adjusting their secretion quickly in response to changes in relative humidity.²¹ This suggests that the effect of relative humidity on nectar secretion may vary depending on the plant species and the region it originates from. Relative humidity likely plays a significant role in a plant's ability to secrete nectar, and depending on the plant's water availability, an increase in humidity could either enhance or hinder nectar production.

The volume of nectar in the future could change with climate change because of fluctuations in temperature and relative humidity. Since both factors are positively correlated with nectar volume, there could be implications for plants allocating more resources toward nectar secretion. This also means that nectar supply will not remain constant. Due to climate change, weather patterns are becoming increasingly unpredictable. As both temperature and relative humidity impact nectar volume—and are themselves inconsistent—there is a possibility that plants will not be able to maintain a consistent nectar supply.

How do temperature and relative humidity affect the concentration of nectar?

I found that both temperature and relative humidity had significant negative effects on the concentration of nectar (Figures 4 and 5). Since higher temperatures yielded larger volumes of nectar, it is unlikely that evaporation or water loss were responsible for this trend. Interestingly, a prior experiment on sunflowers found that nectar concentration increased with temperature, identifying an optimal temperature for sugar concentration at 32 °C¹⁵ that is much higher than any of our recorded temperatures. The many individuals of the Asteraceae family in our study did not seem to follow this positive relationship between temperature and nectar concentration. Other work has shown that drought-stressed plants produce fewer flowers and that their nectar contains

a lower proportion of sucrose, although the overall volume of nectar initially remains the same.²² The decrease in nectar concentration that I observed with increased relative humidity is more consistent with prior work — pollen loads collected by *Melipona rufiventris* included lower concentrations of nectar sugars as relative humidity increased.¹³ This trend may be due to increased condensation entering the nectaries, diluting the sugar content.

The concentration of nectar could change in the future due to climate change, as temperature and relative humidity are expected to fluctuate. Since both of these variables show a significant negative correlation with nectar concentration, there could be major implications for the composition of nectar. A decrease in nectar concentration may influence which pollinators are attracted to which flowers. If a flower no longer provides enough energy to meet a particular pollinator's needs, that pollinator may stop visiting it. This shift in pollinator behavior could reduce pollination success, impacting the genetic diversity of plant communities and limiting their reproductive output.

How does visitation change with temperature, relative humidity, volume of nectar, and concentration of nectar?

I found that relative humidity and nectar volume had significant influences on the proportion of pollinator visitations (Figures 7 and 8). In contrast, temperature and nectar concentration did not have significant impacts on visitation rates (Figures 6 and 9). I believe the significant increase in visitations with higher relative humidity may be due to the typically dry conditions of the study area. An increase in atmospheric moisture and water availability could reduce water stress for pollinators, potentially enhancing their activity levels. A study examining shifts in plant-pollinator interactions in response to water availability found that pollinator visitations were highest at intermediate water levels.²³ This year, there was a decrease in monsoon activity, so the observed relative humidity levels may represent an intermediate point for the pollinators, prompting an increase in visitation rates. The area where my study takes place experiences frequent drought and is generally very dry. A manipulation study also found that relative humidity influences hawkmoth behavior. When all other environmental conditions were held constant, hawkmoths altered their visitation patterns in response to humidity, showing increased visitation rates at higher relative humidity levels.²⁴

Additionally, visitation may increase with nectar volume because more available nectar supports more pollinator visits. Over the course of a day, greater nectar volume provides a more consistent resource, sustaining pollinator activity and attraction. Optimal foraging theory suggests that when pollinators forage, they aim to visit the flowers that offer the greatest reward. They will leave a flower once they believe another flower offers better or more abundant resources.²⁴ Therefore, a higher volume of nectar on average may sustain the extent of time over which a pollinator expects that plants of a certain species contain nectar and is worth visiting. However, a study on various *Lamiaceae* species found no significant correlation between nectar volume and honeybee visitation rates. Instead, they found that other floral traits, such as the type and proportion of sugars in nectar, had a more significant influence on pollinator preference.²⁵

All together, my results suggest that pollinator visitation is likely to be most affected by changes in relative humidity. Relative humidity had a significant impact on visitation rates directly and also influenced nectar volume, which in turn influenced pollinator visitation. Thus, with increased variation in humidity and precipitation due to climate change, the interactions between plants and pollinators may shift. For plants, this could lead to reduced genetic diversity and lower reproductive success. For pollinators, it may mean losing a reliable food source, prompting changes in foraging behavior. Pollinators will need to seek alternative food sources that offer sufficient quantity and energy, which may result in shifts in plant-pollinator relationships. In some cases, pollinators may not find adequate nutrition, and plants may not receive the pollination they require. These disruptions could lead to long-term changes in ecosystem composition.

There were several limitations in this study. As this was our first time conducting this type of test, the initial rounds of sampling had to be discarded due to mistakes and trial-and-error learning. We also encountered difficulties extracting nectar using the same microcapillary tubes throughout. Specifically, tubes with a diameter of 0.5 μ l frequently became clogged with pollen, preventing nectar concentration readings from being obtained. As a result, there was a significantly larger number of individuals for which nectar volume was recorded ($n = 126$) compared to those with concentration data ($n = 56$). Collecting more data across varying environmental conditions and on the same plants could strengthen the dataset and improve the significance of the findings. Additionally, this study was conducted in a very dry and hot region, and this summer was notably hotter than in previous years. In future studies, I would like to include soil moisture as a variable. While relative humidity was measured, combining it with soil moisture data could provide insights into subsurface conditions affecting nutrient uptake and nectar production. There also appeared to be a major decline in the number of pollinators observed during the study period, which may have influenced both the visitation rates and the overall quantity of pollinator data collected. Compared to other studies, which often use experimental manipulation to determine optimal environmental conditions, our study was observational. I am interested in exploring not just optimal levels, but the tolerance ranges of nectar production and pollinator visitation under varying conditions. It is possible that the environmental range in temperature and relative humidity captured during our study was not wide enough to fully observe these tolerance thresholds.

This study is important for understanding how environmental changes, such as shifts in temperature and relative humidity, influence plant-pollinator interactions. By comparing the impacts of temperature and humidity, we gained insight into how these factors affect both plant traits (such as nectar volume and concentration) and insect behavior. Specifically, this study found that the volume of nectar was influenced in a positive correlation by temperature and relative humidity. It also found that the concentration of nectar is influenced by a negative correlation with temperature and relative humidity. Lastly, visitations were positively correlated and influenced by the volume of nectar and relative humidity. While this study offers a snapshot of how the system responded over a single season, examining multiple systems across longer timescales will be essential to reveal broader patterns and better understand how plant-pollinator relationships are shifting alongside environmental changes.

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Table 1:

Different plants with their amount of individuals and their volume and concentration ranges of nectar.

Plant	N (volume)	N (concentration)	Volume range	Concentration Range
<i>Delphinium barbeyi</i>	12	12	0.16-1.32	0.431-0.911
<i>Erigeron elatior</i>	10	8	0.16- 1	0-0.742
<i>Erigeron speciosus</i>	26	14	0-4.84	0-0.678
<i>Helianthella quinquenervis</i>	15	NA	0-0.0547	NA
<i>Heliomeris multiflora</i>	16	9	0.00781-3.6	0-0.276
<i>Hymenoxys hoopesii</i>	15	NA	0-0.781	NA
<i>Ligusticum porteri</i>	12	3	0-0.44	0-0.528
<i>Potentilla fruticosa</i>	10	10	0.04-1.96	0-0.528
<i>Potentilla pulcherrima</i>	10	NA	0.0156-0.19	NA

Table 2:

Environmental factors influence the volume of nectar. Bold means that they were statistically significant.

	Estimate	Std. Error	df	t value	p value
Intercept	-30.6544	7.6654	121.5847	-3.999	0.00011
Temperature	0.5414	0.1977	120.4978	2.739	0.00710
Relative Humidity	0.5430	0.1174	119.8480	4.625	9.54e-06

Table 3:

Environmental factors influence the concentration of nectar. Bold means that they were statistically significant.

	Estimate	Std. Error	df	t value	p value
Intercept	3.20738	1.40641	49.12840	2.281	0.0270
Temperature	-0.07569	0.03757	48.99283	-2.015	0.0494
Relative Humidity	-0.04137	0.01987	50.02224	-2.082	0.0425

Table 4:

Different factors influence the proportion of visitations. Bold means that they were statistically significant.

	Estimate	Std. Error	z value	p value
Intercept	-7.27389	2.66043	-2.734	0.006255
Temperature	0.08478	0.06721	1.261	0.207181
Relative Humidity	0.12446	0.03999	3.113	0.001855
Volume	0.39315	0.10983	3.580	0.000344
Concentration	-0.59151	0.45853	-1.290	0.197045

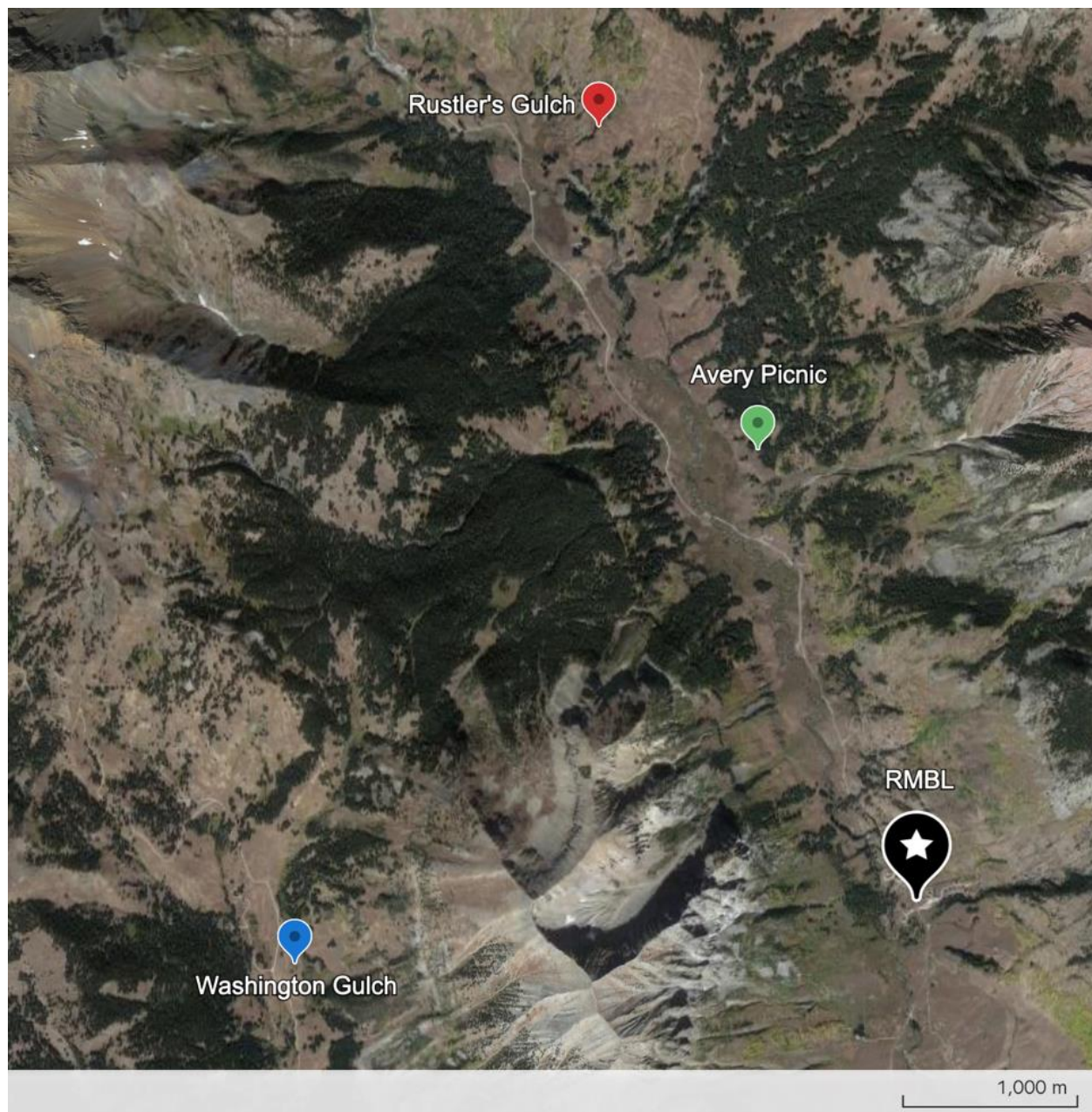
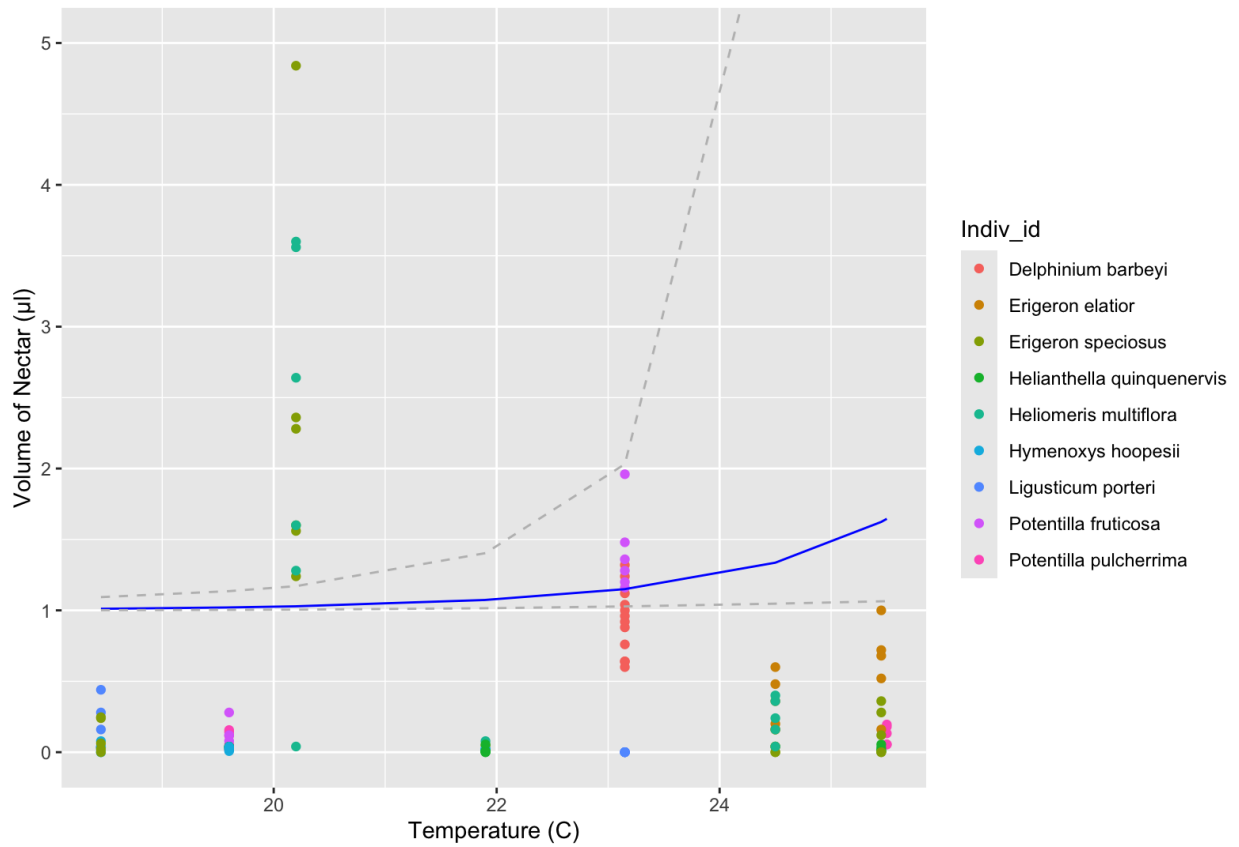


Figure 1. These are the locations at which my sites were located.



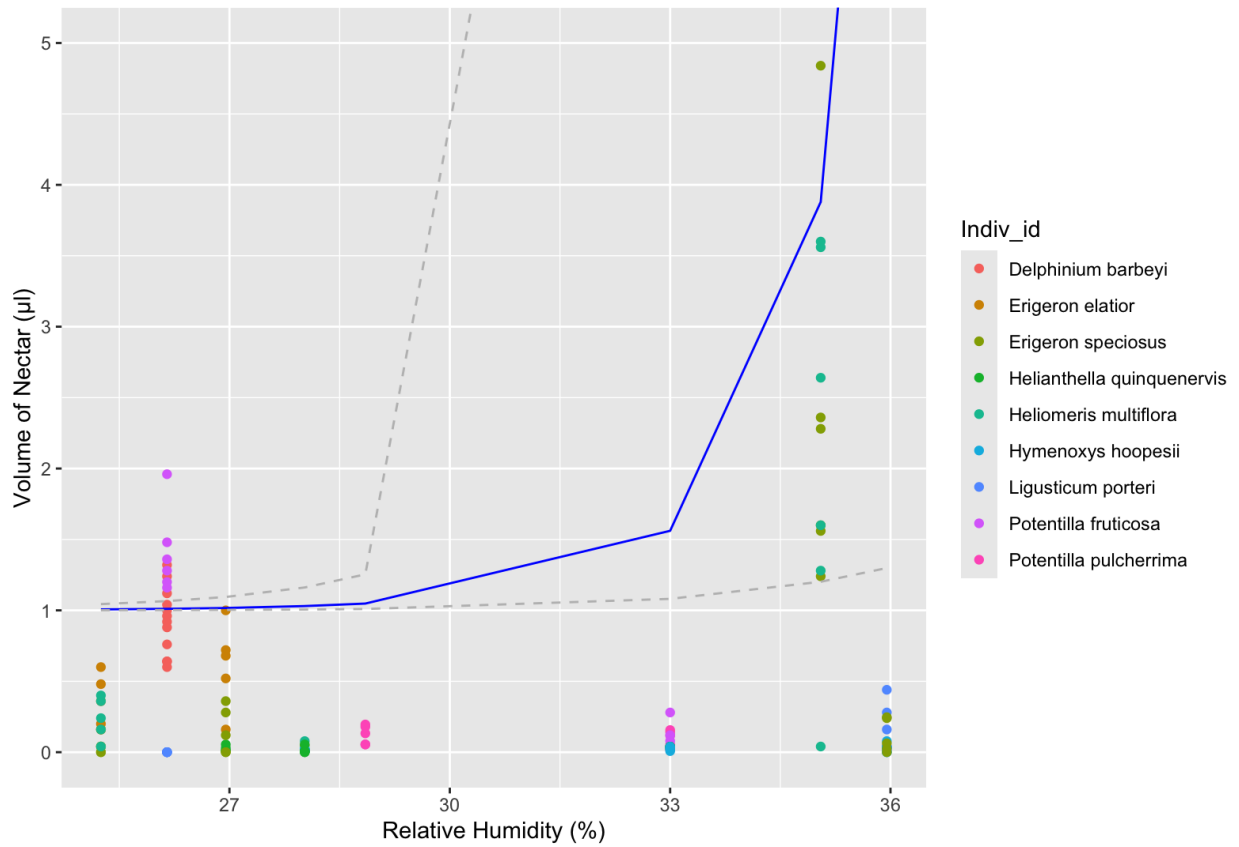


Figure 3. Depicts a significant relationship between nectar volume and relative humidity ($p = 09.54 \text{ e } -06$). The blue line represents the predicted data, while the different dots are the actual data point (the different colors represent different flower species).

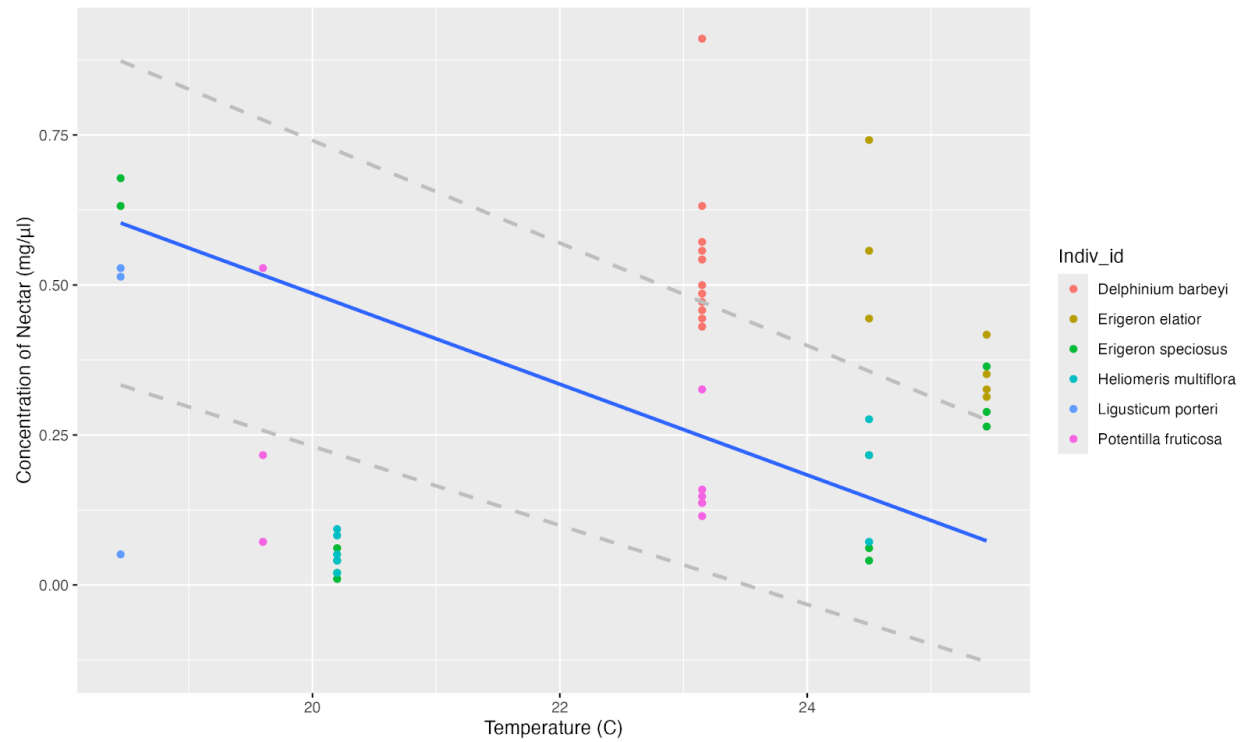


Figure 4. Depicts the relationship between nectar concentration and temperature. The result was not statistically significant ($p = 0.0494$). The blue line represents the predicted data, while the different dots are the actual data point (the different colors represent different flower species).

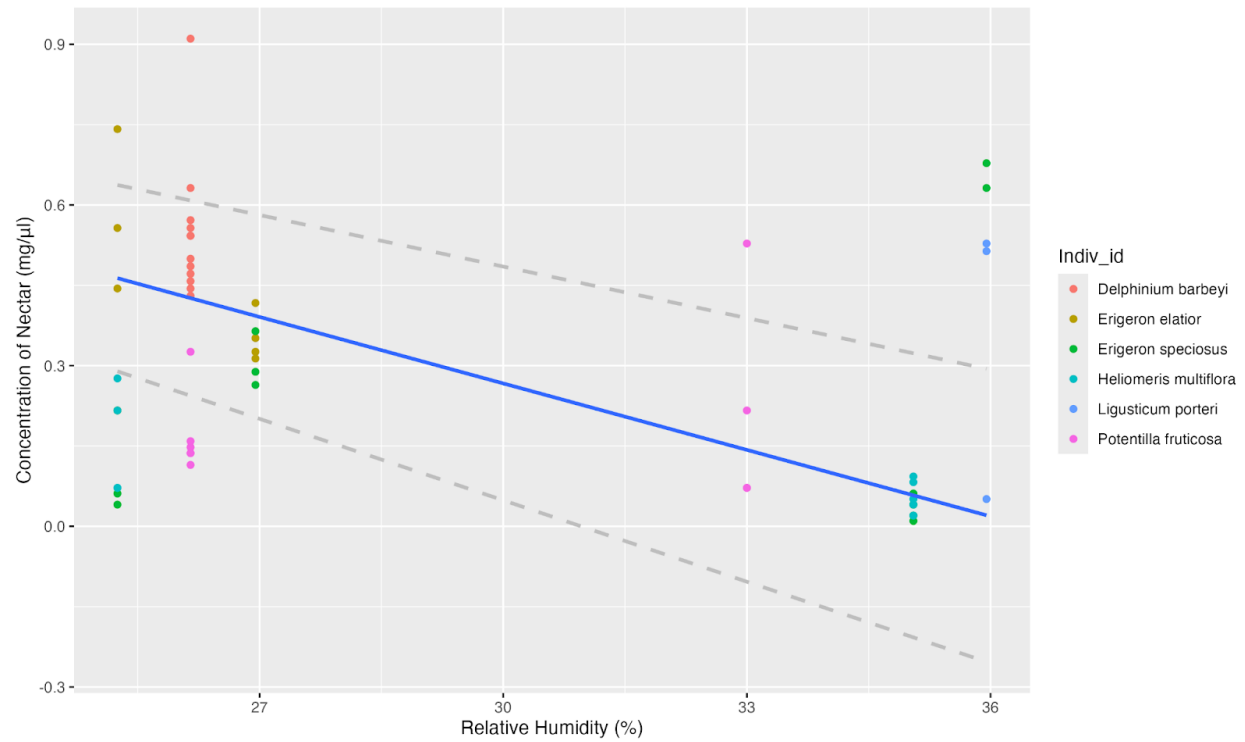


Figure 5. Depicts the relationship between nectar concentration and relative humidity, which was not statistically significant ($p = 0.0425$). The blue line represents the predicted data, while the different dots are the actual data point (the different colors represent different flower species).

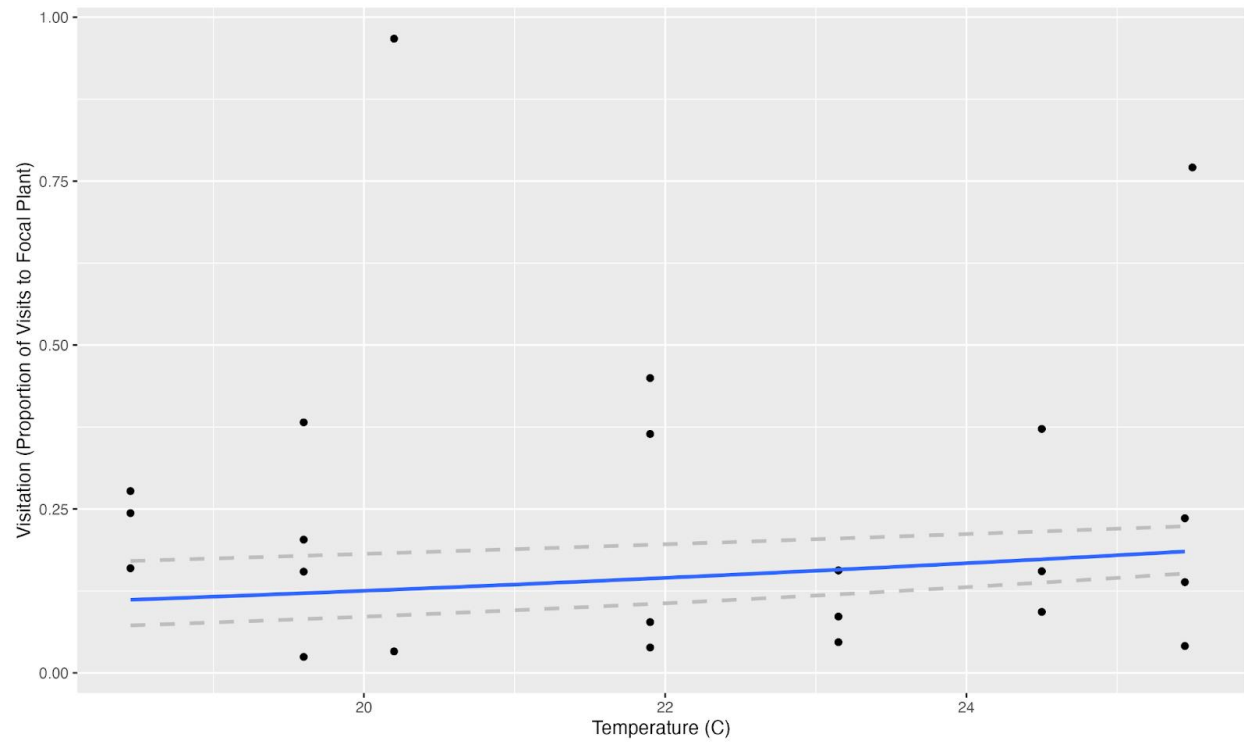


Figure 6. Depicts a non-significant relationship between pollinator visitation and temperature ($p = 0.207181$). The blue line represents the predicted data, while the different dots are the actual data point.

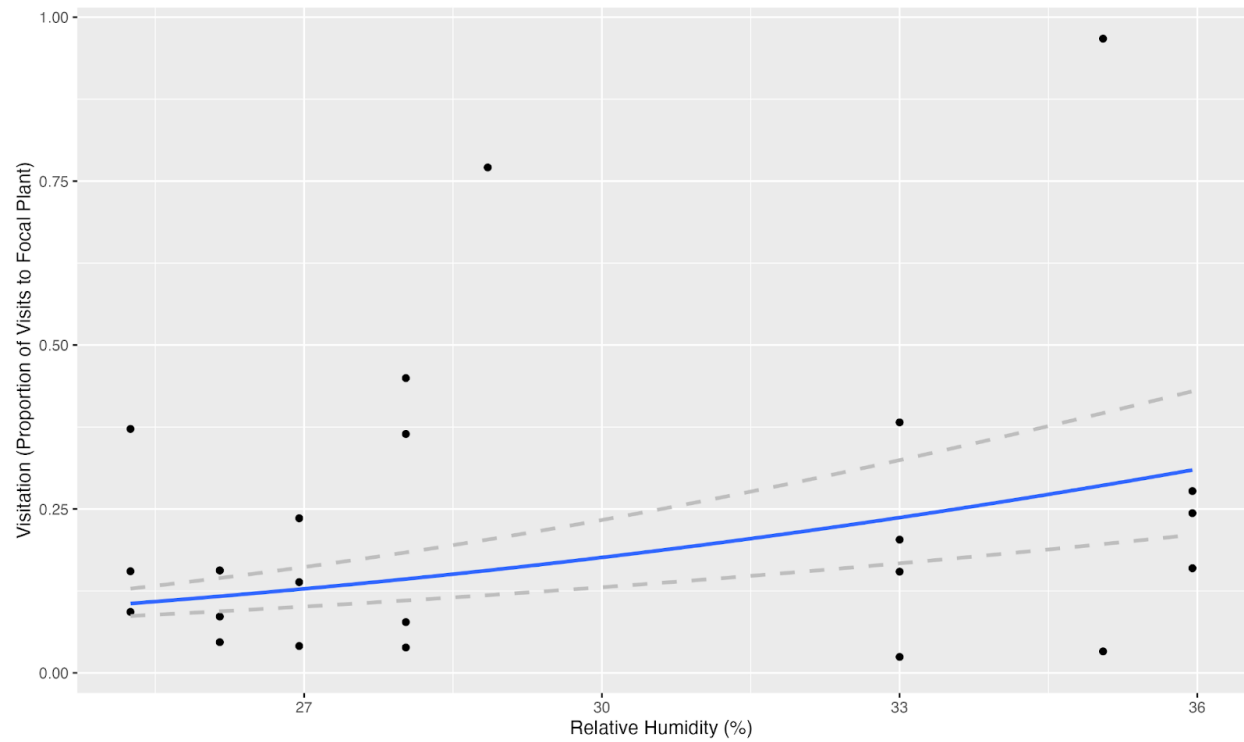


Figure 7. Depicts a significant positive relationship between pollinator visitation and relative humidity ($p = 0.001855$). The blue line represents the predicted data, while the different dots are the actual data point.

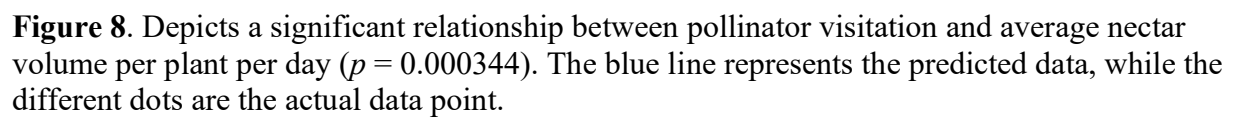


Figure 8. Depicts a significant relationship between pollinator visitation and average nectar volume per plant per day ($p = 0.000344$). The blue line represents the predicted data, while the different dots are the actual data point.

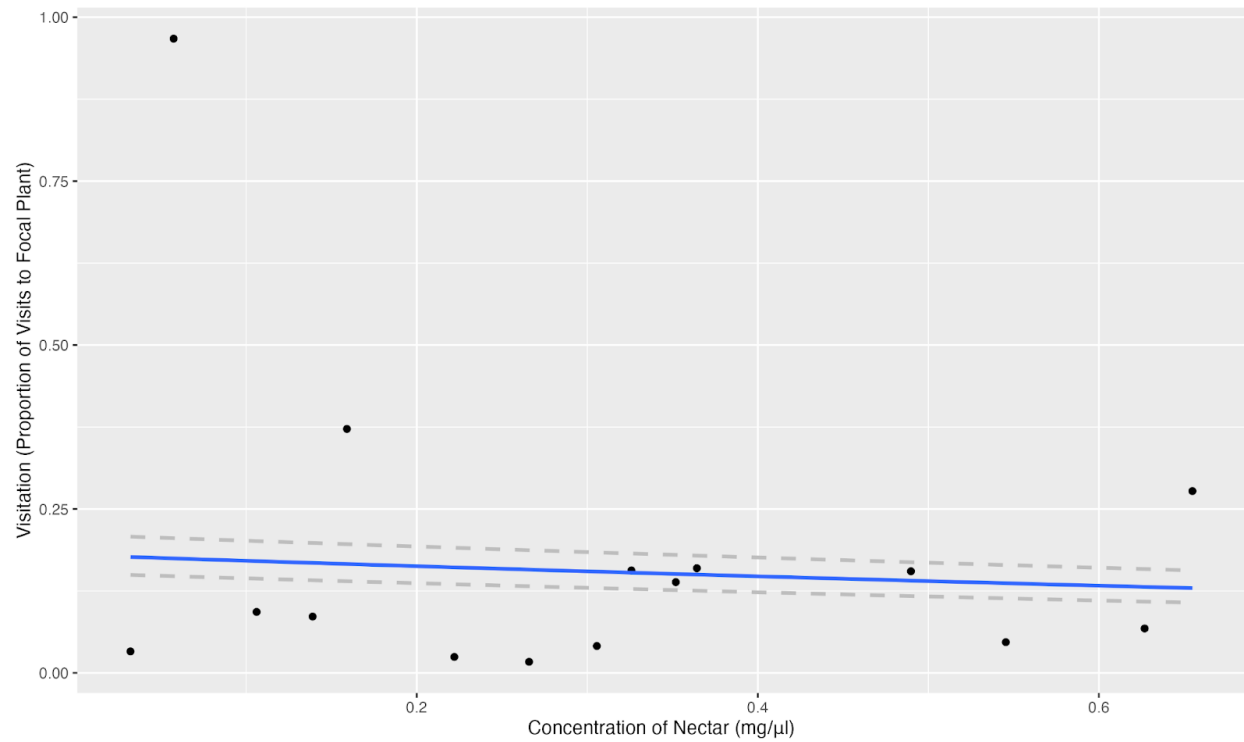


Figure 9. Depicts a non-significant relationship between pollinator visitation and nectar concentration ($p = 0.197045$). The blue line represents the predicted data, while the different dots are the actual data point.