

Fall 2018

# Differences in temporal and territorial feeding patterns of various tropical Trochilidae species as observed at two different ecosystems in Soberanía National Park

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*SIT Study Abroad*

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Differences in temporal and territorial feeding patterns of various tropical *Trochilidae* species as observed at two different ecosystems in Soberanía National Park

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In conjunction with SIT Panama Fall 2018  
To be reviewed by Aly Dagang

## Abstract

This study aims to illustrate differences in feeding patterns and displays of territorialism at two artificial feeding sites, located in two ecosystems; one site in a secondary forest of Soberanía National Park, the other in a residential area in the nearby town of Gamboa. Four 1-hour observation periods were recorded each day for four days at both sites. During each period of observation, the allocation of time to the three activities of perching, flying, and feeding was recorded, along with the number of visits to the feeders. Notes were taken on patterns of territoriality as connected to species and sex. Significance was found in the different allocations of time at both locations. Significantly more time was spent perching at the Park Feeders, and significantly more time was spent flying at the Lodge Feeders. Additionally, while there was no correlation found between the period of observation and the number of visits to the feeders at the Lodge, there was correlation found at the Park feeders, as the earlier the observation period, the more visits were recorded to the feeders. Overall, *F. mellivora* was the clear dominant species and males exhibited the majority of territorial displays at both sites, however observationally, individuals were more aggressive for longer periods of time at the Lodge Feeders.

## Acknowledgements

For flexibility in the face of my ever-changing topics and support leading up to project commencement, I would like to thank our director Aly Dagang. Thank you to Rhay Perez for providing the equipment needed to make this project possible. I would also like to thank Chelina Batista for providing prompt feedback with enthusiasm on everything I presented. I would not have been able to analyze cross ecosystem data without access to the Soberanía hummingbird feeders provided by Karen Avila of Avifauna, thank you for your permission. Finally, thank you to my family back home and my fellow SIT Panama Fall 2018 students and friends for providing support when I most needed it.

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## Introduction

Family *Trochilidae*, commonly known as hummingbirds, are amongst the smallest birds in the world, with some of the highest levels of maneuverability. Their small bodies give them the ability to fly and hover in patterns and directions that are unattainable to almost all other birds (West and Butler 2010). Many species are sexually dimorphic, such as *Florisuga mellivora*, the White-Necked Jacobin, in which the males feature a striking blue body and white tail feathers, whereas the females have a duller green body and grey underbelly. This distinctive feathering pattern, as well as specific flying patterns, are part of involved displays of courtship (Hurly et al. 2001).

Many factors of morphology relate to the specific functions of the *Trochilidae* in nature. The ability to maintain hovering speed can be attributed to the small body size of the birds (averaging between 5 and 20cm), increased heart rates, high frequency of wing beats, and high rates of oxygen consumption. The ability of hummingbirds to absorb oxygen at such high speeds, specifically in rapid dives, is the result of a pulmonary diffusion capacity more similar to that of bats than other birds (Altshuler and Dudley 2002; West and Butler 2010). The birds average flight speed has been recorded around 11.5 m/s, with much higher speeds to reach flowers. These high speeds must be recompensed by the reward of nectar in order to prove energetically valuable. Even slight modification in body mass and type due to molting or weight gain can alter

the birds' ability to efficiently maneuver and hover. The characteristically thin bill of the hummingbird provides the ability to enter the small space of the flower corolla and feed on nectar. Certain species of hummingbird, such as *Ensifera ensifera* have evolved alongside certain nectar producing flowers to have longer bill lengths (Gill 1985).

The tongue of the hummingbird is also highly specialized. Previous journals reported that the tongue brings nectar from the flower in a way similar to a capillary tube via capillary action. More recent research provides that the tongue tip actually functions to create a liquid trapping mechanism through the application of rapid configuration change (Rico-Guevara and Rubega 2011). This newfound recognition of the real mechanism through which hummingbirds achieve feeding efficiency proved significant in altering the understanding of energy allocation and nectar extraction.

### *Feeding*

*Trochilidae* flight, as a function of body size, requires not only immense exhaustion of metabolic strength in constant hovering, but also an intense aerobic capacity to maintain breathing at high speeds (Altshuler and Dudley 2002). Due to this continual energy use, hummingbirds have developed the ability to select nectar sources based on the sucrose concentration that will maximize their immediate energy intake (Tamm et al. 1986). Hummingbirds spend at least 20% of their time feeding, which makes nectar selection an activity that must be as energy efficient as possible (Diamond et. al. 1986).

Hummingbirds exhibit clear preference in certain aspects of nectar differentiation. It has been shown that certain species of hummingbird prefer a nectar sugar concentration around 50%. This is interesting, as the concentration from nectar producing flowers is typically around 20%. Additionally observed, however, is that while the birds prefer a concentration higher than is typically found in nature, their ability to differentiate nectar sources significantly improved when concentrations hovered around the natural 20% level, whereas they were not as discriminating when concentrations were higher (Blem et al. 2000). While it was previously understood that hummingbirds will always prefer the higher concentration of sugar, Tamm et al. (1986) observed that hummingbirds prefer the highest concentration up to a certain threshold of sugar absorption. Typical breakdown of sugar concentration in nectar producing flowers is about 15% fructose, 11% glucose, and about 74% sucrose (Freeman et al. 1984). The data collected about a wide variety of nectar producing plants suggested that the nectar might have developed from selective pressures and the process of adaptive convergence. Hainsworth and Wolf (1976) supported this breakdown of sugar, as hummingbirds in artificial settings seemed to prefer sugar compositions that reflected the compositions found in nature.

While hummingbirds do not show any preference to different amino acids present in the nectar, they show a significant avoidance to three types of amino acids. Additionally, the size of the corolla, which affects the rate at which nectar could be extracted, affected the differentiation of nectar sources. The species preferred higher concentrations of nectar generally, however once the corolla became too restrictive for adequate feeding efficiency, birds would move to prefer lower concentrations with more easily accessible nectar. This preference for different lengths of corollas as can be used most efficiently for hummingbird nectar extraction gives further evidence to the theory of coevolution of nectar producing plants and nectar feeding organisms (Hainsworth and Wolf 1976).

Some studies have noted that certain species, such as *C. anna* supplement nectar supplies with small insects. It appears that this hunting of alternative food sources is determined by

availability of quality nectar food sources, time of day, and weather conditions (Wheeler 1980). This study noted that nectar from feeders was consumed the most on clear days, while on days with even slight drizzle, the birds seemed to forage more for other food sources. Certain species, while it is quite possible they do supplement with insects, have not been observed feeding on insects during an observation period.

One major inhibition of a variety of studies, including Hainsworth and Wolf (1976) study of food selection, and Tamm and Gass' (1986) study of hummingbird energy intake rates observes the species in an unnatural, laboratory environment, possibly prohibiting natural feeding patterns. Hummingbirds can generally extract nectar at a faster rate from feeders than from flowers, altering the regular necessity of inserting their bills in multiple flowers despite unknown nectar concentrations. Additionally, although visits to feeders negatively correlated with the higher floral abundance, during times of lower floral abundance, feeders significantly dominated over remaining flowers in visits (McCaffrey and Wethington 2008). This might result in unfulfilled pollination in outstanding floral populations due to the presence of feeders.

The presence of artificial nectar might also impact the spatial organization of hummingbirds in relation to the feeders. From as far as 75m from a feeder to the source, hummingbird abundance increased steeply (Sonne et al. 2015). The study also reports, however, that increased hummingbird abundance due to the feeders subsequently increased the visits to flowers within 125m of the feeders, therefore negating the possible adverse effect of feeders on pollination. Spatial distribution of hummingbirds was highly affected by the presence of feeders (Inouye et al. 1991). This was observed most notably at the beginning and end of the high floral season, during which the low floral season coincides with the season most popular for feeder use. Further suggested is that hummingbirds will fly further distances to artificial feeders than they would to flowers in seasons of low floral abundance.

Hummingbird energy allocation is also tied to the natural design of flowers. Overall, hummingbird activity is correlated to floral patch size. As a result of the high energy expenditure of flight, territory is typically established at preferred feeding patch (Jiménez et al. 2012). Time spent feeding might be a function of patch quality, suggesting that higher patch quality would result in less time feeding, but more time defending the territory from intruding species (Schemske 1975).

Although the consequences of feeders as they skew population data and affect spatial organization have been noted, few studies have considered the effect of artificial feeders on the natural feeding patterns and time allocation of hummingbirds.

Hummingbirds have been noted to have the ability to differentiate different sources of nectar based both on their sugar concentrations and the quantity of nectar available. Pleasants and Zimmerman (1979) noted the presence of high and low concentration flowers coexisting in the same flower patch, coining the terms 'hot spots' and 'cold spots' for quantity of nectar. Hummingbirds are rewarded differently based on the presence of nectar in these flowers, and evidence suggests that certain nectar seeking organisms might have the ability to selectively feed from fuller flowers (Corbet et al. 1984). The volume of nectar present in a flower may fluctuate on a day-to-night basis, as well as in conjunction with varying humidity levels (Corbet, 2002).

The arrangement and design of inflorescence has influence on hummingbird feeding. Two-dimensional floral arrangements saw a higher level of different flower visits and revisits than three dimensional floral arrangements, suggesting that this arrangement pattern has influence on the feeding and pollination patterns of the birds (Hainsworth and Wolf 1983).

In addition to physical characteristics of environments such as floral arrangements and sugar concentrations, temporal factors are also significant in studying the feeding patterns of hummingbirds. The time of day is suggested to have a noteworthy impact on the frequency and duration of visits to nectar sources. Quantity of nectar consumed increased until mid morning, at which point the quantity consumed decreased through late afternoon, until a short feeding period between 16:00 and 18:00. This study was conducted on *Calypte anna*, a species native to the western coast of North America (Wheeler 1980). In contrast, it has also been observed that the number of visits was fairly even throughout the whole day, from sunrise to sunset. This study recorded around 80 to 120 visits per feeder per hour, recording a visit as any time a hummingbird used a feeder (Miller and Miller 1971). Schemske (1975) studied the temporal patterns of the Cinnamon Hummingbird, recording that the large majority of time observed (71%) was spent perching, while only around 9% of time was spent feeding. These values were consistent with those found by Pearson (1954) and Stiles (1971).

### *Territorialism*

*Trochilidae* are one of the few families of which inter and intraspecific patterns of competition can be understood, due to their outward and prominent displays of aggression and territorialism in the presence of almost any food source (Stiles & Wolf, 1970). Patterns of territoriality observed in hummingbirds at flower patches may be determined by the number of flowering buds present at a site. However, once a territory is established, the same amount of energy goes into defense throughout the whole period of territoriality, regardless of any decrease in the flower value (Trombulak 1990). Hummingbird territoriality seems to be fairly fleeting, observed to occur on an hourly basis, rather than a long-term seasonal basis (Stiles & Wolf 1970). It also occurs mainly in the mornings, when the number of visits is greater and the energy cost of territorialism is subsequently higher (Trombulak 1990). A study by Cody (1968) noted, however, that over a four-day period, the same territories were established by the same species of hummingbirds, in a site with interspecific competition. In this study, the territories were non-overlapping both inter and intraspecifically and between sexes. Additionally, the hummingbirds exuded clear preference over the chosen feeding sites. This site preference was also illustrated by Miller and Miller (1971) and Schemske (1975), where observations clearly supported that *Trochilidae* establish a preferred feeding site and repeatedly return to this site, with little observed variance and exploration.

There have been a number of studies that attempt to determine the factors involved in the selecting of a territory. The energetic value of a patch, as determined by the nectar energy content in joules and the number of inflorescences present, remained consistent from the beginning to the end of territorialism (Trombulak 1990). This exemplifies that the future viability of a patch is not considered in deciding to defend and maintain defense. The study suggests that it is important to consider the availability of other food sources in attempting to determine the motivation behind establishment of territory. It is possible that hummingbirds avoid being territorial whenever abundant food source is available.

Different species of *Trochilidae* are known to show different levels of territorialism. For example, *Selasphorus rufus* is highly territorial and rarely observed outside of established territory, while *Selasphorus calliope* only established weak territory twice over the course of the 17-day study, with each period of territorialism lasting less than one day (Martin 1988). Additionally, some species show territorial displays to only members of the same sex, while

others show aggression towards any species that enters the territory. *S. rufus* males have been observed to aggressively chase any other males to enter the feeding site, while performing courtship J shape dives in the presence of females (Hurley et al. 2001). Camfield (2005) noted that *Selasphorus platycercus* was almost always completely excluded from certain feeding sites by aggressive behavior of *S. rufus*, suggesting a hierarchy of defensiveness. Powers and Conley (1994) supported this observation in concluding that with the presence of a dominant species, the subordinate species will feed at a lower quality site, so as to decrease the energy expended in a futile attempt at defense.

Mechanisms utilized in defense of a food source vary to include chases, vocalization, hovering, and physical attacks (Camfield, 2005). The pattern of defense may change as physical territory shifts. Additionally, patterns of territorialism shift with the availability of food source. When food sources were unlimited, typically aggressive males avoided intraspecific aggression and were able to feed efficiently without the added energy expenditure of defending territory. On the other hand, when nectar was limited, more than four times the amount of interspecific aggressive chases occurred within the territory (Powers and McKee 1994). Additionally, a decrease in food supply by *Calypte anna* led to a decrease in low energy defenses and an increase in chases along with an increase in the time between feedings (Ewald and Orians 1982). This notion of the effects of competition was also noted by Schemske (1975) in that *A. rutila* spent significantly less time in their preferred feeding zone when a competitor was present in the area versus when a predator was not present. Additionally, by playing the chirps of territorial hummingbird *E. curpeiceps*, an increase in the aggression and a decrease in the foraging time of hummingbirds can be observed (Tsai 2009). It was also observed, however, that the increase in aggression and decrease in foraging was most conspicuously tied to the presence of intraspecific competition versus interspecific competition. This might lead to the conclusion that hummingbirds will more readily engage in combative territorialism with members of the same species. The energy required for *Trochilidae* flight and hovering means that additional time spent in competition is energetically expensive and wasteful.

The amount energy used in defending territories is positively related to the quality of the food source. These defensive tactics at higher quality food sources included longer chases, and defenses more often accompanied by chirps and aggressive hovering (Camfield 2005). This expenditure only occurs to a certain threshold, however. If, for example, too many intrusions occur in a territory and the amount of energy used is greater than the amount of energy there is to gain, the territorial activity will end (Brown 1964).

### *Species Overview*

#### White-Necked Jacobin (*Florisuga mellivora*)

Males and females, although similar in morphology as juveniles, molt to sexual dimorphism around 14-weeks (Bleiweiss 1991). Males mature to have bright blue backs with a white patch on the upper neck, white stomachs and a white under-tail. Females develop green iridescent feathers on the back and a scale-like pattern on the breast. Some females actually maintain the blue feathers typical of the male, making the species partially sexually dimorphic (Ridgely and Gwayne 1989). *F. mellivora* ranges from through Peru, south Bolivia, and southern Brazil. The birds typically feed in pairs, observed in late afternoon congregating in larger groups high in trees (Cotton 2001). The culmen length, as averaged from both males and females is 19mm. This

species has been observed actively defending *Erythrina micropteryx*, and is also known for occasional feeding on various insects (Snow and Snow, 1972).

#### Rufous-Tailed Hummingbird (*Amazilia tzacatl*)

This hummingbird is common throughout Neotropical lowlands of Central and South America. There are five subspecies of *A. tzacatl*, with two of the five being endemic to different parts of Panama. (Miller et al, 2011). Male and female *A. tzacatl* are monomorphic, both displaying iridescent green throat feathers, orange bill with black tip, and characteristic rufous color tail feathers. These birds are known to be extremely territorial and aggressive when defending preferred feeding site (Stiles & Skutch 1989). They do, however, occasionally form nesting communities in groups of *A. tzacatl* (Weller 1999).

#### Violet-Bellied Hummingbird (*Damophila julie*)

This species can be observed from western limits of Coclé province in Panamá to its eastern limits of Magdalena Valley in Colombia. It has also been reported in eastern Peru (Hilty and Brown, 1986). Male and female *D. julie* are slightly sexually dimorphic; the male is mainly green with a bright violet chest while the female is green with a greyish underbody (Wetmore, 1968). Little information has been recorded about the behavior of this species of hummingbird, although they are typically observed as birds that forage mainly close to the ground (Hilty and Brown, 1986).

#### Long-Billed Hermit (*Phaethornis longirostris*)

Little information has been recorded about this species of hummingbird. Their known range is from south-eastern Mexico through northern Panama and north-western Colombia, and a small portion of western Ecuador. Males are known to gather in leks and have a very distinct song (Araya-Salas 2013). *P. longirostris* forages mostly in the understory and rarely visits the same flower patch twice in one day (Skutch 1964). The species is notably recognizable by its long curved bill, facial striping, and long white tail feathers.

### Research Question

How are patterns of *Trochilidae* territorialism and temporal feeding different at artificial feeders in two varying ecosystems in Soberanía National Park?

### Methods

#### *Description of Study Site*

The study was conducted in Soberanía National Park, a 22,000-hectare park with about 8,000 hectares of primary forest at the mouth of the Chagres River. The park is located in a tropical area with a short dry season with annual rainfall of 2616 mm per year (Karr 1982; Rand & Rand 1982). The park occupies most of the former US Canal Zone and is divided into northern and southern parts by the Chagres River. The northern portion of the park is evergreen lowland forest, which deviates to semi deciduous lowland forest in the south. The study will take place in the lowland portion. The park is largely free from human activity, however the land along the northern and eastern sides of the park has been converted to cattle ranching and agriculture.

(BirdLife International 2018). The feeders are located approximately 0.6 km off the well-known Pipeline Road. At the site, three feeders hang off a high raised roof, about two meters apart from one another, surrounded by secondary forest of moderate canopy coverage.

The second portion of study was conducted at Soberanía Lodge, located in the town of Gamboa at the end of Jadwin Road. The Lodge is in a residential area, however is in very close proximity to a slightly forested area. The feeding station has three feeders that hang off a low rising roof, about two meters apart from one another. Two days were spent attempting to locate a forested patch of flowers with nectar used by *Trochilidae*, however the attempts were unsuccessful.

### *Observation*

Every day for nine days of study, I conducted four, 1-hour observation sessions of the birds, Early Morning (6:15-7:15), Mid Morning (8:30-9:30), Mid Afternoon (14:00-15:00), Early Evening (16:00-17:00); five days were conducted at the Lodge feeders, and four days were conducted at the Park feeders. General climatic conditions were recorded at the feeders during each hour long observation session. A high count of the birds present during the given hour was also taken, so as to estimate the total number of individuals present at the feeding site.

Specific methods were used to study the feeding patterns. I noted the feeding visits from when a hummingbird arrives at the feeding site to when it leaves, leaving being defined as when it leaves the area/feeder to visit/perch on another feeder or leave the area entirely. (McCaffrey, & Wethington, 2008). The time of day of all feeding visits was recorded. Time allocated to (1) perching, (2) feeding, and (3) miscellaneous flying was recorded using a stopwatch (Schemske, 1975). Miscellaneous flying was recorded when occurring within a one-meter radius around the feeders. Every day, the times spent doing each activity were recorded in overall seconds for each period of the day, then summed up for the days total, then finally summed over the course of all four days of observation.

Additionally, notes were taken on the territoriality of the birds, observation were made on the interspecific and conspecific interactions between birds. Specifically, the territorial patterns of chasing and physical altercation were noted (Camfield 2005). This is meant to provide information on the difference of territorial patterns in different ecosystems, and to have a basis of comparison to literature. These notes were taken in conjunction with observations on species and sex of the hummingbirds, so as to link territorial patterns to certain species.

The results will be analyzed using a one-way ANOVA test, along with analyses of correlation between observations.

### Ethics

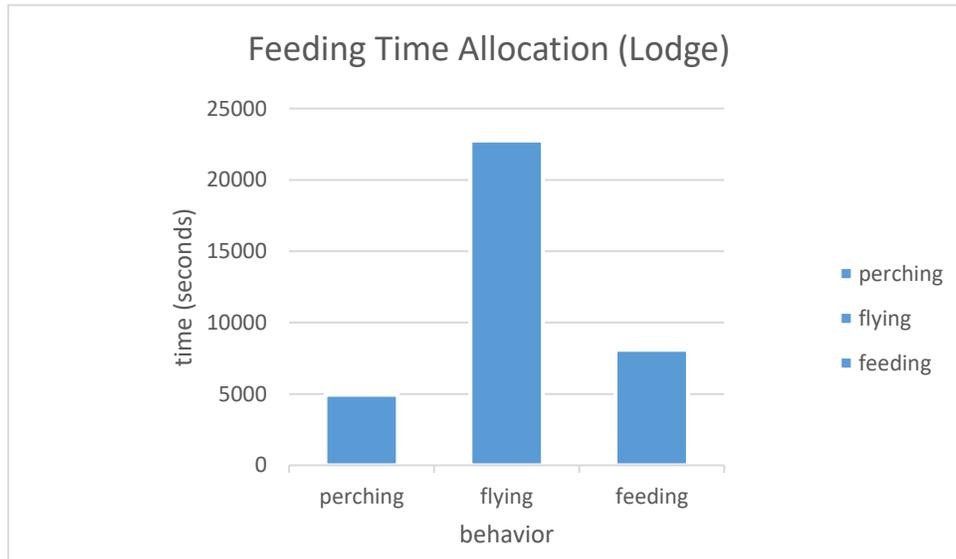
So as to limit the pressure felt by *Trochilidae*, only observational research was conducted. Additionally, while observing at the Lodge feeders, observation was done behind a mesh barrier, to leave the area undisturbed and limit the effect of human presence on the feeding patterns. At the Park feeders, a similar attempt was made to limit human effects by conducting observation approximately three meters away from the feeders, outside the path of flight of the birds. While recording video of the birds, the camera was placed as far away as possible so as to still get detailed video coverage. Video was only taken three times at each site in increments of 15

minutes, so that the presence of the camera did not alter the hummingbird patterns. This project was approved by the IRB/LRB.

## Results

### *Lodge Feeding Time Allocation*

The majority of daily research surrounded the breakdown of time spent in various activities while feeding. The times spent flying, perching, and feeding by *Trochilidae* was recorded at both the Lodge Feeders and the Park Feeders. Every day, the times spent doing each activity were recorded in overall seconds for each period of the day, then summed up for the days total, then finally summed over the course of all four days of observation. At the Lodge Feeders, a total of 4,945 seconds were spent perching, 22,759 seconds were spent in miscellaneous flying within a one-meter radius around the feeder, and 8,097 seconds were spent feeding. The respective percentages are as follows: 13.81%, 63.57%, and 22.62%. This data is representative of 16 total hours of observation over four days. The values in seconds are represented in the bar graph below (Figure 1).



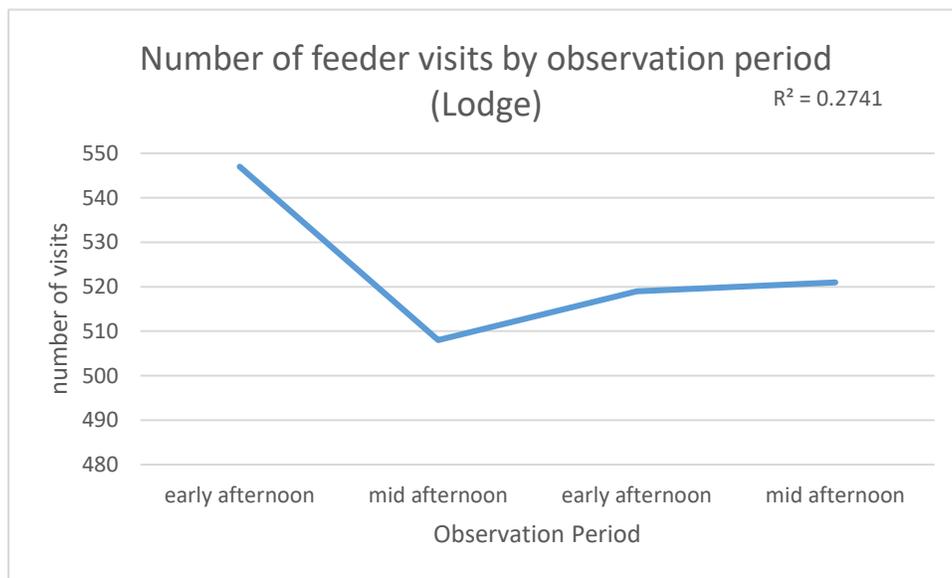
**Figure 1.** Feeding time allocation in seconds of all species of hummingbird present at the Lodge Feeders from November 10, 2018 to November 13, 2018, between the hours of 6:15-7:15, 8:15-9:15, 2:15-3:15, and 4:15-5:15.

The values clearly exemplify that the majority of feeding time at the Lodge Feeder during these time periods was spent flying. Observationally, it was noted that the majority of feeding was conducted while hovering, which was counted in the flying time. This means that the time spent feeding while hovering was recorded for both flying and feeding. Occasionally, the birds fed while perching, which means that time spent feeding while perching was recorded for both feeding and perching. These overlaps were counted in order to get a clear picture of feeding activity.

The results of the one-way ANOVA test on this portion of the data showed no significance ( $p=0.05$  or less) in the allocation of time spent on different activities during the different periods of observation. This shows that at the Lodge feeders, the birds consistently

showed the same patterns in temporal allocation, regardless of time of day. Observationally, it was noted that during periods of extreme heat, the activity of all species was much lower; only 8 total minutes of activity was recorded on this day, whereas the median of total recorded activity at the Lodge feeders was 37.75 minutes.

The visits to the feeders were recorded at each observation period. The median number of visits to the Lodge Feeders was 129.75, with a standard of deviation of 39.16. When plotted on a line graph (Figure 2) with visits as a function of time of day, little correlation was found with an  $R^2$  value of 0.27. Figure 2 illustrates that the number of visits to the feeder were fairly consistent throughout the day. During the period of observation mentioned above that only recorded 8 total minutes of activity, only 30 visits were recorded. After removing this data point from the data set, the standard of deviation is reduced to 30.46 and the median number of visits is increased to 135. This is slightly more representative of the typical number of visits to the feeders.



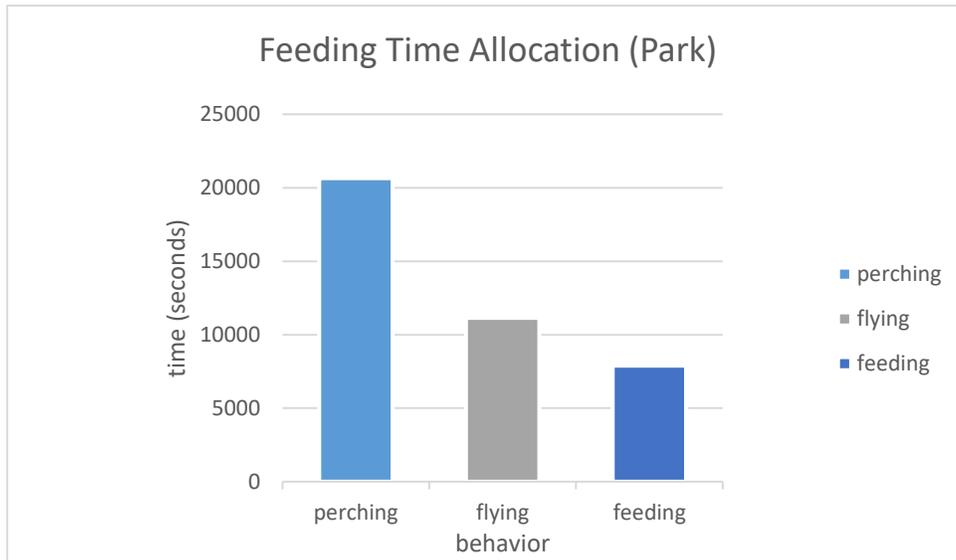
**Figure 2.** Number of visits recorded at the Lodge Feeder at different observation periods throughout the day.

No valuable difference in the climactic conditions recorded were experienced throughout the four days of observation at the Lodge Feeders. Therefore, no data can be presented on the correlation between climactic conditions and number of visits.

#### *Park Feeding Time Allocation*

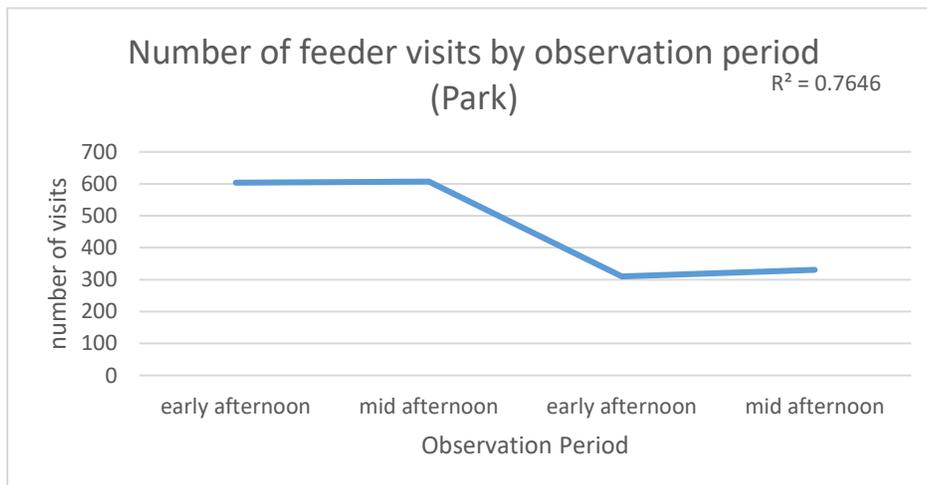
Total time allocated to different activities at the Lodge feeders resulted in 52.03% of time perching, 28.08% flying, and 19.89% feeding. This data is representative of 16 hours of observation over four days. The graphic below (Figure 3) displays the time allocation information. The values clearly represent that the majority of time was spent perching, followed by flying, and the least amount of time spent feeding.

While the results of the ANOVA test showed no significant difference between the times spent perching or flying over the four observation periods, there was a statistical difference noted between the times spent flying when the two morning periods were combined and analyzed against the two afternoon periods combined. The p value obtained was 0.023. This means that a significantly larger amount of time was spent flying in the morning observation sessions at the Park than during the afternoon sessions.



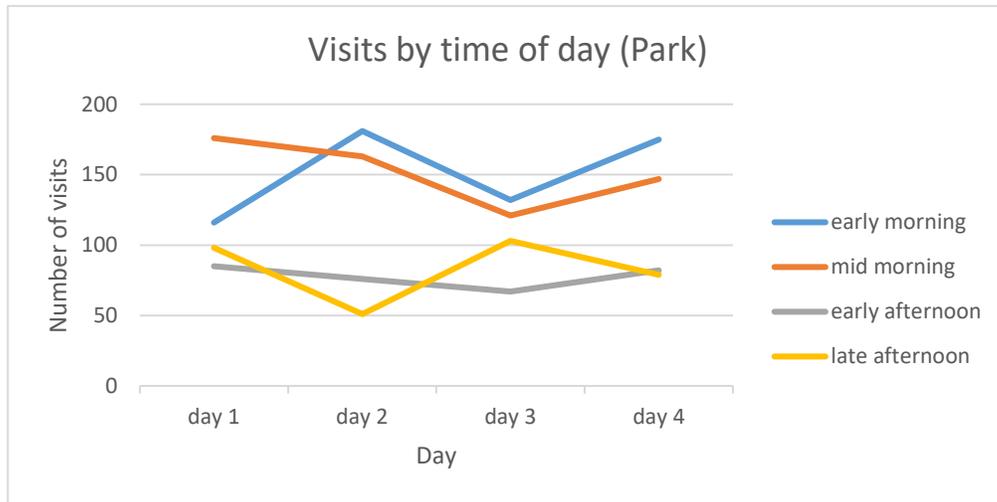
**Figure 3.** Feeding time allocation of all species of hummingbird at the Park Feeders, from November 14, 2018 to November 17, 2018 during the four aforementioned observation periods.

The median number of visits at the Park Feeders per hour-long observation session was 97 with a standard of deviation of 38.9. The maximum number of visits was 181, which was achieved during the early morning observation period on the second day. The lowest number of visits was 51, which was achieved during the late afternoon observation on the second day. When plotted on the figure below (Figure 4), with number of visits as a function of time of day, a strong correlation was found with an  $R^2$  value of 0.764. This shows that the hummingbirds visited the feeders at a higher frequency during the earlier periods of observation.



**Figure 4.** Number of visits recorded at the Park Feeders at different observation periods throughout the day.

When plotted on the line graph below (Figure 5), showing the number of visits during each observation period on the four different days of observation, it is illustrated that the majority of visits occurred in the first half of the day, while less occurred in the two afternoon observation periods. There is a clear split in the frequency of visits.



**Figure 5.** Number of visits at the Park Feeders on each of the four days of observation, during each of the four periods of observation.

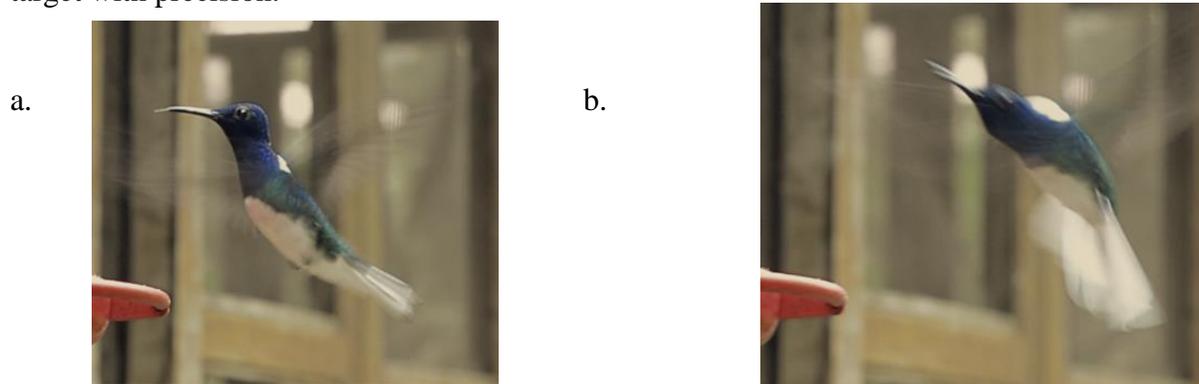
When comparing the values of time allocation recorded at the Park and the Lodge Feeders, some statistical significance was found. The p value resulted from a one-way ANOVA test between the perching times at the Lodge and the Park Feeders was 0.029, which shows that the perching times at the Park Feeders were statistically larger than the perching times at the Lodge Feeders. The p value that resulted from an ANOVA test comparing the flying times at the Lodge versus Park feeders was 0.037, which shows a statistically significant increase in the amount of time spent flying at the Lodge versus the Park Feeders. The p value that resulted in testing the feeding times at the two sites was 0.896, which shows no statistically significant difference in the time spent feeding at the two locations.

#### *Territorialism at Lodge Feeders*

After observing the feeders at the Lodge for a total of 16 hours, many notes were taken on the patterns of territorialism of all *Trochilidae* species present. Although this data is more qualitative than quantitative, clear patterns of behavior were present.

Of the four species present at the Lodge feeder, the dominant and most aggressive species and sex was the male *Florisuga mellivora*. The male *F. mellivora* frequently utilized chases and dives to drive other individuals out the the area of the feeders. Occasionally, a male would claim territory at the feeders by perching on a metal pole around 2-meters from the feeder. Subsequently, the male would drive out any individual that would come within 1-meter of the feeder, inhibiting any feeding that might otherwise occur. These territories rarely lasted more than 30 minutes. It was difficult to discern whether or not the same individuals were habitually

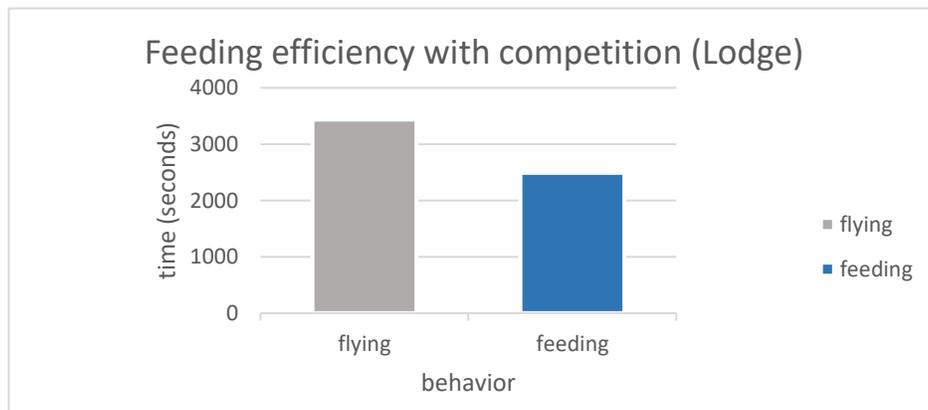
setting up territory, due to small size and limiting distinguishable characteristics between individuals of the same sex and species. Additionally, it was evident that the male *F. mellivora* mainly engaged in physical altercation with other members of the same sex and species. The species showed well-defined patterns of territorialism and aggression. Before chasing or diving at another individual, male *F. mellivora* would arch it's back and then accelerate towards the target with precision.



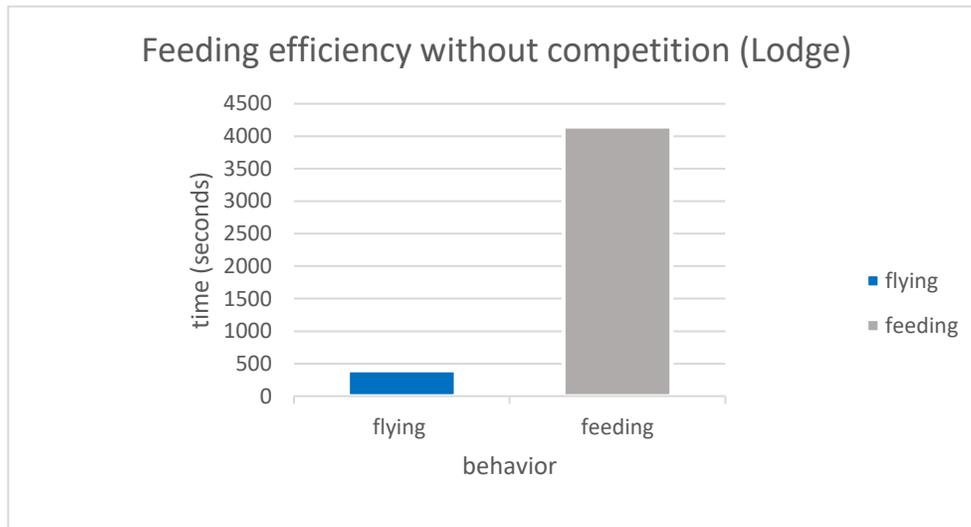
**Figure 6a, 6b.** Male *F. Mellivora* engaged in typical flight at the Lodge Feeder site in figure 6a. Male *F. Mellivora* engaged in flight typical of chasing or diving behavior, with back arched.

Except when defending established territory, the male *F. mellivora* would rarely chase or dive at a member of a different sex or species. The majority of territorial behavior was intraspecific and intra-sex. It was also observed that the individuals would rarely allow another individual to feed alone. Whenever one individual bird approached a feeder to feed, more would quickly follow suit. There were often long periods of time during which five individuals were attempting to feed at the same time. The other species recorded, *A. tzacatl* and *D. julie*, along with the female *F. mellivora* rarely engaged in displays of territorialism and would fly off if chased by a male *F. mellivora*. All individual birds of all species exhibited strong preference for the middle bird feeder at the Lodge. Rarely did any individual utilize one of the two other feeders present.

Additional temporal data was recorded with regards to feeding efficiency with and without competition for all species combined. Competition, in my data, was defined as any time other individuals were within a 1-meter radius around the feeder. The data is illustrated below.



**Figure 7.** Feeding efficiency at the Lodge feeders with competition. Time spent flying versus time spent feeding.



**Figure 8.** Feeding efficiency at the Lodge feeders without competition. Time spent flying versus time spent feeding.

The median value of feeding efficiency with competition, determined by dividing time spent feeding by time spent flying in approximately one minute intervals was 20.07%. The median value of feeding efficiency without competition, obtained the same way, 57.43%. This shows that a much greater proportion of time is spent feeding when there is no competition.

#### *Territorialism at Park Feeders*

The male *F. mellivora* was the dominant and most aggressive sex and species at the Park Feeders. Seldom, a male *F. mellivora* would establish a territory by perching on a nearby tree or on the railing below the feeders. These individual periods of territorialism never lasted longer than 30 minutes during the observation periods. The individuals seemed to have more aggressive patterns of territoriality in the morning observation periods, when, as mentioned before, there was a significantly greater number of visits everyday. In the afternoon, not only did the number of visits decrease, but the level of territoriality seemed to also decrease. Birds were more likely to visit the feeders alone, without another bird in the immediate vicinity.

A majority of time was spent perching on branches in trees away from the feeders, and the birds had a clear preference on which portion of the trees they would always return to. *F. mellivora* tended to chase other species away from the feeders when engaging in displays of territorialism, and did not just display aggressively to its own species. For the majority of the time, the individuals were receptive and allowing of other individuals feeding at the same time, for long periods of time. Although not quantified, it appeared observationally that the feeding efficiency with and without competition did not show incredibly well defined distinctiveness. The other species recorded, *A. tzacatl*, *D. julie*, and *P. longirostris*, along with the female *F. mellivora* would rarely engage in displays of territorialism. *A. tzacatl* was recorded chirping on multiple occasions, which may have been a display.

No individual birds seemed to take preference to any of the three feeders located at the Park feeding site; each feeder was utilized fairly evenly.

## Discussion

### *Comparative Ecosystem Data of Temporal Feeding Patterns*

The two study sites I observed were located in two very different ecosystems; one site was secondary forest with dense canopy cover and the other was a residential area with few short trees nearby. These two sites saw a significant difference in the time allocated by various species of *Trochilidae* to flying and perching. One possibility that might explain this significant difference is the contrast in habitat functionality for the birds. The Lodge Feeder site provided the birds with little stimulation or place to congregate other than directly around the feeders, whereas the Park Feeders are surrounded by a large area of forest. The observational data that the birds at the Park Feeders spent more time perching in surrounding trees than the birds at the Lodge feeders also supports this.

Little scholarly information is to be found about the relationship between type of ecosystem and feeding behavior. Many experiments performed on *Trochilidae* in a laboratory or artificial feeding station rarely admit the possible error present by altering the natural feeding site. Studies have noted, however, that results were fairly consistent when comparing time between meals in the laboratory and in the field, which does not substantiate my conclusions (Wolf and Hainsworth 1977). Tinoco et al. (2009) found that, in studying different habitats of *Trochilidae*, including those interrupted by human activity, the distribution of the particular species remained without significant difference, as long as the shrubs preferred by the species was still present. This coincides with the data collected that almost the same species, at the same level of abundance, was measured at the Park and Lodge Feeders. This paper also found, however, that, in studying three separate habitats, the feeding behavior did not differ to a statistically significant extent, concluding that feeding behavior is consistent regardless of habitat change. This study was conducted in all natural feeding habitats, with preferred nectar producing flowers, which might be a reason explaining the consistency amongst habitats and lack of similarity with my data.

Poor habitat quality in *Selasphorus rufus* resulted in long stopovers in migration and lower body mass (Russell et al. 1993). Additionally, habitat quality holds effect on population density, overall showing important implications of habitat on hummingbird behavioral and population dynamics. The changes in hummingbird feeding activity has not been studied in this vein of research, however, changes in certain behaviors such as body size, stopover length, and population suggest that differences in feeding behaviors might be present, as the amount of needed energy fluctuates based on expenditure.

When analyzing the breakdown of activity based energy expenditure in the two habitats, the results found at the Park Feeders more closely align with previously researched behaviors of feeding at natural nectar sources. *Trochilidae* typically spend 70-80% of time perching, while predictably less than 20% of time flying for different pursuits (Schemske 1974; Pearson 1954). The Park Feeder habitat holds similarities with the ecosystems studied in the mentioned results, a developed forested area in the natural habitat of *Trochilidae*. This might be why the Park data is most similar to any research previously done, and the Lodge data is not consistent with typical hummingbird patterns of feeding.

### *Visitation Frequency*

The visitation frequency recorded at both artificial feeding sites far exceeds the number of visits typically seen to natural nectar producing flowers. Previous studies have placed hummingbird

visitation frequency around 2-15 visits per hour (Schemske 1974; Campbell et al. 1997). This is drastically different from the range recorded in this study of 51 to 204 visits per hour at the artificial feeders. This could be explained by the data suggesting that visitation rates increase with higher success and usefulness of food source (Garrison & Gass 1999). Additionally, hummingbird population in a given area is known to increase in the presence of artificial feeders, which could result in higher visitation frequency (Sonne et al. 2015).

While there was no statistically significant difference found between the total visitation rates of the hummingbirds at both feeding sites, there was significant difference found between the correlation of observation period and visitation frequency. At the Lodge Feeders, no correlation was found between the time of observation and the visitation frequency. This could be due to the lack of other food sources in the area, or the lack of habitat stimulation offered by the residential area. It has also been shown that sugar concentration has an effect on the visitation schedule of *Trochilidae*. With higher concentrations, *Trochilidae* show steady decline in number of visits throughout the day, while lower concentrations of sugar in nectar show peak visitation times at the beginning and end of the days (López-Calleja et al. 1997). Although the concentrations of sugar at the two feeding sites were not measured on a daily basis, with further research, this might prove the reason behind the differences in feeding frequency.

Some studies have revealed clear patterns in hummingbird daily feeding schedules and peak times, while others have revealed visitation data to be fairly consistent throughout any given day. Miller and Miller (1971) noted no pattern in visitation frequency when observing *Trochilidae* at artificial feeders in an area lacking dense forest coverage. A study by Wheeler (1980) observed, however, that nectar consumption increased until around 9:30, at which point it steadily decreased throughout the day, also observed at artificial feeders in an area lacking forest coverage. Few additional studies have listed feeding frequency as a function of time of day, so further data to support either conclusion is lacking. It is possible, however, that the presence of a natural functioning ecosystem for the *Trochilidae* is what created the temporal patterns of visitation at the Park Feeders.

### *Patterns of Territoriality*

Although displays of territoriality including chasing and diving were high, especially amongst male *F. mellivora*, the frequency of establishment of species-specific territory was low. A male *F. mellivora* established territory on approximately six occasions over the course of the 8 days of observation at both observation sites. There are many explanations that have been offered to dictate how and why *Trochilidae* or other nectar feeding organisms decide to establish territory, determine the size of territory, and eventually abandon territory. Certain territorial animals have been known to abandon territory when food sources are abundant, out of the lack of need for ownership of a territory. It is understood that some level of food scarcity must be present in order to encourage behavior of territoriality (Brown 1964). Defense strategies in hummingbird territoriality can cease in the presence of overwhelmingly abundant competition, as was seen at both the Lodge and Park Feeders. It is possible that as the *Trochilidae* at the two sites were unable to form an impenetrable defense, and therefore would abandon any territory established out of lack of control of the resources. Territory also is known to increase in bounds in *Trochilidae* when food scarcity increases (Hixon 1983). As food was always abundant at both feeding sources and was always refilled when close to empty, it is possible that the *Trochilidae* did not feel the pressure of food limitation needed to jumpstart the establishment of long-term territory. The short bursts of established territory defenses by *F. mellivora* mirrors the

understanding that *Trochilidae* typically hold on to territory on an hourly basis, rather than establishing a more permanent area of territory for a longer period of time (Stiles and Wolf 1970).

*F. mellivora*, as previously mentioned, was by far the dominant hummingbird observed during each observation periods. It regularly utilized chases, dives, and chirps to defend the territory from other individuals, both inter and intraspecifically. The displays, however, were mainly intraspecific, being targeted towards other male *F. mellivora*. This is supported by the data that intraspecific competition typically impacts aggression more than interspecific competition (Tsai 2009). There has been data found to support some defense employed by *F. mellivora*, however no study has ever noted this species as a dominant species amongst all others (Snow and Snow 1972). This intraspecific competition does not line up with the data observed that intraspecific competition is limited when food sources are unlimited, as mostly all of the territorial displays that occurred during the observation periods at both sites were intraspecific. (Powers and McKee 1994). There is also limited data to supplement the behaviors observed in the other species of *Trochilidae* present at the feeding sites. There have been observations to note that *A. tzacatl* are typically extremely aggressive individuals that dive at other birds or even insects that invade their territory (Stiles and Skutch 1989; Primack and Howe 1975). These displays of aggression were not observed at the Lodge or the Park Feeders. It was observed that this species was not as abundant as the other species, and as this species is known to form loose nesting colonies, it might be possible that the lack of other individual *A. tzacatl* discouraged the natural behavior of aggressive territorialism (Weller 1999). The Lodge Feeders also saw a variety of other families of birds, other than *Trochilidae*. The sightings included multiple individuals of the family *Tyrannidae* and two individuals of the family *Picidae*. This added competition that was present at the Lodge and not the Park Feeders might have contributed to the different patterns of feeding that were based in territorialism and competition. Observationally, the hummingbirds did not approach the feeders when a member of the *Tyrannidae* or *Picidae* were perched on the feeders.

The *Trochilidae* clearly showed a preference for a specific feeder at the Lodge Feeders. This is true of hummingbird territoriality, as it has been noted that this family of birds often establishes a preferred feeding site to which they often return (Miller and Miller 1971; Schemske 1975).

As illustrated by the data collected at the Lodge Feeders, the presence of competition has an effect on the feeding efficiency of *Trochilidae*. It is well understood that feeding becomes limited in the presence of competitors (Schemske 1975). Although the defense of territory and displays of aggression towards competition increases the amount of energy spent and therefore increases the amount of energy required to be obtained by feeding, the amount of time spent feeding is negatively affected by the amount of competition present at any given time.

#### *Possible Limitations and Error*

Throughout the study, multiple logistical situations offered the presence of possible error in observations and data recording. During filming of the species, three 25-minute sessions per observation site, a camera was placed on a tripod within 1-meter of the feeders. The presence of the camera might have altered the natural behavior of the birds and therefore altered the authenticity of temporal feeding data recorded during that time. Additionally, although observations were generally made from an inconspicuous distance, it is possible that the birds were able to sense the presence of a possible intruder and did not display genuine patterns.

After presenting recorded data, a few possible sources of error must be accounted for. This includes the difficulty in determining accurate counts of temporal patterns of a species that is very quick and fleeting. It is necessary to account for some error that resulted from an inability to stop a timer with complete speed accuracy. Additionally, visitation frequency data was difficult to obtain due to the speed of the birds. The study was also limited by the amount of time that observation could be conducted daily by one researcher. If possible, it would have been interesting to note hummingbird feeding and patterns of territoriality earlier in the morning and later in the evening. Additionally, data could have been collected in the middle of the afternoon, which might have revealed different patterns as this was typically the warmest portion of the day. One final source of error and limitation of the study is that the sugar concentrations of the nectar at the two sites was not determined. There is a plethora of data to support the influence of sugar concentration on the patterns of *Trochilidae*, therefore this lack of knowledge on these levels might have led to error in recognizing such patterns.

### Conclusion

Although the explanations behind the data recorded are not entirely clear, there was a significant difference in temporal feeding patterns observed at the Lodge and Park Feeders. It is possible that this is due to the difference in ecosystems, including both flora and fauna, present at the two sites. The Park Feeders offered a more natural habitat for the birds to reside in, whereas the Lodge Feeders offered limited stimulation besides the feeders themselves. In order to get a clearer image of the effect of ecosystems on feeding patterns, more diverse and detailed studies need to be conducted, with observation of the same collection of species feeding at two different sites. It may also be important to add more stations of data collection in more habitats, so as to confirm this pattern and possibly offer new patterns of feeding based on habitat. Additionally, it would be interesting to conclude whether or not differences in feeding are more closely tied to different ecosystems or to the presence of natural feeding sources of nectar producing flowers. Anthropogenic interference into *Trochilidae* foraging alters natural habits of the birds, however more information is needed to know exactly to what extent, and how these changes are affecting essential processes such as pollination.

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