Flowers and Feeders: A Comparison of Hummingbird Feeding Activity

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ABSTRACT
Hummingbird feeders are the best way to see high species abundance and diversity, but few studies examine the differences in species abundance, diversity, feeding patterns, and aggression between flowering plants and artificial feeder sites within the same habitat. Are there significant affects on local hummingbird ecology by the presence of feeders? This paper explores possible answers to this question by investigating discrepancies between the two types of site and the implications of said discrepancies. A high count method was used to estimate species abundance and diversity along with qualitative observation was used to analyze aggression. The study found that, in general, higher abundance and diversity than at feeder sites than can be found at flowering plants. Feeding trends at the two sites remained similar while aggression displays took place largely only at the feeder sites.

RESUMEN
El uso de comederos de colibríes es la manera más efectiva para ver abundancia y diversidad de especies en una nivel muy alta, pero nadie ha estudiado las discrepancias entre abundancia, diversidad, horarios de consumiendo, ni agresión entre sitios que tienen comederos artificiales y sitios que tienen flores en que comen los colibríes. Este ensayo explora las implicaciones posibles de éstas diferencias. Una cuenta de máximo ha usado para estimar la abundancia y diversidad de especies y observación calidaza ha usado para analizar agresión en cada tipo de sitio. El estudio descubrió que por lo general, hay abundancia y diversidad más arriba en sitios con comederos artificiales que en sitios con plantas floridas. Horarios de consumiendo en los dos tipos de sitio remandaron similar pero actos de agresión por el gran parte solamente pasó en sitios con comederos.

PURPOSE

The purpose of this survey is to examine the difference in hummingbird activity at artificial feeder sites and natural feeding sites at various flowering plants. Special attention is paid to species abundance, diversity, feeding time, and aggression displays.

HYPOTHESIS

It is expected that the abundance, diversity, feeding time, and aggression displays will vary greatly between the two types of sites. It is projected that more kinds of species and more individuals will visit the artificial feeder sites than will visit the flowering plants surveyed. Similarly, the feeding schedule of hummingbirds at the artificial sites is anticipated to be unnaturally standardized; the birds will disregard those factors that typically dictate the ordinary ebb and flow of foraging such as temperature change. It is also suspected that there will be more numerous and forceful displays of aggression at the feeders than at the flowers. All of these incongruities exist because feeders are a higher resource than flowering plants in the forest.

INTRODUCTION

General Study Area

All hummingbird surveys were performed on the property of the Wildsumaco Wildlife Sanctuary at an elevation of approximately 1450 meters in the foothill rainforest of the eastern slope of the Andes Mountains in Ecuador. The property is two kilometers south of the Gran Sumaco National Park and also at points abuts the Gran Sumaco buffer zone. The land is slightly east and downslope from both the Antisana Ecological Reserve and the Cayambe-Coca Ecological Reserve. This area, protected by the Wildsumaco Wildlife Sanctuary Foundation, contains primary forest, secondary forest, and cow pasture with the dominant plant life being *Bambusa (*in naturally disturbed areas*)*, Rubiaceae, Melastomataceae, Piperaceae, and Narupa palm (Vallejo 2008)(Olsen, pers com) (Neill 2008). Before the land was bought and protected by the foundation in 2006, it was used for agriculture, primarily the cultivation of naranjilla. Deforestation for timber as a cash crop and clearing of forest for naranjilla agriculture remain some of the biggest threats to the immediately surrounding areas of the Wildsumaco refuge. All surveys took place between the seventh and 19th of November, 2008.

Despite the various threats to this unique ecosystem, it boasts high biological diversity across taxa, but most impressive is its 415-species bird list (Nilsson 2008). Of those 415 species, 38 are hummingbirds, ranging from the rarely seen Lazuline Sabrewing to the very common Sparkling Violetear.

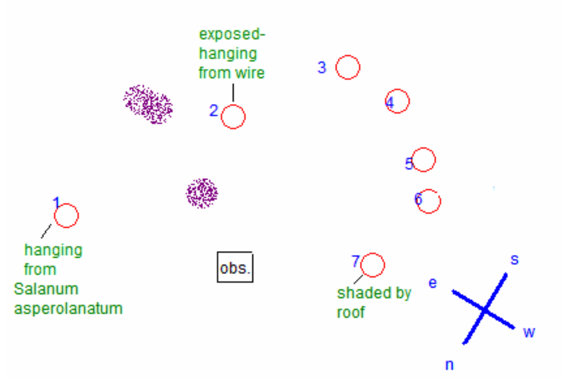
STUDY SITES

Three six-hour surveys were performed at each of four study sites. Two artificial feeder sites were observed as well as two natural feeding sites. These natural feeding sites contained different types of hummingbird pollinated plants. In hopes of accounting for some of the highly specialized relationships between flowers and these avian pollinators, the natural feeding sites were chosen to encompass as many ecological niches as possible.

<u>Feeder Site A- The Residence House</u>

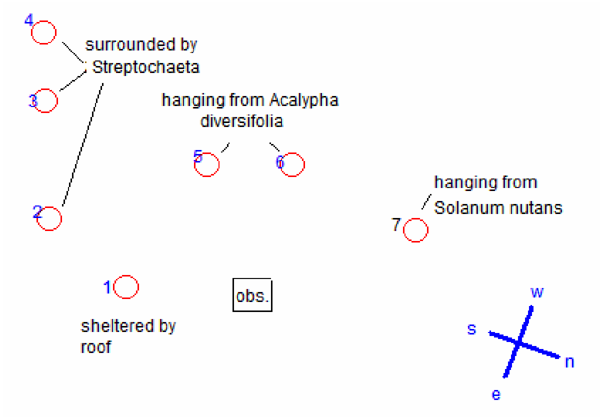
This artificial feeding site, with a perimeter of approximately 81m and an area of about 276 m^2, was located in a clearing surrounded primarily by cecropia trees, a large fruiting

Heliconia in the southwest border of the clearing, as well as many *Salanum asperolanatum*. There were also three flowering *Mintostachis sp.* plants in the clearing between feeders one and two. The observation point was located in the northwest edge of the clearing so that all seven feeders were clearly visible at all times. Each of the seven feeders held 16 ounces of artificial hummingbird nectar of one part sucrose and four parts water. Feeding access varied from feeder to feeder. Feeder one contained eight access points while feeders three, four, five, and six all contained only six access points. Feeders two and seven contained only four access points. All feeders were of the saucer model except for feeders one, two, and seven which were of the bulb feeder model (refer to Appendix A). Below is a visual rendering of the site.



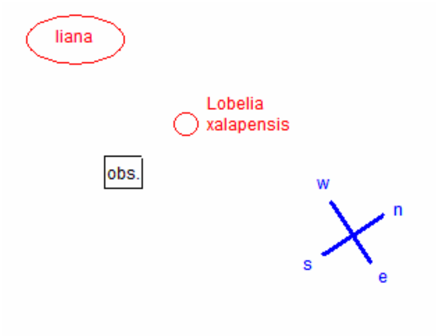
<u>Feeder Site B- The Guards House</u>

This artificial feeder site, with a perimeter of 90 m and an area of 233 m^2 was surrounded primarily by cecropia trees, *Acalypha diversifolia*, *Solanum nutans*, and *Poaceae streptochaeta*. Like Site A, there were seven feeders all of which held 16 ounces of artificial hummingbird nectar of the same mixture. All feeders were of the saucer model with six access points each except for feeder one which was a bulb model and had four access points. The observation point was located at the east northeastern edge of the clearing so that all feeders were visible at once. Below is a visual rendering of the site.



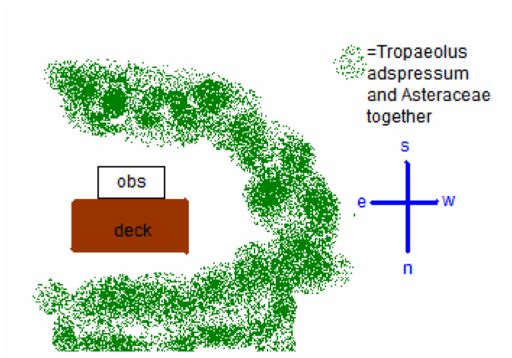
<u>Flower Site A</u>

This site was located about 0.8 km due east of the two artificial feeder sites. This distance was deemed necessary to avoid surveying populations whose movement might be affected by the nearby presence of artificial feeders. Two flowering plants were observed at this site- a liana, of family Ericaceae, located about 10m northwest and 15 m up from the observation point, and a *Lobelia xalapensis* 5m directly north of the observation point and about 2m off the ground. Observers laid down so as to have a good view of the lianas and to be less obtrusive to visitors of the nearby *Lobelia xalapensis*. Below is a visual rendering of the site.



<u>Flower Site B</u>

This natural feeding site contained an abundance of flowering *Topaeolus adspressum* growing on numerous flowering Asteraceae. From the observation point, blooms were visible to and excess of 180 degrees. *Tropaeolus adspressum* and Asteraceae plants ranged in height from less than .5 meters to about six meters off the ground. When tested for nectar, 70% of the *Tropaeolus adspressum* flowers contained nectar. Below is a visual rendering of the site.



METHODS

Surveys were performed at four sites total in shifts of six consecutive hours either in the morning (from 6:00 to 12:00) or in the afternoon (from 12:00 to 18:00). At each site, three six-hour surveys were performed so that an equal number of mornings and evenings were observed at artificial feeders and natural feeding sites. For example, two 6:00-12:00 surveys and one 12:00-18:00 surveys were performed at Feeder Site A while one 6:00-12:00 survey and two 12:00-18:00 surveys were performed at Feeder Site B. Likewise, one 6:00-12:00 survey and two 12:00-18:00 surveys were performed at Flower Site A while two 6:00-12:00 surveys and one 12:00-18:00 survey were performed at Flower site B. The purpose of the study is to compare hummingbird activity, abundance, and behavior at artificial feeder and natural feeder sites so all data gathered at Feeder sites A and B are treated as one unit. Similarly, all data gathered at Flower Sites A and B are treated as one unit in the analyses.

During the surveys, the high count method was employed. By using max count, the observer avoided counting the same individual more than once within each ten minute interval as individual identification was not feasible. At every ten minute interval, the observer recorded the maximum number of individuals of each species she observed simultaneously during those ten minutes. For example, if during one ten minute interval, the observer saw three Sparkling Violetears feeding at once during minute three, but five Sparkling Violetears feeding at once during minute six, the observer would record five as the high count for Sparkling Violetears for that ten minutes. The observer would perform the same process for all species observed in each ten minute period for each ten minute period. To facilitate analysis, three 10-minute counts were lumped into a single 30 minute count. The only materials used in this study were a pair of 8x32 Celestron binoculars and a Swarovski AT-80mm scope to better see and more accurately identify hummingbirds.

Notes were taken on weather every hour or whenever there was a notable change in temperature, cloud cover, or precipitation. Similarly, note was made of any inter and intra-species interactions at both the feeder and flower sites. The aggression gradient was based on Sparkling Violetears as reference points as they are typically the most abundant and the most aggressive species present.

To make sure the flowers at chosen flower feeding sites were producing nectar, the observer tested production by tasting ten flowers and recording what proportion of flowers tasted sweet of nectar.

Protocol Changes

Due to scheduling complications, 42 hours of observation took place between the two feeder sites while only 36 hours of observation took place at the flowers. Averages of high counts were used to effectively eliminate the occurrence of sampling bias in the results due to this alteration.

RESULTS

The purpose of this study is to examine the differences in species composition, species abundance, inter and intra species aggression, and other aspects of hummingbird behavior between visitors to artificial feeders and visitors to flowers. In order to more closely examine diversity and abundance, the high count method was employed, recording the maximum number of individuals of each species seen every ten minutes. In order to ease data examination, only the high counts for every half hour were analyzed. Species aggression and behavior were observed and recorded continuously throughout the study.

Below is a representation of the average hourly high counts for each species at both the feeder and the flower sites. In this table (table I), all high count observations for each species in all surveys at the feeders were averaged to yield the hourly mean at the feeder sites. Likewise, all high count observations for each species in each survey at the flower sites were manipulated in the same manner to yield the values presented in this table.

Feeders	**Time**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
	Sparkling Violetear	2.83	2.83	2.33	2.50	2.17	1.83	1.67	1.17	1.50	1.50	1.00
	Gould's Jewelfront	0.33	0.33	0.50	0.17	0.17	0.17	0.17	0.17	0.17		0.17
	Fork-tailed Woodnymph	0.83	1.00	1.17	1.17	1.00	1.00	1.17	1.33	1.17	1.17	1.00
	Many-spotted Hummingbird	1.00	0.83	0.83	1.00	1.17	1.00	0.83	0.83	0.67	0.83	0.67
	Golden-tailed Saphire	1.83	2.17	2.50	2.17	2.33	2.67	1.67	1.50	1.50	1.17	1.83
	Napo Sabrewing	1.00	0.67	1.00	0.83	1.00	0.83	0.67	0.67	0.67	0.67	0.83
	Green Hermit	0.33	0.33	0.33	0.67	0.67	0.50	0.50	0.67	0.33	0.50	0.33
	Black-throated Brilliant	0.50	0.33	0.33	0.33	0.17	0.83	0.50	0.50	0.67	0.50	0.67
	Violet-fronted Brilliant	0.33	0.33	0.33	0.33	0.17	0.33	0.67	0.67	0.50	0.50	0.50
	Gray-chinned Hermit									0.33	0.17	0.17
	Violet-headed Hummer		0.17			0.17		0.17				
	Booted Racket-tail	0.17	0.17	0.17	0.33	0.33	0.50	0.33	0.17	0.67	0.33	0.33
	Ecuadorian Piedtail							0.33	0.33	0.17	0.33	0.17
	Lazuline Sabrewing											0.17
	Glittering-throated Emerald											
Flowers												
	Time	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
	Sparkling Violetear	0.33	0.33	0.33	0.33	0.33	0.17					
	Gould's Jewelfront											
	Fork-tailed Woodnymph			0.17	0.17	0.17	0.17	0.33	0.17	0.17	0.17	
	Many-spotted Hummingbird											
	Golden-tailed Saphire	0.17		0.17		0.17	0.17	0.17	0.17	0.17	0.17	
	Napo Sabrewing		0.17									
	Green Hermit		0.17		0.17	0.33			0.17	0.17		
	Black-throated Brilliant	0.17	0.17	0.17			0.17		0.17	0.17	0.17	
	Violet-fronted Brilliant			0.17								
	Gray-chinned Hermit	0.17	0.50	0.33	0.17	0.17	0.17	0.33	0.17	0.33	0.50	0.50
	Violet-headed Hummer							0.17	0.17	0.33	0.17	0.17
	Booted Racket-tail							0.33	0.17	0.33	0.17	0.33
	Ecuadorian Piedtail		0.17		0.17	0.17			0.17		0.17	0.33
	Lazuline Sabrewing											
	Glittering-throated Emerald	0.17	0.33	0.17	0.17	0.33	0.17	0.17	0.17	0.17	0.17	0.17

Table I. This table illustrates average species abundance for each hour during the twelve hour observation day. The first and last half hour were removed to create hour intervals to augment ease of viewing. The high counts for every species at each location were averaged and put into this table. To create high count averages for the feeders, averages of both feeder sites A and B were taken into account. Likewise, to create high count averages for the flowers, averages of both flower sites A and B were taken into account.

In order to more easily compare and contrast daily visitation patterns, the average sum of all hummingbird individuals across species observed at each half hour for feeders and flowers were graphed (Figure II**)**. The max count of each species each half hour was averaged and then all averages across species were added together to reach the average sum of all individuals seen in that half hour period. This was created in order to discern general feeding trends at both the flower and feeder sites.

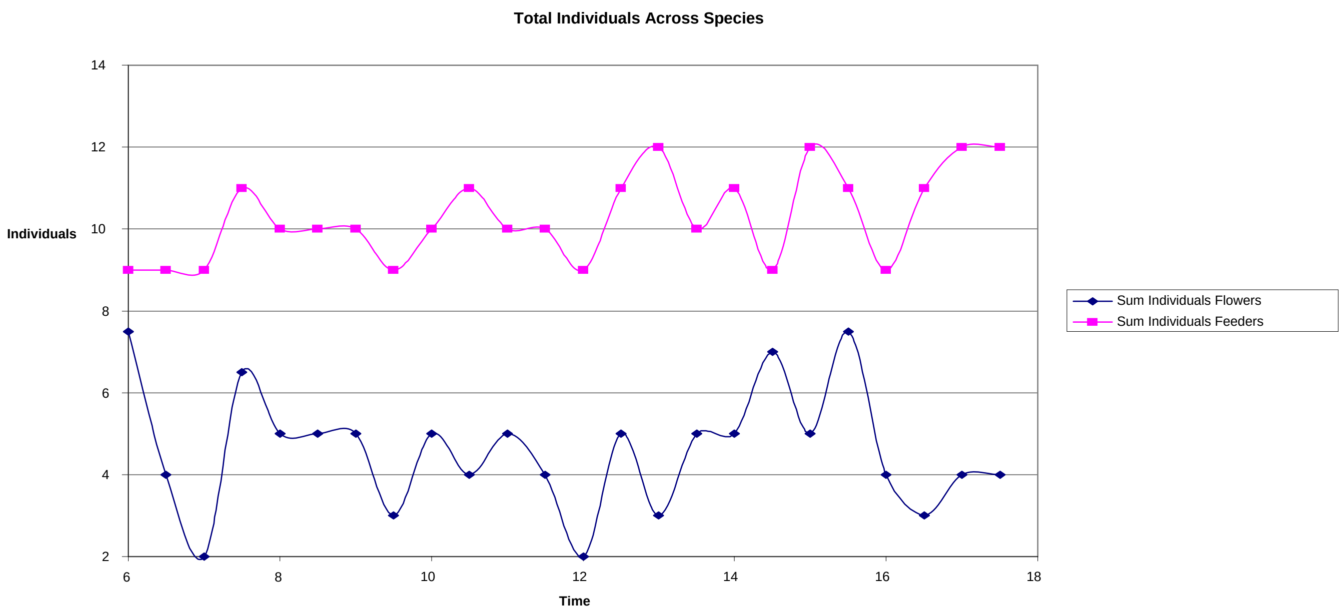


Figure II: This graph illustrates the average total of individuals of all species of hummingbird observed at each half-hour interval at both feeder and flower sites.

Overall species composition and abundance was examined in figure I, but further attention was paid to the differing abundances of territorialist and traplining species at both types of sites. The relative abundance of the following four species at the flower sites were graphed to illustrate how frequently the most territorial species (the Sparkling Violetear and the Many-spotted Hummingbird) came into contact with the least territorial species (the Green and the Gray-chinned Hermit).

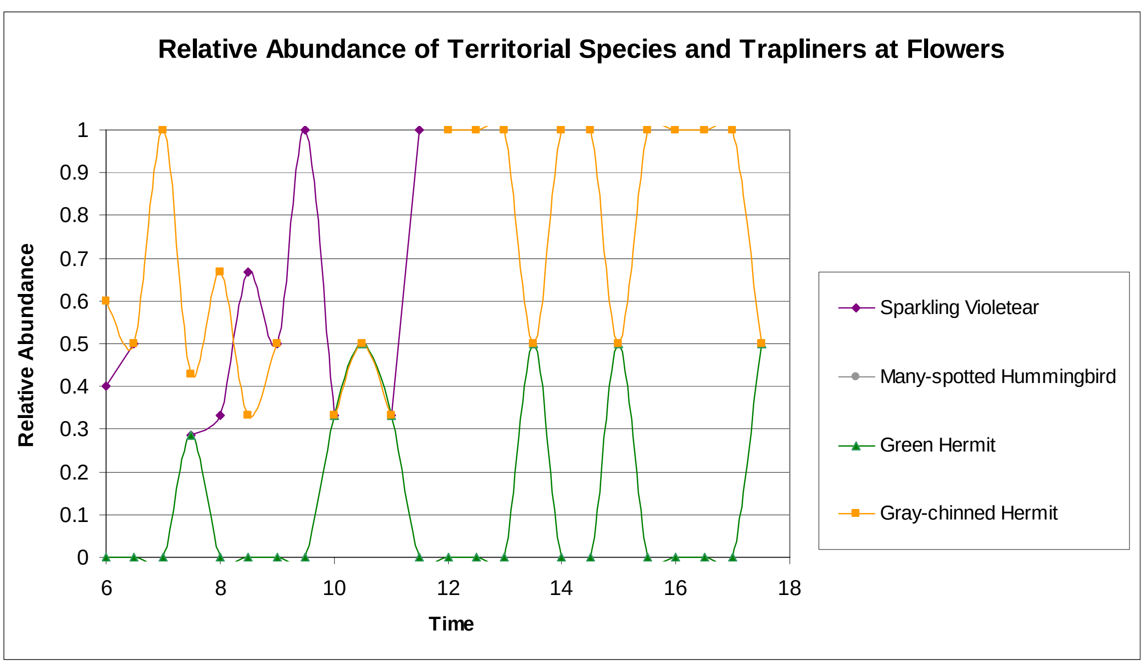


Figure III. This graph illustrates the relationship between the average relative abundance of the most aggressive species observed (the Sparkling Violetear and the Many Spotted Hummingbird) and the traplining species (the Gray-chinned and Green Hermits) at the flower sites.

During this study, qualitative observation was made on hummingbird aggression and interactions. Figure III is a table of all species seen at both feeder and flower sites. All species have been placed in aggression classes based on these observations. The only species excluded from this graph are the Glittering-throated Emerald and the Lazuline Sabrewing. The Glittering-throated Emerald was not classified because it was only observed feeding alone—never interacting with another individual of its own species or of other species. The Lazuline Sabrewing was only observed once the entire study providing an insufficient amount of interaction observations to classify its aggression level. Most if not all of the observations made on the inter and intra-species interactions of these hummingbirds were made at the feeders as typically the flowers were visited by one individual at a time.

Most Aggressive	Aggressive	Least Aggressive
Black-throated Brilliant (11.5 cm)	Fork-tailed Woodnymph (9.5 cm)	Booted Racket-tail (7 cm)
Many-Spotted Hummingbird (10 cm)	Golden-tailed Saphire (9 cm)	Ecuadorian Piedtail (7.5 cm)
Napo Sabrewing (11.5)	Gould's Jewelfront (9.5 cm)	Gray-chinned Hermit (7.5 cm)
Sparkling Violetear (12 cm)	Violet-fronted Brilliant (11.5 cm)	Green Hermit (11.5 cm)
		Violet-headed Hummingbird (7.5 cm)
**The Glittering-throated Emerald was never seen interacting with other individuals of any species. The Lazuline Sabrewing was seen only once in all 78 hours of observation. Therefore, this study lacks sufficient observation to place either species in an aggression class.*		

Figure IV. Based on behavioral observations in the field, this table groups all species seen at both flower and feeder sites (with the exception of the Glittering-throated Emerald and the Lazuline Sabrewing) on a scale of most aggressive to least aggressive. The species are listed in alphabetical order in each category.

DISCUSSION

The level of species diversity at any given site presents a myriad of ecological questions. What species are there? How do they interact? For which and what kinds of niches are they competing? What is the affect of this combination of species on the surrounding wildlife? In the case of the hummingbird, this question is of particular interest. Hummingbirds are some of the most important pollinators for many plants of the neotropics. Perhaps one of the best known examples of this extreme inter-dependence is the relationship between the *Eutoxeres* (sicklebill) hummingbirds and the *Heliconia* plants. The bills of these birds are decurved so as to fit perfectly into the flower and become sufficiently covered with pollen in the hopes that the next visit to *Heliconia* flowers will yield successful pollination. This is only one example of the often highly specialized relationships between hummingbirds and the plants they pollinate in the tropics.

But what happens when these important pollinators stop their usual business at these flowers in the forest? Hummingbird feeders are the best way to see these typically elusive and beautiful birds. In the western hemisphere, hummingbirds are a great boon to the ecotourism industry as there is no hummingbird equivalent anywhere else on the planet. Without feeders, many visitors to the west would never see these tiny birds. Hummingbird feeders represent a case of the most important question facing the ecotourism industry: People need to know about and experience the natural world in order to begin to feel accountable for it, but is this very exposure to the environment simultaneously destructive? Is it worth it? Though these feeders are the best way to see hummingbirds, do we risk harming pollination ecology in the surrounding areas? I believe we can begin to answer these questions through comparing and contrasting species diversity, abundance, and behavior both in areas where feeders are present and in natural feeding areas.

Comparative Species Diversity and Abundance

The data collected in this study shows that the feeders have both higher richness and abundance than the flowers. Species richness was not as astoundingly different as anticipated; a total of 14 different species of hummingbirds were observed at the artificial feeding sites over the course of the survey while only 12 different species of hummingbirds were observed at the flowers during observation hours at the flower sites. Neither Gould's Jewelfront, Lazuline Sabrewing, nor Many-spotted Hummingbird were observed at the flower feeding sites, but the Glittering-throated Emerald was only observed at the flower feeding sites and never at the artificial feeders (Table I).

Gould's Jewelfront is rarely seen even in its more ordinary habitat—the terra firme lowland forests of eastern Ecuador. According to Ridgely's Birds of Ecuador, its presence in the Sumaco Wildlife Refuge is an anomaly to begin with because 1450 meters is above this species' typical altitudinal range (Ridgely 2001). If this bird were to be seen at all, it makes sense that it would be seen at the feeders instead of the flowers because of the high individual and species density witnessed there. The same principle applies to the sighting of the Lazuline Sabrewing at the feeders. Though this bird is fairly common in Venezuela, it is an enigma in Ecuador. Ridgely writes of the Lazuline in his field guide:

> Uncertain. …despite the considerable amount of recent fieldwork in this region, however, there is only one single report of the species that can be regarded as certain, a female seen for several days in Jun. 1999 at Cabanas San Isidro…we thus give it an Ecuadorian status of Data Deficient (Ridgely 2001).

There have only been two other sightings of this bird on the Wildsumaco property both of which were also at the feeders.

The Glittering-throated Emerald was only seen at the flowering sites and never at the feeders. I propose the following as possible explanations of this occurrence:

A) The Glittering-throated Emerald was only ever only observed at flowering Site B feeding on the *Tropaeolus adspressum*. It is possible that this species of hummingbird has a beak specialized for the feeding on and pollination of the

Tropaeolus adspressum. When there is such a large patch containing so many blooming *Tropaeolus adspressum*, why would a *Tropaeolus adspressum* specialist bother competing with so many other species for the popular sucrose solution at the feeder? At the flowering site, it could instead feed in near solitude expending no energy on competition.

B) For this group of hummingbirds, the Glittering-throated Emerald is of an odd size. At eight centimeters, it would fall squarely between the size of those birds classified as aggressive and those birds classified as least aggressive. The feeding strategies of these two aggression classes are very different. The aggressive species (anywhere from 9 to 11.5 cm) mostly try their luck and challenge the largest, most aggressive species for spots at the feeders. The least aggressive (from 7 to 7.5 cm excluding the traplining Green Hermit) species typically try to inconspicuously move onto the feeders, fleeing as soon as they are noticed. Assuming the same correlation between aggression and size applies to the Glittering-throated Emerald, this would mean the bird is too small to compete with most aggressive species, as do the aggressive species, and too large to discreetly move into position to feed at the feeders, as do the least aggressive species. This would imply that the Glittering-throated Emerald individuals are just the wrong size to compete appropriately at a feeder with the species makeup present at these study sites.

Though species diversity at the flowers was not as comparatively low as projected, a larger and more impressive discrepancy lies in the difference in species abundance between flower and feeder sites. The highest average species abundance at the flowers is the Gray-chinned Hermit at 08:00, 16:00, and 17:00 when average abundance reaches 0.5 while the highest average species abundance at the feeders is that of the Sparkling Violetear at 7:00 and 8:00 when the average abundance reaches 2.83. Of all of the average species abundance counts at the feeders, only 50.6% of them lie below 0.5 while 97.7% of average species abundances at the flowers are less than 0.5 (Figure 1). Again, this is due to the ability of the feeders to support a larger number of feeding individuals at once. Each of the feeders contains access points each of which allow the visiting bird to imbibe the sucrose solution. This is not the case with flowering plants. Even a large flowering *Heliconia* never contains as much nectar as one might think upon first looking at it. Often, flowering plants practice what Feinsinger refers to as "bonanza-blank" pattern putting nectar only in a few of its blooms rather than all of them (Feinsinger 1983). This practice is energy efficient; it takes a lot of energy to produce nectar in each flower on a plant. Additionally, this system has pollination advantages. If there are fewer flowers that contain nectar, a hummingbird will have to visit many flowers before it actually finds the nectar. The more visits a hummingbird makes to a flowers, the higher the chances it will achieve successful pollination. Therefore, there is not only less nutrients available in amount at flowers, there are also fewer points at which the hummingbirds may obtain these nutrients. This is not the case at artificial feeders.

Comparative Hummingbird Feeding Schedules

Overall visitation patterns at artificial feeders were expected to diverge wildly from those patterns observed at flower feeding sites due to the presence of such an unnaturally high resource value. Hummingbirds, or most animals for that matter, should be more inclined to remain in areas that contain high resource values like the feeders. It is less efficient to expend energy by trying to collect it in many different places than it is to linger and eat at the same spot. A study by Ewald et. al found there was a strong relationship between resource values at feeders and visitation to those feeders by Anna's hummingbirds. As resource value at these artificial feeders was decreased, the number of hummingbirds at those feeders decreased. As resource value increased, the hummingbirds visited more often (Ewald et. al 1978).

My study continues examining this same question by looking at feeding schedules at both artificial hummingbird feeding sites and natural feeding sites like flowers. What happens to feeding schedules when sucrose levels are as high as 20% at artificial feeders when naturally occurring feeders like flowers produce nectars with a significantly lower concentration of sugar? Data collected in this study found that, fortunately, the patterns remained quite analogous between the two types of sites but dissimilarities do certainly exist in species abundance.

If feeding schedules at the feeder sites and flower sites were shown to be drastically different, one may assume that the presence of unnaturally high value resources (feeders) in these sites disrupt the natural feeding patterns of the hummingbirds. This would have many ecological implications. For example, this would mean that that these hummingbirds are spending so much time at these feeders that they effectively decrease the amount of time they are spending pollinating plants. If this incongruity in time investment was pronounced enough, it could seriously disrupt the pollination ecology of an ecosystem that is so highly dependent on hummingbirds as a vector.

This study did not find a significant difference in feeding patterns in hummingbirds at the two sites. There are apparent slow feeding times as well as peak feeding times that the two sides hold in common. The graph in Figure IV was created to explore this question and depicts these similarities. In both cases, slower feeding times occur at 7:00, 9:00, 12:00, and around 16:00. Feeding increases around 8:00, 15:00, and at the end of the day near 18:00 in both sites as well.

Periods of High Visitation	Periods of Low Visitation
• 8:00 • 15:00 • 18:00	• 7:00 • 9:00 • 12:00 • ~16:00

Feeding was shown to slow in the middle of the day due to intensified heat and sunlight. Energetically, it is inefficient for a bird to exert energy on feeding while simultaneously maintaining homeostasis. The energy demand of a hummingbird is tremendously high for many reasons. A study by Greenewalt found that, depending on weight, a hummingbird's wings may beat anywhere between 15 and 80 times per second (Crespo 2003). The heart rates of Hummingbirds are equally impressive, reaching up to 1,260 beats per minute (Kricher 1997). One of the first studies performed on metabolic rates of hummingbirds found that Anna's Hummingbirds have a metabolism of 68 cc/g/hr while the Allen's Hummingbird can have a metabolism of anywhere between 23 and 165 cc/g/hr; this is the highest recorded for any vertebrate in the world (Pearson 1950). This is only a sample of two species, but hummingbirds in general have been shown to have the highest metabolic rate of all homoeothermic animals on the planet (Lasiewski 1967). The most basic of their life functions are carried out to the extreme. Like that skinny kid in middle school that had such a high metabolism he never quit eating, these hummingbirds are the avian world's version of the proverbial bottomless pit.

The rise in feeding in the last hour can be attributed to the birds' need to garner energy before dark and roosting for the night. It has been found in various studies that metabolisms of hummingbirds are highest at dusk because of increased activity such as more frequent flying and feeding (Pearson 1950). Hummingbirds must spend a lot of energy on temperature regulation in the nights Though some hummingbirds have been known to enter the low-energy torpid state at night manage homeostasis, this phenomenon is largely seen only at higher altitudes or in environmental temperatures lower than 24 Fº (Hilty 1994, Pearson 1950). Neither of these requisites applies to the area where this study was performed. The Wildsumaco Wildlife Refuge is relatively low in elevation and the temperature rarely drops below 60 Fº at any time during the year so it is unlikely that the hummingbirds here practice torpor. However, it is still important for the birds studied to indulge before the sun goes down for the night.

The biggest difference between the feeding patterns at the two sites lies in the species abundance. At all times in the day, the species abundance at the flowers is far lower than the species abundance at the feeders (figure II). While the abundance at the flowers never rises above eight individuals in one half hour, the abundance of individuals at the feeder sites never falls below nine. This phenomenon is easily explained by the abundance of energy available at the artificial feeder sites. There is more energy available at these sites; they can therefore support a higher number of feeding individuals.

This supports the theory that feeders draw an unnaturally high number of individuals to the feeders but does not find that the basic feeding schedules of the birds are significantly altered by the feeders.

Prevalence of Different Feeding Strategies at Feeders and Flowers

An increase in species abundance and diversity at feeding sites dramatically changes the behavioral dynamics there in. A study on Rufous and Broad-tailed Hummingbirds by Camfield in 2006 showed that as abundance increased due to resource value increase at the feeders, the number of aggressive acts performed by the hummingbirds likewise multiplied. Additionally, the chasing of competitors intensified, illustrated by the general elongation of chases by hummingbirds (Camfield 2006). This would suggest that if there are more species and individuals present in any given site, competition between individuals complicates feeding arrangements. It suggests that no longer does the individual hummingbird only have to consider the resource value of the feeding source; it must now budget its energy expenditure to account for competition efforts—including but not limited to escape tactics, marauding maneuvers, and various aggression displays. The singular, isolated flower in the forest with less sugar and challengers may become more appealing to the hummingbird as competition grows.

In the natural world, resource value differs between plants; artificial feeders are not the only instance of value variance. This variation and the consequent competition has given rise to the formation of five different hummingbird feeding strategies:

territorialism, territorial parasitism, generalism, thievery, and traplining. These divisions are typically fluid and territorialists often become territorial parasites through marauding the feeding areas of other territorialists (Hilty 1994). At the feeders, there were countless instances of Napo Sabrewings forcing Sparkling Violetears out of their dominant, protective perches above the feeders. Adult Black-throated Brilliants often appeared out of the depths of the forest and literally knocked the territorial Many-spotted Hummingbirds off of the feeders and almost to the ground. Even the typically thieving Ecuadorian Piedtail was observed chasing a juvenile Black-throated Brilliant from the liana. The most noticeable feeding strategies employed by the hummingbirds observed in this study were territorialism and traplining.

-Territorialists

The larger more aggressive territorialists tend to dominate the highest resource value sites, which in this study are represented by the feeders (figure IV). Each of these territorialists had their own aggression tactics. The Many-spotted Hummingbird scared away its competitors by making itself appear to be almost two times its actual size. Individuals of this species were seen to puff out their grayish/white chests and fly slowly towards their challengers. They would hover as near to the challenger as they could until the other bird became so intimidated it flew away to another feeder. Sometimes the tactic would fail or the challenger would be so intimidated it would fly away before the Many-spotted Hummingbird even began its threatening display.

The Sparkling Violetear was typically seen to choose a perch right above or very near to a feeder and stand guard. Whenever a hummingbird of the same or another species approached the feeder, the Sparkling Violetear would leave the perch and fly quickly and noisily at the hummingbird. The attack was usually so sudden and startling that the competitor would fly away immediately. In the case that the other hummingbird did not instantly retreat, the Sparkling Violetear would hover in front of its challenger and threateningly fan out the purple feathers behind its eyes in hopes of surprising the other hummingbird into retreat. After the Sparkling Violetear had successfully frightened off the other bird, it would return to its original perch.

The Black-throated Brilliant and the Napo Sabrewing seemed to employ the same defense strategy: brute force. Both would simply fly directly at the intruder to scare it away from the feeder though the Black-throated Brilliant was observed to be more aggressive in its chasing. Many times, the Black-throated Brilliants would crash into their adversaries if they did not move quickly enough while the Napo Sabrewings typically moved slowly enough to allow their rivals to move out of the way. In the case of both species, these aggressive attacks did not occur only when they were feeding or wanted to feed. Often, they would chase intruders away from the feeders and return to a perch near the branch to stand guard as did the Sparkling Violetears. Creating a hierarchy within this aggression class is difficult as the observation hours of each species were so drastically different. Sparkling Violetears were seen the most followed by the Many-spotted Hummingbirds. Napo Sabrewings were observed fewer times and Black-throated Brilliants even less. The sampling bias in this case does not allow the observer to appropriately arrange a hierarchy within this class.

-Trapliners

Instead of lingering at one food source and defending it from competitors such as the territorialist Sparkling Violetear or Many-spotted Hummingbird, hermits practice a feeding strategy referred to as traplining. This foraging strategy is defined by daily visits to many different understory flowers that are typically of too small resource value to support territorialists. This means trapliners expend a lot of energy on travel from flower to flower, but little to no energy on defense or aggression because they hardly ever run into other individuals on their travel routes (Hilty 1994). The different feeding times of the different types of hermits suggest that the travel routes of these two trap-lining species are arranged so that one will visit the flowers while the other is absent (Figure II).

At both the feeder and flower sites, the hermits seemed to visit almost regularly. Because observers lacked markers to discriminate, it is unknown if each observation was the same individual or if they were different individuals. It is certainly possible that these hermit observations were of the same few birds as hermits typically establish feeding routes that they repeat through out the day and across time (Hilty 1994).

Though the Green and Gray-chinned Hermits were some of the most regular and abundant feeders at the flower sites, this was not at all the case at the artificial feeders. The Gray-chinned Hermit was observed on only six occasions over the course of 42 hours. Its relative abundance is miniscule. The Green Hermit was seen slightly more often but never for long. Its non-confrontational demeanor left it susceptible to intimidation by even the smallest of the hummingbirds.

Irregularities in Feeding Patterns

In this study, the Many-spotted Hummingbird was never observed at the flowers while the Sparkling Violetear was only ever observed at the flowers before 12:00. Both hermit species were observed throughout the whole day. The strange appearance of the Sparkling Violetear only before noon may be a product of energy partitioning of the bird. The territorialist feeding strategy demands a lot of energy. In order to answer that energy demand, it may be that the Sparkling Violetear must feed as much as possible in the morning before venturing out and searching for a particularly high resource value that they may defend and dominate. The Many-spotted Hummingbird was not seen at all at the flowers likely because of its tendency to avoid energy intensive foraging and settle for one high energy resource instead of moving around.

Of the relationships represented in figure III, the most notable is the relationship between Gray-chinned Hermit and Green Hermit; their feeding schedules are almost the inverse of each other. This is mostly true through out the entirety of the day but especially noticeable from 12:00 to 18:00. This is perhaps a function of the large bird’s need for more energy before roosting at night than a single clump of flowers can provide. The two species were never seen feeding at the same time. There was one instance at Flower Site B in which two Gray-chinned Hermits were seen at once. They were close to one another but did not exhibit any aggression towards each other. In fact, they did not interact at all on any level.

Aggression

Hummingbirds are particularly aggressive birds (Kricher 1997) and when feeders draw such a high abundance of diversity of hummingbirds, interactions are bound to get interesting. In this study, most of the aggression observations were made at the feeder sites. The flower sites were rarely visited by more than one individual at a time making it difficult to make any aggression observations.

Qualitative observation found that the species that make up the most aggressive class of hummingbirds are the largest hummingbirds with the exception of the Violet-fronted Brilliant and the Green Hermit (Figure III). A study performed on hummingbird feeding dynamics and aggression in La Reserva Ecológica Río Guajalito yielded similar findings in the relationship between size and aggression. The largest hummingbirds in Nuechterlein's study, the Fawn-breasted Brilliant and the Hoary Puffleg, were shown to be the most aggressive while the smallest birds in the study, the Booted Racket-tail and the White-bellied Woodstar, were almost never observed partaking in any kind of aggressive acts (Nuechterlein 2008).

It is possible that the Violet-fronted Brilliants' surprisingly timid demeanor is due to its age as most of the Violet-fronted Brilliants seen in this study were classified as juveniles rather than adults. My theory is that this lower level of aggression is attributable to the fact that juveniles are less aggressive than adults in general. Younger birds are not as accustomed to fighting for their food as they have more recently been fed by adults. This aggression is a learned behavior that develops with more exposure to competition. Juveniles are, in fact, smaller than their adult counterparts, but size can not account for this feeding irregularity as there were a few instances in which the smaller but feisty Golden-tailed Saphire chased a juvenile Violet-fronted Brilliant off of a feeder.

At 11.5 cm the Green Hermit was one of the larger species observed but was not seen to be aggressive toward other species. This is easily explained by its non-territorial trap-lining feeding strategy (Hilty 1994). With these few exceptions, there is an obvious positive correlation between hummingbird size and aggression intensity.

A study by Wolf, Stiles, and Hainsworth on tropical highland hummingbird communities found that it is far more costly for large birds to forage than smaller ones (Wolf et. al 1976). This would explain why larger birds hold stake in dominating and zealously defending one feeding site rather than avoiding conflict and expending energy flying to less contentious sites. In this study, the majority of visitors to the flowers were smaller in stature such as the Ecuadorian Piedtail, the Gray-Chinned Hermit, or the Golden Tailed Sapphire.

In conclusion, it is true that feeder sites provide a better option for those birders who wish to see greater species abundance than a natural flowering site might offer. The general difference in species diversity at the two sites is minimal, only 14 to 12, but there is certainly more diversity observed in less time at the feeders. Based on the data collected in this study, I can not support the theory that feeding schedules of birds are dramatically altered by the presence of a high resource values at hummingbird feeder sites as the general trends are similar between the two. The qualitative observations made in this study illustrate that the larger birds are typically more territorial than the smaller ones, but that these feeding strategies are not stagnant.

While this design of this study does not allow for the establishment of direct causational relationships between the presence of feeders and the discrepancy between abundance, diversity, and aggression at the two sites, these differences certainly merit future investigation over a longer period of time.

POSSIBLE FUTURE STUDIES

To better examine the change in hummingbird feeding dynamics between feeder and non-feeder sites, I propose a different study design. Sites with sufficiently diverse flowering plant life would be chosen and surveyed using the same methods as this study. As soon as sufficient data is collected at these sites, artificial feeders should be erected in these sites. The surveys should continue in the same manner. The observers should analyze what species are displaced or what new species now come to this site. The change in frequency of visits to the flowers should also be noted. It would be possible to find direct causational relationships between the presence of feeders and changed hummingbird activity. What birds remained? Are the feeders selecting birds with a specific feeding strategy?

Other qualitative data suggests that considerable study should be done on hummingbirds and their reaction to natural disturbance at and away from artificial feeders. Such natural disturbance could include but is not limited to predation or extreme and sudden change in weather. There were a few instances during the study when raptors were present near or even in the survey site. Some species seemed to respond while others didn't. Likewise, I did not have enough time to fully examine the hummingbird's reaction to extreme weather. There was only one survey in which sudden, heavy rain occurred. This was not a sufficient sample size to fully analyze hummingbird behavior in these situations.

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APPENDICES

i.) Feeder model types

Bulb Model Feeder Saucer Model Feeder

ii.) Plants Observed

Site A: Ericaceae- liana (left) and *Lobelia xalapensis* (right)

 

Site B: *Topaeolus adspressum* (left) and Asteraceae (right)

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