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Resource Quality and Defense: Feeding Behaviors and Female Territoriality in Two Species of Tropical Hummingbird

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Feeding Behaviors and Female Territoriality in Two Species of Tropical Hummingbird

ABSTRACT:

The study "Resource Quality and Defense: Feeding Behaviors and Female Territoriality in Two Species of Tropical Hummingbird" investigates the feeding behaviors and territoriality of hummingbirds at a flowering shrub of the Gesneriaceae family, *Besleria solanoides.* Four 1.25-hour observation periods were completed each day, rotating between four different observation sites. During each observation period, the sugar concentration of nectar and number of flowers on each bush was measured, and each time a hummingbird entered the area the following data was recorded: species, sex, time of arrival, duration of visit, number of flowers probed, number of perches, duration of longest perches, any vocalizations and territorial behaviors. Two species of hummingbird fed at *B. solanoides* throughout this study: booted racket-tails (*Ocreatus underwoodii)* and violet-tailed sylphs (*Aglaiocercus coelestis).* The linear regression run between visitation frequency and number of flowers showed a significant, positive correlation, and the regression of visitation frequency and nectar sugar concentration was insignificant, showing that these species value quantity of flowers over quality of nectar at this particular resource. Very few male violet-tailed sylphs visited *B. solanoides,* but instead were seen feeding on inflorescences of other plants, possibly because *B. solanoides* was declining as a resource at time of the season. Unexpectedly, females of both species were predominantly the territorial individuals, and three individuals were distinguishable based on physical traits and perching locations. These three females visited their bush more times than all other visits combined, and exhibited territorial behaviors, lengthy perches, and vocalizations.

RESUMEN:

La investigación "Resource Quality and Defense: Feeding Behaviors and Female Territoriality in Two Species of Tropical Hummingbird" enfoca en los comportamientos de la alimentación y la territorialidad de los colibríes que visitan un arbusto floreciente de la familia Gesneriaceae, *Besleria solanoides.* Yo hice cuatro periodos de observación de 1,25 horas cada día, en cuatro sitios diferentes. Durante cada periodo, yo medí la concentración del azúcar en el néctar y conté el número de flores de cada arbusto, y anoté la siguiente información sobre cada visita de colibrí: la especie, el sexo, la hora de llegada, el número de flores visitadas, el número de veces que se posaba, cualquieras vocalizaciones y comportamientos territoriales. Dos especies de colibrí visitaron *B. solanoides* durante este estudio: booted racket-tails (*Ocreatus underwoodii*) and violet-tailed sylphs (*Aglaiocercus coelestis*). El análisis de correlación entre la frecuencia de visitación y el número de flores en el néctar mostró una relación significativa y positiva, mientras que el análisis entre la frecuencia de visitación y la concentración del azúcar reveló una relación insignificante, significando que la cantidad de flores es más valiosa que la calidad del néctar para estos colibríes. Muy pocos machos de la especie violet-tailed sylph visitaron *B. solanoides,* pero se alimentaron con otras plantas, posiblemente porque *B. solanoides* no tenía muchas flores en este periodo de transición entre las temporadas. Las hembras de las dos especies fueron los dueños territoriales de estas plantas, y yo podía distinguirles debido a sus características físicas y las ubicaciones de sus posaderos. Estas tres hembras visitaron más veces que las otras visitas combinadas, y usaron comportamientos territoriales, se posaron por mucho tiempo, y vocalizaron.

ISP topic codes: Biology 609; Ecology 614; Forestry and Wildlife 608

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INTRODUCTION

Hummingbirds depend largely on the sugar in nectar for their daily sustenance, and due to their near-constant movement and high metabolism, it is vital that they spend at least 20% of their waking hours feeding, which, for some species, means feeding for a few minutes 14-18 times per hour, with rest periods spent "crop-emptying", or digesting (Diamond *et al.,* 1986). In order to feed at such a high frequency, they must locate both high quality and high quantity nectar sources throughout the day and be able to quickly adjust to changes in the environment (Powers & McKee, 1994; Noble, 2010). Due to the finite number of flowering plants that exist in a given area, there are two main types of feeding behavior niches that allow multiple species of hummingbird to coexist: territorial and trap-lining. Territorial feeding occurs when a hummingbird protects large quantities of flowers (usually on a single plant or localized patch) from other hummingbirds, and generally spend time guarding or perching within their chosen plant (Stiles & Wolf, 1970). Trap-lining consists of a hummingbird feeding at unprotected flowers in a circuit, usually specializing in high quality nectar sources that may only be accessible to hummingbirds with long, curved bills (Snow & Snow 1972). This study analyzes the feeding behaviors of two different species of hummingbird at the flowering shrub *Besleria solanoides,* focusing particularly on visitation rates, feeding behaviors and resource choice, with respect to the quantity and quality of the resource (as represented by the number of flowers and nectar concentration, respectively).

Besleria solanoides is a large, flowering shrub (~1-4m tall) of the family Gesneriaceae, occurring in clusters from approximately 1600 to 2100 meters throughout the Chocó cloud forest of Ecuador and in other high-elevation regions of tropical Latin America (UC Davis, 1998; Londono & GBIF, 2013). Each tree produces hundreds of small, tubular orange flowers (Appendix, Figure C) that have an average corolla length of 15.25 mm long, and during the month of observation had a mean concentration of 10.28% (Wolbert, 2016). Although it has not been verified through observation due to the limited research on this species, the orange color and tubular flower structure may indicate that it is hummingbird pollinated (Martén-Rodríguez *et al.,* 2009; Altshuler, 2003) along with 60% of the ~3000 other species in the Gesneriaceae family (San Martin-Gajardo & Freitas, 1999). Whether hummingbirds are the true pollinators or not, *B. solanoides* may be a valuable resource for hummingbirds due to the accessibility of the nectar and the quantity of flowers on each bush.

Due to the small size of these flowers, we predicted that small hummingbirds would visit most often, while large hummingbirds would not visit much at all, due to the fact that, while small hummingbirds feed on any flowers from which they can draw nectar, large hummingbirds rarely feed on small flowers, because the cost of hovering outweighs the energy gain from such a small volume of nectar (Snow & Snow, 1972). The hummingbirds that reside at the altitude range of this study and are the smallest are booted racket-tails (abbr. BRT) and violet-tailed sylphs (abbr.VTS). Booted Racket-tails (*Ocreatus underwoodii*) are hummingbirds in the puffleg group (also known as the Racket-tail puffleg), with green coloration on the body and white feathering around the legs called "leg puffs" (Johnson, 2011). In this region of Ecuador, males have solid green bodies and preen their two long, iridescent blue tail feathers into a "racket" shape, with only the tips having a full, rounded feather. Females have more inconspicuous coloration, with a mostly white breast and green back and cap, without the extended tail. They are a solitary, promiscuous species, and feed from mostly small, brightly colored flowers that are

often tubular-shaped (Johnson, 2011).Violet-tailed sylphs (*Aglaiocercus coelestis*) are also solitary, promiscuous birds that are typically found from 900 meters to 2100 meters (Johnson, 2010). Males have solid greed, iridescent bodies with a few long, iridescent blue tail feathers that are often longer than their bodies, and green, iridescent strip that runs from the top of their beak to the crown of their head. Male VTS are generally 18-21 cm long including the tail, so body length is often around 9 cm long (Johnson, 2010). Females are mostly green with a rusty-orange abdomen, with white on the upper chest and tail tips, as well as a blue, iridescent crown. This species feeds "on nectar taken from brightly colored, scented small flowers [...] (often red-colored and tubular shaped)" and may also feed on spiders and small insects (Johnson, 2010).

Both species are have relatively short, thin beaks, small bodies, (VTS are slightly larger than BRT) and short wings. Feinsinger and Chaplin (1975) found that short wings are correlated with higher wing disc loading, which entails faster, more energy consuming wing beats, and allows for faster movement and change of trajectory. This is useful for aggressive, territorial species that must often engage in high-speed chase, but is not efficient for hovering; trap-lining hummingbirds (which feed on unprotected resources, and generally have lower wing disc loading) "expend less energy in hovering per gram body weight than any territorial bird" (Feinsinger & Chaplin, 1975). Thus, territorial birds perch whenever they are not feeding or interacting (often aggressively) with other hummingbirds. Additionally, unlike larger hummingbirds that need higher sugar concentrations to counter-balance the cost of hovering, with their small body sizes, these are able to feed on both small flowers and large flowers, taking advantage of any accessible resource (Atshuler *et al.*, 2004; Snow & Snow, 1972). Due to their thin, short beaks, they are likely to feed mainly on small flowers, although certainly not exclusively (Snow & Snow, 1986). In contrast, larger hummingbirds with longer, more curved beaks, tend to specialize in flowers with longer, more complex corollas (and also pollinate the flowers) due to symbiotic co-evolution (Gill, 1988; Kiester & Schemske, 1984). Due to their physical traits, I will thus predict that both booted racket-tails and violet-tailed sylphs are generalist, territorial hummingbirds. Thus, I hypothesize that I will observe high frequency and duration of perching, aggressive, territorial interactions among hummingbirds, and attempts to feed on many different types of flowers (in addition to *B. solanoides).* I further predict that, due to the previous studies of territoriality in male hummingbirds, that males will visit with higher frequency to *B. solanoides,* and more aggressive interactions will consist of males chasing away other individuals (Pitelka, 1942; Powers, 1987).

Additionally, I would like to know how the feeding behaviors of each species differs--the duration of feeding times, visitation frequency, if individuals will defend these resources, and whether these behaviors correlate with different traits of each plant. Tamm and Gass (1986) found that hummingbirds prefer the highest nectar concentration when given the choice with artificial feeders. Thus, I predict that hummingbirds will visit *B. solanoides* individuals that produce the most concentrated nectar with the highest frequency, and that I will see the most territorial interactions protecting the plants with more concentrated nectar. However, I also predict that plants with greater numbers of flowers will attract a higher frequency of visits, and that this may prove a more important criteria for hummingbirds than nectar concentration, due to the frequency at which hummingbirds must feed. Further, in this study I will investigate inter- and intraspecific interactions among hummingbirds, to determine if hummingbirds will defend resources from other species as well as their own. I predict that the generalist species will in fact exhibit territorial behavior towards individuals of other species, as well as members of their own

species, because any hummingbird can feed on the nectar from these flowers (due to the short corolla length), and, thus, is a competitor (Stiles & Wolf, 1970). I predict that due to their larger size, male VTS will be able to defend their territories from individuals of their own species, and of smaller species (BRT) most effectively. I expect that male BRT will also defend territories, but will be less successful at keeping hummingbirds of other species away, due to the fact that BRT are the smallest species in this region.

METHODS

Description of Study Site

This study was conducted at the Santa Lucia Ecuadorian Cloud Forest Reserve, near the town Nanegal, in the Northwest of the Pichincha province on the Western slope of the Andes in Ecuador (Appendix, Figure A). The study was conducted from the 5th to the 24th of November. The elevation range was approximately 1700 meters to 2,200 meters, and the climate was tropical and generally cloudy, with minimal variation in temperature. Rainfall occurred nearly every day for the first week, but the second and third weeks did not rain at all, with open, sunny skies and little cloud cover except for the afternoons (during which data was not taken).The average annual temperature in the surrounding area is approximately 20.2 ^{o}C and average annual rainfall is 2086 mm (Climate-data.org). The research site consisted of several transects through mountainous terrain, each about 2 or 3 kilometers long, consisting of mostly secondary growth, reforested pasture (trees planted among grasses that previously were used for grazing livestock), and some primary forest.

Selection of B. solanoides

This project focuses on studying the feeding behaviors of hummingbirds with relation to the flowering plant *B. solanoides,* and monitoring the interspecific and intraspecific interactions among various species of hummingbirds that visit this plant, specifically tracking territorial movements and indicators of aggression. The first task consisted of locating *B. solanoides* and determining the relative value (in terms of nectar production and flower count) of each bush, so that the best bushes that would attract the most visitors were chosen for this study (in order to comply with time constraints). However, this proved difficult because most *B. solanoides* were transitioning from bloom to fruit at this time of the year, so most plants contained very few inflorescences. Each individual that had more than 40 flowers (there were many others with less) was marked with a GPS point for identification (BES1-25), and altitude measurements were recorded. After a few test sessions, in which an hour to an hour and a half was spent watching various bushes, it was determined that single plants with less than 400 flowers were not worth watching (1 visit or less in an hour), and that patches with multiple plants (with one bush with more than 400 flowers) were ideal.

Nectar extraction

At the beginning of each observation period, the nectar concentration of each individual of *B. solanoides* under study was measured by first removing a flower at the peduncle (to include the corolla and receptacle), then using a 3-mL plastic pipette with a VWR Ergonomic High-Performance 10-1000uL micropipette tip attached (Appendix, Figure E) to extract whatever nectar could be found inside the nectaries (usually around 2-5 uL), and finally measuring the

concentration of sugar in the nectar with a Vee Gee BX-50 Refractometer (Appendix, Figure D). The extracted nectar was placed on the blue, translucent plate on the inside of the refractometer, the lid was closed, and the percentage was determined upon turning the apparatus to the light and peering through the eye-hole. This practice was performed in duplicate whenever possible, but soon proved unreasonable due to the extremely limited number of reachable flowers. Both tools were rinsed with boiled water before and after every use.

Observation Periods

After nectar concentration was measured, each bush or patch of bushes was watched for a period of 1.25 hours. For each period, the following general data was collected about the surrounding environment: the trail on which the patch of plants resides, a description of the habitat and the current climatic conditions. Information about each plant was also collected, including: approximate number of flowers on each plant, the concentration of nectar of each plant, and the approximate percentage of unopened flowers of each plant. Additionally for each hummingbird visit (which entailed the entire time and all activities of one hummingbird from arrival (first sighting in the area) until exit (flying out of sight) the following data were collected: the sex and species name of each visiting hummingbird, the time of arrival, visit duration, number of flowers probed, number of perches without feeding, and behavioral notes ("normal" behaviors included (1) flying around the food source, (2) feeding, and (3) perching, while "aggressive" or "territorial" behaviors included: (1) perching and chirping (2) ramming (flying full speed into an intruding individual) (3) chasing and (4) vocalization (5) other displays such as the puffing of feathers or hovering displays) (Pitelka, 1942; Camfield, 2006).

Four 1.25 hour periods were completed each day: "Early Morning" (6:15-7:30am),"Mid-morning 1" (8:15-9:30am), "Mid-morning 2" (9:45-11:00am), "Late Morning (11:20am-12:35pm). Afternoon sessions (2:00pm to 5:00pm) were attempted, but so few sightings were recorded during this time that it was determined that activity was too low to record significant interactions, and human resources were limited (only one observer), so more than 5 hours of observation per day was difficult.

Comparative Data

Comparative data was adopted from the study "Trends in Nectar Concentration and Hummingbird Visitation: Investigating Different Variables in Three Flowers of the Ecuadorian Cloud Forest: *Gusmania jaramilloi, Gasteranthus,* and *Besleria solanoides* " by Sophie Wolbert (2016), collected from several camera traps placed within Santa Lucía during an ongoing project that began in 2013. Each species of hummingbird that visited *B. solanoides* was noted, along with the number of visits to show a proportion of visits by each species.

Data Analysis

To clearly represent the data, pie charts were used to show the proportions of total visits to each species of plant and by each species of hummingbird. Bar graphs were used to compare large differences between groups, and chi-squared tests were performed to determine the statistical value of differences between the sexes of BRT and VTS. Linear regressions were run between nectar concentration and number of visits per observation period, and number of flowers and number of visits per observation period. Correlation coefficients and p-values were reported,

at the 95% level. Scatter-plots with visit durations were created, to show the distribution and mean of visit duration with outliers. Territorial behaviors were reported, structured by interactions of known territorial individuals (recognized by physical characteristics and perching locations) with intruding hummingbirds. Unexpected behaviors were also reported.

RESULTS

Selection of B. solanoides

Before any proper observation of hummingbirds could begin, it was necessary to locate viable observation sites. First, I walked the length of all four accessible trails in the Santa Lucia reserve, and marked GPS points for all *B. solanoides* individuals with more than 40 flowers (Figure 1; Appendix, Figure B). Additionally, I recorded elevation measurements, number of flowers, and if each was (or was not) located in a "patch" with other individuals within a radius of ~3 meters (Appendix, Table 1).

Figure 1. Google Earth representation of study site. All notable *B. solanoides* individuals are pictured (BES1-25), but individuals in patches often do not show all numbers (*ex:* BES18,19,20 all so close together that BES18 does not show up). The Santa Lucia Lodge is located on the ridge between BES4 and BES16.

I discovered that most plants were transitioning into the fruiting period of the season; according to my advisor, Holger Beck, the average *B. solanoides* has more than 400 flowers at the peak of the flowering season, and at this time of year it was evident that most individuals had far fewer than 400 flowers. Thus, approximations of flower numbers of each individual were noted and considered a determining factor in the value of each shrub as a resource for hummingbirds (Appendix, Table 1).

After a few test observation periods at various sites, I determined that, in order to attract more than one visit per hour and to increase the possibility of viewing territorial interactions (Camfield, 2006; Feinsinger & Chaplin, 1975), only *B. solanoides* individuals with more than 400 flowers, or patches with at least one individual with greater than 300 flowers would be considered viable observation sites. Thus, two individuals (BES21 and BES25), and two patches (Patch A with individuals BES18, 19, 20 and Patch B with BES22, 23, 24) were considered for this study. All four of the sites were located on one slope of the reserve, on the "parqueadero"

trail within 200 meters in elevation (BES21: 1878m, BES25: 1693m, Patch A: ~1891m, Patch B: ~1726m), all below the altitude of the lodge (which rests at ~1950msnm).

Comparative data

I wanted to determine whether my results reflected the normal activity of hummingbirds to *B. solanoides*, so I utilized data collected by Wolbert (2016) with camera traps at the Santa Lucia Reserve. Out of 69 visits, 38 visits (56%) were VTS, 23 visits (34%) were BRT, and 8 visits (11%) were species other than BRT and VTS (Figure 5). Female and male VTS visited equally (19 visits each) along with female BRT, while male BRT only visited 4 times.

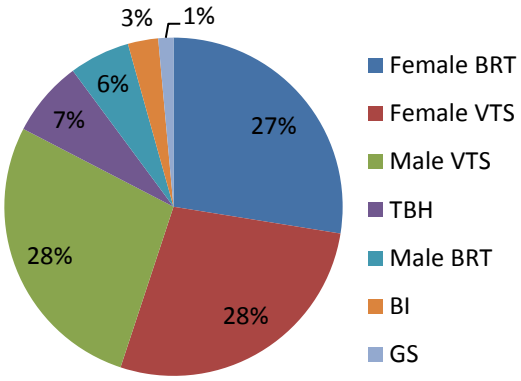

Figure 2. Proportion of visits to *B. solanoides* as detected by camera traps (Wolbert, 2016). number of visits: 69. BRT: booted racket-tail (female: 19 visits, male: 4), VTS: violet-tailed sylph (female and male: 19 visits), TBH: tawny-bellied hermit (5 visits), BI: brown inca (2 visits), and GS: gorgeted sunangel (1 visit). **The majority of data is from before 2016, throughout all seasons, as the data comes from an ongoing study that began in 2013.**

General visitation data

I recorded all sightings, behaviors and interactions of hummingbirds at each observation site at four different times of day for 1.25 hours, twice for each site. After the completion of all observation periods (more than 40 hours of observation), the data reveal that the only species that fed at *B. solanoides* were VTS and BRT (Figure 3), which is inconsistent with the camera trap data previously stated.

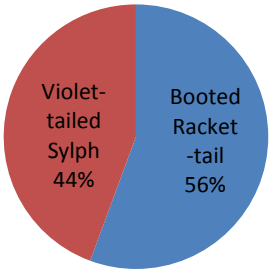

Figure 3. Percentage of total visits by each species to *B. solanoides* at all observations sites. Total number of visits: 142.

It is notable that other species were spotted close by on 19 occasions, sometimes feeding on other inflorescences, sometimes hovering, and other times perching momentarily on *B. solanoides* shrubs, but never feeding. Species in the area included: Brown Inca, Tawny-bellied Hermits, Green-crowned Brilliants, and Fawn-breasted Brilliants (Figure 4).

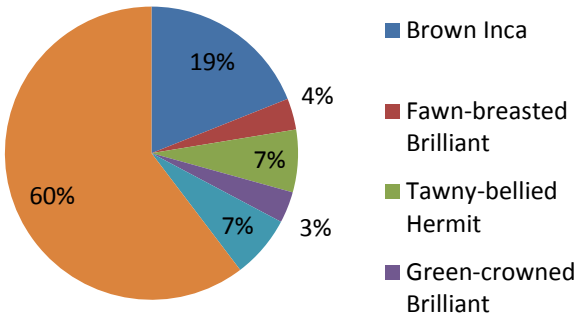

Figure 4. Documented visits of all hummingbird species to plants in the area that were not *B. solanoides* during observation periods. Representative of visitation only to areas in sight of the chosen observation sites for *B. solanoides.* Total number of recorded visits to plants other than *B. solanoides:* 58.

There were many documented visits to different plants in the area by all species of hummingbird. Most often were visits to a species of Maranthaceae called *Calathea ischnosiphonoides* with large, white inflorescences on stalks, and an invasive species of Malvaceae with red, bulbous flowers that hang opening-down (Figure 5).

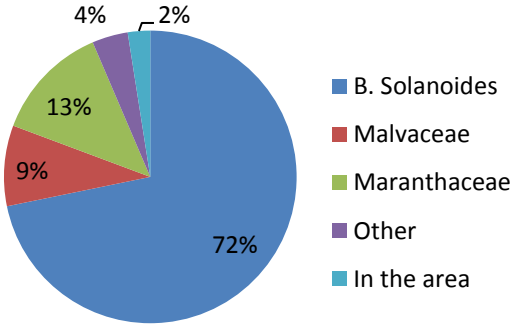

Figure 5. Percentage of all hummingbird sightings in the area, including visits of all species of hummingbird to all species of identifiable plants. Total number of hummingbird sightings: 202.

Visitation by sex

Of all visits to *B. solanoides* by BRT and VTS, I discovered that the majority of individuals were female (Figure 6), which contradicts the expected result that males would dominate visitation due to higher aggression and territoriality. Furthermore, while female and male BRT visited equally, male VTS barely visited *B. solanoides,* while female VTS had the highest number of visitations (Figure 6).

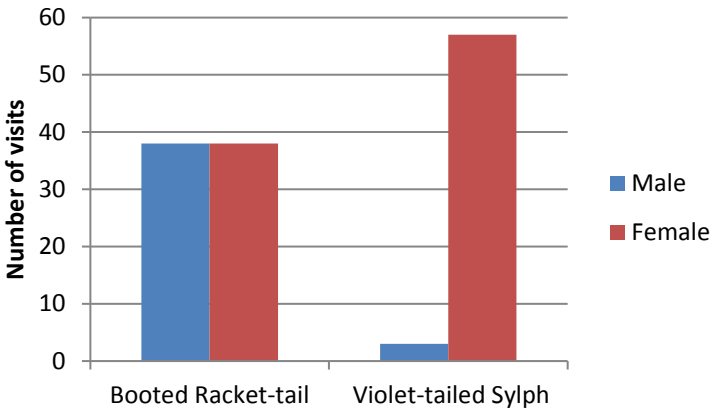

Figure 6. Visitation by sex. Red: female, Blue: male.

To ensure a significant difference in the visitation by VTS, a chi-squared test was run, with a null hypothesis that visitation would be the same for each sex of both species. The chi-squared test revealed that the BRT data supports the null hypothesis exactly (λ^2= 0.0), while the VTS data rejects the null hypothesis; there is a significant difference in visits between the sexes (λ^2= 48.6, greater than 99.9% CI cut-off of 10.8). Additionally, there is a statistically significant difference between female VTS and female BRT (λ^2= 3.8, 95% CI cut-off of 3.8), and female VTS and male BRT (λ^2= 3.8, 95% CI cut-off of 3.8).

Male VTS were more often seen feeding at other plants, including the common species of Maranthaceae previously mentioned, epiphytes, and trees (Figure 7).

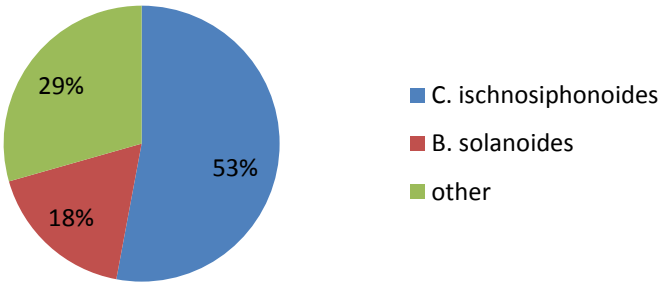

Figure 7. Number of sightings of male violet-tailed sylphs to various plants. Total number of sightings: 17.

Correlation analyses

To test the hypothesis that hummingbirds would visit *B. solanoides* individuals with higher concentrations of nectar at a higher frequency and with greater numbers of flowers would attract a higher frequency of visits, linear regressions were run between these two factors and number of visits. The linear regression between nectar concentration and visitation frequency did not produce a significant correlation (p-value > 0.05, 95% CI). However, one can interpret that

there is a trend of a weak positive correlation (R= 2.0) between nectar concentration and number of visits, which might result in significance if the sample size was increased (Figure 8).

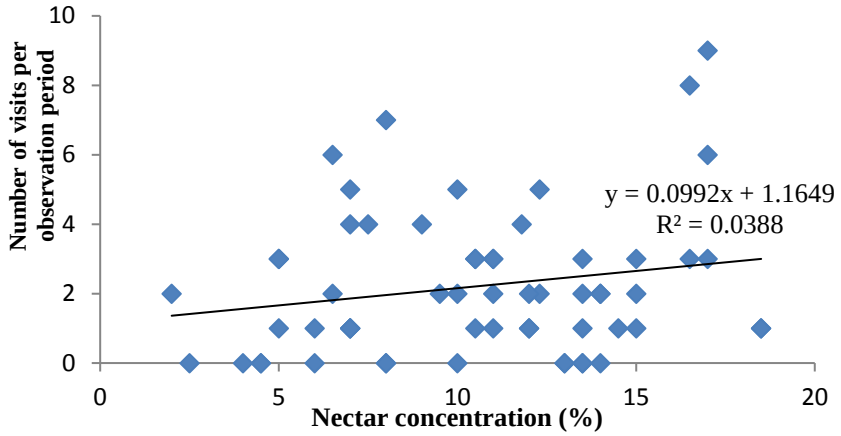

Figure 8. Nectar concentration versus visitation frequency (p-value= 0.13, 95% CI [-0.030, 0.23]; Correlation coefficient (R) = 0.20).

The linear regression between number of flowers and number of visits revealed a significant trend (p-value < 0.05, 95% CI), and a moderate positive correlation (R= 0.56) (Figure 9).

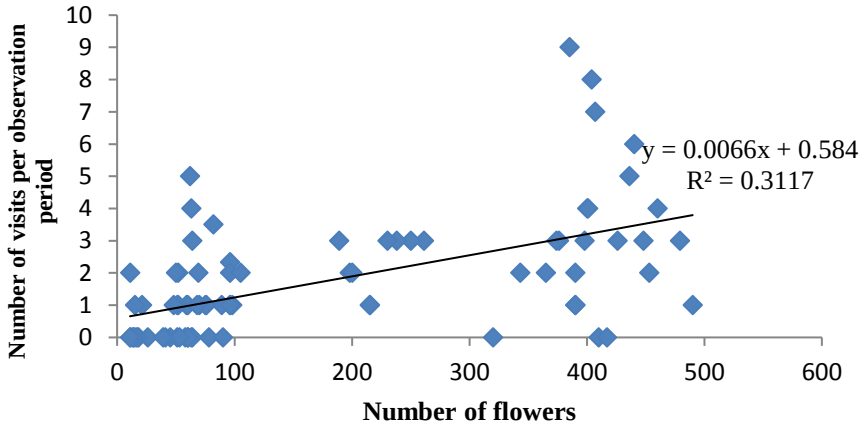

Figure 9. Number of flowers versus number of visits per observation period (p-value= 6.1 x 10^{-8}, 95% CI [0.0044, 0.0087]; Correlation coefficient (R) = 0.56)

Visit duration

The range of duration of visits by BRT to *B. solanoides* was 3 seconds to 11 minutes and 1 second, and the range of duration of visits by VTS was 3 seconds to 14 minutes and 41 seconds. These, however, are outliers; the mean durations were 1 minute 37 seconds and 1 minute 28 seconds, respectively (Figure 10 A & B).

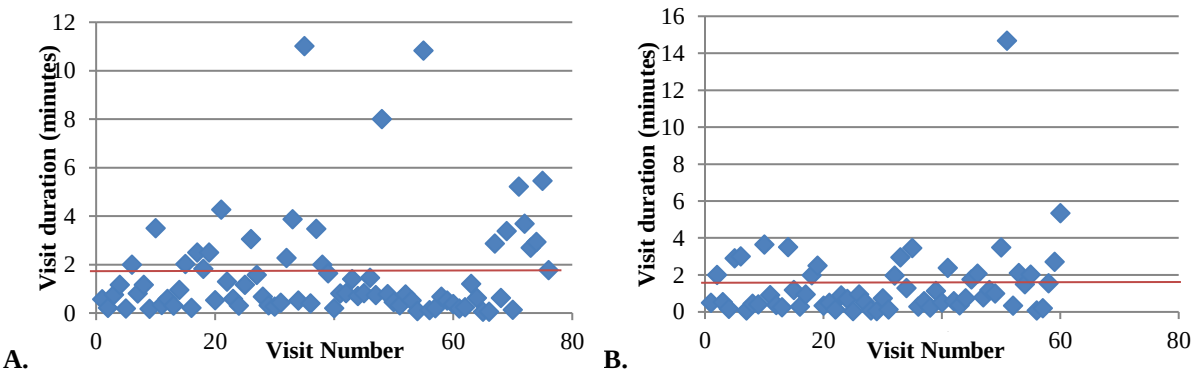

Figure 10. Scatter-plot of duration of each visit to *B. solanoides.* **A.** Visits by booted racket-tails **B.** Visits by violet-tailed sylphs. Mean durations indicated with red lines.

Territorial behaviors

Throughout this study, I spent enough hours watching and waiting at the same bushes that I eventually was able to distinguish individual hummingbirds based on physical characteristics and perching locations. I am confident that these individuals were the territory holders, based on interactions with other hummingbirds, behaviors, and vocalization. I was able to distinguish four individuals who each defended *B. solanoides* bushes: a female VTS at BES18, a female BRT at BES21, a male BRT who took the territory at BES21 from the female, and another female VTS at BES25. In the scatter-plots of visit duration above (Figure 10), these individuals stayed for the longest visits, often perching for many minutes within or next to their bush. During these long perches, the individual performed a range of behaviors: resting, preening, glancing around, wiping their bill, sticking their tongue out, and sometimes chirping.

The first sighting of the territorial female VTS at BES18 occurred on November 10th, during which I noted that she perched on the same branch (mid-bush) quite often, and that she had two small bright white feathers on the top of her head, where normally female VTS have solid-green, iridescent feathers (Appendix, Figure E). Three separate territorial interactions were observed: a female BRT attempted to probe a flower on BES18 at 6:37 am on Nov. 10th and the female VTS immediately chased her off, and at 6:41 am on the same day a tawny-bellied hermit approached her territory and she chased it off as well. On November 17th at 7:18am, the territorial female chased away a male VTS who had approached her territory. All three times, the chase began with a full-speed charge towards the intruding hummingbird, which may have resulted in contact (ramming) if the intruder had not flown quickly away. The female VTS visited 14 times (Figure 11) and was spotted near BES18 (flying, feeding on other plants or guarding) 5 times from Nov. 10th to 22nd. She did not perch while eating but while perched in the bush she gave a single chirp on 4 occasions, and called back to another VTS on two other occasions. By November 23rd, BES18, which originally had more than 400 flowers, had only 52 left; by then it is possible she abandoned the territory.

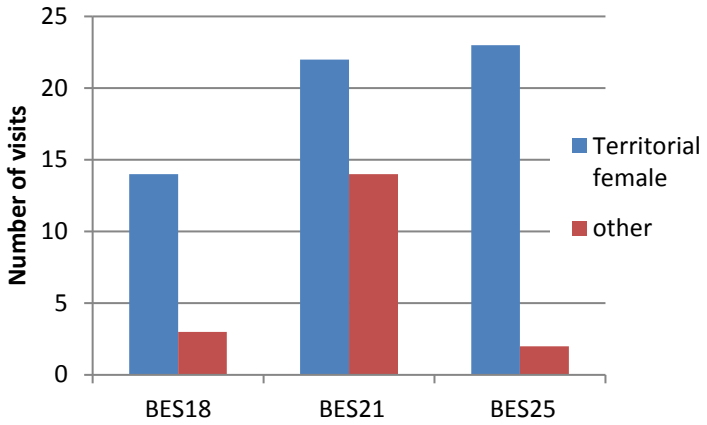

Figure 11. Proportion of visits of each territorial female vs. visits of other individuals. Female VTS at BES18, female BRT at BES21, and female VTS at BES25. The other visits to BES21 are all a male BRT, which may be the individual took over the female's territory.

The first visit of the territorial female BRT to BES21 occurred on November 10th. This female had a mostly white breast without any green flecks, except for the very edges, and a solid, green cap that began mid-cheek (Appendix, Figure F). She visited 22 times (out of a total of 36 visits, of which the other 14 were by a male BRT) (Figure 11) and often chirped as she fed. This female perched often, often stayed for long visits (8 visits longer than 2'00"), and when she perched for long periods she usually perched in the same spot, in the middle of the bush. Her longest visits were 8'00" and 11'01" shown above (Figure 10), with long perches of 5' 24" and 4'22" respectively. The first time I saw the female in the vicinity of another hummingbird, she was perched in BES21 on Nov. 17th, and at 6:41 am, and a tawny-bellied hermit flew by and hovered a couple feet from the bush. She watched but did not react, and the hermit did not attempt to feed, and flew away. On November 18th at 9:19 am, she was perched in BES21 and a male BRT began to feed. The female chased him away almost immediately, chirping. Soon after, she returned and perched, and at 9:25 am, a male VTS perched on Maranthaceae right next to BES21, and she watched him until they both flew off in opposite directions, without either exhibiting aggression. On November 22nd, the female chirped a descending call at 6:05am. A male BRT also sang the descending call upon arrival at 6:23am, when the female was not present, and departed after feeding. At 6:45 am, I think I may have witnessed a change of ownership: the female was feeding and the male BRT flew up to her, both hovered silently, face-to-face, and then the male chased her away from the bush. The male BRT quickly came back after the chase at 6:47 am and fed until he was deep inside the bush, and then the female arrived at 6:48 am as he was leaving. She fed on the front of the bush for 2 minutes and 6 seconds and then left. On November 23rd at 8:21, the male BRT chased the female BRT away from the bush immediately as she arrived, after which she was not seen again. The male BRT also visited for long durations: 3'23", 5'27", and 10'50", with the longest perch of 3'16". It is difficult to know whether all 14 visits by a male BRT to BES21 were the same individual, as I was not able to identify him based on physical characteristics. Additionally, the female chirped while feeding until the male took her territory, and once he had gained the territory he began to chirp while feeding.

The territorial female VTS at BES25 was first seen on November 14th, and she was distinguished by a rusty-orange color on her breast that went higher onto the throat than usual, with dark-green flecks on the small sliver of white on her throat, and a slightly more upturned beak than usual (Appendix, Figure G). The female VTS visited 23 times (Figure 11), 12 times for longer than 2'00", with the longest visits of 14'41", 5'26", and 3'30" (Figure 10) and the longest perches of 11'03" seconds, 3' 39" seconds, and 2'08". At 12:35pm on November 14th, she chased off a female BRT, chirping. Then, on November 16th at 6:44am, she perched below a male BRT who was feeding, chirped once, and he immediately flew away. She often perched on the same branch just behind BES25, and would preen herself and chirp. On November 18th at 9:49 am, she perched in the normal place, did an ascending call and then the harsh, record-scratching warning call that often can be heard among VTS at the Santa Lucia feeders.

Although I was unable to distinguish other individuals, it is highly likely that other bushes were being guarded by certain individuals throughout the day. BES19 had 14 visits from male BRT, 1 visit from female BRT, and 1 visit from male VTS. I did not witness any interactions among individuals at BES19. At BES20R and L, there were 6 and 7 visits from a male BRT, which were definitely the same individual 3 times (I watched him feed at one bush and move to the other), who also fed at BES19 in the same visit. BES20R was visited by a female BRT 3 times. However, I witnessed no interactions, nor long, drawn out perches or territorial displays. Similarly, BES22, 23, and 24 were visited most often by a female VTS: visiting BES23 11 times, BES22 9 times, and BES24 once-- three of these visits overlap. The only other visitor was a female BRT, once only to BES22, and another to BES22 and BES23. I witnessed one aggressive interaction at this site (Patch B), during which a female VTS was rammed and chased by a bird that I struggled to identify-- it may have been another female VTS but it was extremely difficult to see.

Additional behaviors

In addition to expected behaviors such as feeding on nectar, perching, chasing, and vocalizing, I also witnessed some behaviors that I was not expecting. On three separate occasions I observed hummingbirds that perched, glanced around, flew off perch a couple feet and then straight back to their perch, repeating this behavior several times in a row. The first time I saw this behavior was at 11:12 am on Nov. 11th on the main trail, when a Brown Inca was perched on a stick that was not near any flowering plants, and flew off in this way. I witnessed it a second time on Nov. 17th at 11:03 am, when a male VTS was perched in a relatively open area, a couple meters behind and to the right of BES20R. I watched the male VTS stick his tongue out after each flight. The last time was at 10:01 am on Nov. 21st, when I watched a male BRT perform the same behavior, perched on a branch of BES21. I witnessed another interesting behavior as I was observing the resident female VTS at BES25; she flew off her normal perch towards BES25 and smacked into butterfly that had begun feeding at 10:31 am on 11/22/16. At 10:50 am, she did it twice more as the butterfly continued to return to the bush.

DISCUSSION

Comparative data vs. general visitation data

The comparison between camera trap data and observation reveals a disparity between the hummingbird species that normally visit and those that visit in the presence of a human observer (Figures 2, 3). In the camera trap photos, 5 species were present, while I only observed 2 species feeding (Figure 3). There are various explanations for this result, the first and most obvious being that, due to my presence, some species decided that the risk of predation outweighed the potential energetic benefit of feeding at *B. solanoides* (Lima, 1991). This interpretation seems logical, because the two species that I observed are clearly the predominant species that feed on this plant (89% of visits were VTS and BRT, Figure 2), and thus may largely depend on *B. solanoides* for sustenance. Meanwhile, the other species may not need *B. solanoides* as a main source of food, due to their ability to feed at a larger variety of flowers, with longer corollas; both brown incas and tawny-bellied hermits have longer beaks and larger bodies than VTS and BRT (Ridgely, 2011), and I witnessed both of these species feeding on other resources near the observation sites (Figure 5).

However, this reasoning does not hold true for the last species in the comparative data, the gorgeted sunangel, due to the fact that this species has a very straight, short beak and a small body (Ridgely, 2011), which indicates that it is also a generalist species, and thus most likely would feed on flowers like those on *B. solanoides* for most of its sustenance (Snow & Snow, 1976). Additionally, I did not observe this species at any site for any species of plant. Thus, it is more likely that gorgeted sunangels only reside at higher elevations; while my study ranged from 1693-1891msnm, the camera trap photo was taken at 2174 msnm (Wolbert, 2016), and they are generally known for residing between 1800-2400m, but occasionally will migrate to higher altitudes (Ridgely, 2011).

Due to the fact that the camera trap data was collected continuously from 2013 to 2016 (and thus throughout all seasons), an alternate or congruent explanation could be that tawny-bellied hermits and brown inca do not feed on *B. solanoides* at this particular time of year, due to the fact *B. solanoides* is losing flowers quickly as it transitions into the fruiting season, and thus is declining as a resource. Thus, it may not provide these larger species with sufficient quantity and quality of nectar to outweigh the costs of hovering (Garrison & Gass, 1999).

Visitation by sex

In a related result, I found that, while female and male BRT visited *B. solanoides* equally, male VTS fed at *B. solanoides* significantly less than female VTS (only 3 out of 60 VTS visits were males) (Figure 6), and instead spent most of their time feeding at *C. ischnosiphonoides,* a species of Maranthaceae (Figure 7). I previously predicted that male VTS would be the most territorial and thus visit at the highest frequency to *B. solanoides*, which is not supported by these results. At this particular season, is possible that male VTS have abandoned *B. solanoides* for other inflorescences with higher quality and quantities of nectar, due to the fact that *B. solanoides* is declining in this season (Garrison & Gass, 1999). Additionally, previous studies have shown that although most species can be described as either territorial or trap-lining, niche overlap does occur quite often in response to changing resources (Feinsinger, 1976; Leone & Estevez, 2008). Therefore, I conclude that, in this season, male VTS are spending more of

their time feeding in a trap-lining fashion, and are feeding on sparsely distributed inflorescences over larger areas instead of defending more localized resources. Meanwhile, there was a statistically greater number of female VTS visits than both female and male BRT (Figure 6), which can be explained by the presence of an innate dominance hierarchy (Camfield, 2006; MacNally & Timewell, 2005). The absence of competition from male VTS leaves female VTS with more opportunities to hold territories on *B. solanoides* because they are larger than both male and female BRT and thus will hold dominance over more resources (Cotton, 1998).

Correlation analyses

To determine which criterion (nectar concentration or number of flowers) is more valuable to hummingbirds, I ran two linear regressions: one between nectar concentration and visitation frequency (number of visits per observation period), and the other between number of flowers and visitation frequency, with visitation frequency as a proxy for the perceived value of the resource (Figures 8, 9). The analysis reveals that there is no significant relationship between nectar concentration and visitation frequency, although there exists a trend of a weak positive correlation (Figure 8). Nectar sugar concentration varied widely between flowers within an individual plant, and, for the majority of the time, measurements were only taken from one flower on each plant, so these measurements may not have accurately represented the average concentration of each plant. This may indicate that if the sample size was larger, and if nectar concentration had been measured in duplicate or triplicate and then averaged, than a significant result might be revealed. However, it is also possible that, at this time of the season, hummingbirds value number of flowers over nectar concentration in *B. solanoides.* The linear regression between number of flowers and visitation frequency produced a clearly significant result, with a moderate positive correlation, indicating that the number of flowers does strongly influence the number of times a hummingbird will return to an individual plant, and as the plant loses flowers, hummingbirds will adjust their visitation accordingly (Garrison & Gass, 1999; Lara *et al.*, 2009). Thus, the data suggest that, at this particular month of the season, hummingbirds consistently visit *B. solanoides* bushes with greater numbers of flowers more than those with fewer, and flower number may take priority over sugar concentration in nectar.

Visit duration and territorial behaviors

Once I was able to differentiate the individuals based on physical characteristics, the behavioral observations that led me to believe that these individuals were territory holders consisted of aggressive interspecific and intraspecific interactions, visit duration, and vocalization, each of which, in different ways, indicate protective behavior unique to territorial individuals.

Physical aggression

Of these behaviors, overt aggression is probably the most obvious indicator of territoriality. These behaviors were most clearly shown by the female VTS at BES18, who chased off all individuals that flew close to her territory, regardless of sex or species (male VTS, tawny-bellied hermit, and female BRT). This indiscriminate aggression to protect her territory is consistent with previously observed behaviors of males of territorial species (Pitelka, 1942; Powers & Mckee, 1994), especially when resources were limited. Although territoriality in female hummingbirds has not been studied extensively, some studies have reported female

territoriality during the breeding season around nesting sites (Pitelka, 1942), and Wolf (1969; 1975) discovered in two different studies that fiery-throated hummingbirds and purple-throated caribs both display territorial behaviors to protect food resources during the non-breeding season. Territorial behaviors were also observed in the other females and male BRT: at BES25, the resident female VTS chased off a female BRT in a full-fledged chase. At BES21, the female and male BRT chased one another away multiple times, and once hovered face-to-face in the air for a few seconds before the male chased away the female. This hovering display was most likely a confrontation, in which they assessed who was the stronger individual, which seems to have resulted in the male assuming control over the territory. Other studies have reported similar displays, which involve hovering, flashing of iridescent feathers, or movements such as head rotation (Camfield, 2006; Stiles & Wolf, 1970).

Visit duration

Each of the territorial females visited their territory more times than all other visits combined (Figure 11), often perching for many minutes within or next to their bush. According to previous studies, along with resting and preening, these long perches are used for two purposes: crop-emptying, in which they digest the nectar they have recently consumed, conserving energy, and guarding their territory by through occupation (Diamond *et al.*,1986; Feinsinger & Chaplin, 1975). Additionally, the shortest visits (of a few seconds long) were nearly all visits by territorial individuals, in which the individual would perch or hover at the site for a few seconds, and then leave. Although I did not come across any literature that touched on this topic, my interpretation of this behavior is that these territorial individuals are checking up on their territory to keep other hummingbirds from taking nectar. However, it is difficult to know without further investigation why they do not feed during these surveying visits as well, and whether or not this behavior is truly territorial.

Vocalization

Another important territorial behavior, which is often combined with the other territorial behaviors, is vocalization. The female VTS at BES25 was particularly vocal, and made a range of different chirps and calls. The first, a high-pitched chirp, has been described by others as a general "call" (xeno-canto.org). She used this vocalization to declare her presence to a male BRT who was feeding in her bush, after which he immediately flew away. Because the female VTS at BES18 also used this sound in reply to a call by another VTS, I suspect that it is not an aggressive call, but was used by the female at BES25 to simply declare her presence and territory. On another occasion, the female a BES25 perched and made two calls (that I have also heard male VTS while fighting in the Maranthaceae or at the Santa Lucía feeders): a chattery, agitated call that gets more shrill as it ascends, and a harsh, record-scratching call. I interpret both as aggressive calls, the first more as a declaration of territory or chase call, and the second as an alarm call or warning call (consistent with xeno-canto.org for subspecies *Aglaiocercus coelestis coelestis*). The female BRT at BES21 chirped as she fed, which has been described as "foraging calls" and cried a descending call when flying into her territory, which others have described as a "chase-call" (xeno-canto.org). Because the male BRT that later took over her territory also used this call, I suspect that it is also a territorial vocalization.

Dominance hierarchy

While both female VTS chased away all individuals who neared their territories (BES18, 25), I observed that the female BRT (BES21) was not as quick to aggression. On two separate occasions, I observed her watch, without reacting, as an intruder of a different species came very close to her territory: the first time was a tawny-bellied hermit, and the next was a male VTS. Because neither of these individuals attempted to probe a flower, it is difficult to know whether she would have aggressively defended her territory if they had fed. It is possible that she was just conserving energy by not engaging in chase until they came closer (Powers & McKee, 1994; Wolf & Hainsworth, 1971). However, at the other sites, the female VTS chased away all individuals who came within a meter of the bush, leading me to believe that there may also be more complex interspecific dynamics at play. MacNally and Timewell (2005) describe a dominance hierarchy among heterospecific nectivores, in which the largest species defend the best flowering areas, and smaller -and thus subordinate- species occupy lower quality resources. Due to size difference between male VTS and female BRT, I suspect that a male VTS, if he so chose, would be dominant to the female BRT, as would the tawny-bellied hermit due to size (if it was a territorial species) (Ridgely, 2011). Thus, it is possible that the female BRT recognized her sub-ordinance, and thus did not challenge either individual. This may also explain why the female VTS chased away all intruders-- because she was larger, she may have been higher on the dominance hierarchy, and thus able to chase away more heterospecific individuals. However, the female BRT did defend her territory from a male BRT on numerous occasions. Therefore, an alternative or compatible explanation is that defending the territory from conspecifics, who might take over the territory, was a better use of energy than defending from heterospecifics (Noble, 2010). It seems highly likely that she was more preoccupied with defending from members of her own species, and rightly so, due to the fact that a male BRT, by second to last day of observation, took control of the female BRT's territory at BES21, after which she was not seen again.

Additional behaviors

I observed a few behaviors that I did not expect throughout the course of this experiment, which may offer additional knowledge about these species and their behaviors, both while feeding and guarding territories. I witnessed three different species of hummingbird behaving strangely, in which the bird would begin perched, fly off a couple feet, and glide back to the perch. This behavior has been documented in previous studies, and from these observations I can only deduce that the hummingbirds are eating insects, a behavior called "hawking," in which they behave similarly to flycatchers (MacNally &Timewell, 2005; Wagner, 1946). Flying insects such as flies, gnats and mosquitos, and other small organisms such as spiders have been found in analyses of stomach contents of hummingbirds, with diptera constituting the majority of ingested organisms (Wagner, 1946). During certain times of the season, some species of hummingbirds may even depend primarily on insects for sustenance, especially in the high mountains (Wagner, 1946).

I observed another surprising behavior while watching the territorial female VTS at BES25. The female flew off her perch and rammed directly into a butterfly that was feeding on a flower of BES25, after which I saw her repeat the behavior twice. Pitelka (1942) also observed a similar behavior, in which a territorial male ruby-throated hummingbird struck a bee that had entered his territory (p. 191). Although unusual, this behavior seems logical due to the fact that

nectar-robbing bees and other insects like butterflies also feed on nectar, and thus the female is just protecting her resource. Additionally, if there were dozens of butterflies on the bush, the cost of scaring them away would most likely outweigh the potential energetic gain of the nectar they consume. However, when only one individual insect is feeding, there is a very small energetic cost for the female to scare it away.

Limitations of the study

Although direct observation was a necessary part of this study in order to record all behaviors, my presence may have altered the behavior of these individuals. Because the *B. solanoides* plants of interest were so close to the path, I was forced to stand within 3 meters of all bushes, which may have altered the behaviors of some species and/or individuals. Additionally, due to the structure of these shrubs, it was sometimes necessary to stand directly underneath the bush in order to keep the visiting hummingbird in sight. Additionally, I did not include data I collected regarding number of flowers probed during each visit because at times I was forced to approximate due to the fact that it was difficult to keep the hummingbirds in sight as they flew to different parts of the bush. In terms of technical improvements, for future studies related to territoriality and resource value, mist-netting and tagging individuals (and possibly DNA analysis) is an important addition in order to identify and verify the presence of territorial individuals. Of course, time was a limitation for this study, as visitation rate was low to this plant at this time of year, and only a handful of territorial observations were recorded for each individual. Future studies should include a more comprehensive analysis of territoriality for both sexes of both BRT and VTS, and should include observation periods into the afternoon as well.

CONCLUSION

Although it is difficult to come to concrete conclusions with the limited number of observations and lack of previous knowledge about these species, this study shows that booted racket-tails (BRT) and violet-tailed sylphs (VTS) both depend on *B. solanoides* for sustenance, even at this time of year, as the flowers are falling and the resource is declining. There was a positive correlation between number of flowers on each bush and visitation frequency, and a non-significant, weak positive trend between nectar sugar concentration and visitation frequency, which may become significant with a larger sample size. Both BRT and VTS fit the physical and behavioral description of territorial, generalist hummingbirds, and exhibit aggressive, territorial behaviors. While BRT were only aggressive towards members of their own species, VTS were aggressive towards both conspecifics and heterospecifics. While total visits by male and female BRT were equal, female VTS visited significantly more than male VTS, and it became clear that male VTS were feeding mainly on other resources this season, possibly performing trap-lining-like behavior. Two female VTS and a female BRT were distinguishable by physical characteristics, and performed territorial behaviors such as aggressive chases, vocalizations, and long perches within their territories. These species also seem to follow a dominance hierarchy, in which BRT are subordinate. Lastly, interesting behaviors regarding insects were also observed: hawking (feeding like flycatchers), and ramming butterflies to defend floral resources. This study just scratches the surface of feeding and territorial behaviors in these species of hummingbirds, and the nuances of their behavior still remains undiscovered; there is much more to learn about these species, *B. solanoides*, and the ecosystem as a whole.

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APPENDIX

Figure A. GoogleEarth image of Santa Lucia in relation to the surrounding area.

Figure B. Alternate view of marked *B. solanoides* individuals using GoogleEarth.

Table 1. *B. solanoides* Bush Descriptions

Individual	Approx. initial number of flowers	Elevation	Location (Trail)	Patch or no?
1	~40	1742	Cana de azúcar	Yes
2	~50	1749	Cana de azúcar	Yes
3	~15	1760	Cana de azúcar	No
4	~50	1960	Principal	No
5	~90	1976	Principal	No
6	~80	1976	principal	No
7	243	1860	Auto-guiado	Yes
8	63	1871	Auto-guiado	Yes
9	111	1868	Auto-guiado	Yes
10	~50	1817	Auto-guiado	Yes
11	62	1821	Auto-guiado	Yes
12	~50	1822	Auto-guiado	Yes
13	181	1825	Auto-guiado	Yes
14	~50	1830	Auto-guiado	No
15	46	1832	Auto-guiado	Yes
16	160	1807	Auto-guiado	No
17	126	1871	Auto-guiado	No
18	410	1890	Parqueadero	Yes
19	82	1891	Parqueadero	Yes
20	194	1891	Parqueadero	Yes
21	490	1878	Parqueadero	No
22	238	1724	Parqueadero	Yes
23	400	1731	Parqueadero	Yes
24	64	1725	Parqueadero	Yes
25	460	1693	Parqueadero	No

Figure C. *Besleria Solanoides.* Pictured left: shrub, right: tubular orange flowers.

Figure D. Vee Gee BX-50 Refractometer. For determining sugar concentration in flower nectar.

Figure E. Makeshift nectar extraction device: 3-mL plastic pipette with a VWR Ergonomic High-Performance 10-1000uL micropipette tip attached.

Figure F. Territorial female violet-tailed sylph from BES25. Left: seated on favorite perch, note how rusty orange color rises past collarbone. Right: on BES25, note upturned beak and green flecks inside what is usually all-white throat patch.

Figure G. Territorial female VTS perched in BES18 on favorite branch. Note small white feather on top of head.

Figure H. Territorial individuals of BES21. Pictured left: female BRT, first resident. Right: Male BRT that stole her territory.