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## ABSTRACT

We studied hummingbird communities in Cañitas, Monteverde, Puntarenas, Costa Rica to observe territorial tendencies when given high and low percentage sugar concentration of food resources at artificial feeders along the edge of a forest patch. We wanted to determine if community composition was disproportionately affected by more aggressive, and therefore territorial species. We observed interactions of hummingbirds at artificial feeders of 20 and 33% sugar concentration. We found a disproportionately high number of visits by Rufous-tailed Hummingbirds (*Amazilia tzacatl*) at both sets of feeders (52.5% at 20% feeders and 89.4% at 33% feeders). We found a higher frequency of visits by all species at low reward feeder than at the high reward feeder (1016 visits at 20% feeders and 716 at 33% feeders) and a higher proportion of aggressive interactions at the lower reward feeder. Rufous-tailed hummingbirds were the most territorial species at our study site and their behavior influenced the relative abundance of subordinate species. Contrary to what we expected, we found that frequency of close chases and far chases at different sugar concentration feeders were not different than random.

## RESUMEN

Estudiamos comunidades de colibríes en Cañitas, Monteverde, Puntarenas, Costa Rica para observar tendencies territoriales cuando se les dio concentraciones de recursos alimenticios en comederos artificiales a lo largo del borde de un parche de bosque. Queriamos determinar si la composición de la comunidad estaba desproporcionadamente afectada por especies más agresivas, y por lo tanto territoriales. Observamos interacciones de colibríes en comederos artificiales con 20% y 30% de concentración de azúcar. Encontramos un número de visitas desproporcionadamente alto del colibrí de cola café (*Amazilia tzacatl)* en ambos grupos de comederos (52.5% en los comederos con concentración con 20% y 89.4% en los comederos con 33%). Encontramos una frecuencia mayor de visitas de todas las especies en el comedero con poca recompensa en comparación con el comedero con alta recompensa. (1016 visitas en los comederos con 20% y 716 en los comederos con 33% ).y una proporción más alta de interacciones agresivas en el comedero con poca recompensa. Los colibríes con cola café fueron la especie más territorial en nuestro sitio de estudio y su comportamiento influenció la abundancia relativa de especies subordinadas.. Contrario a lo esperado, encontramos que no la frequencia de persecusiones cercas y persecusiones lejos en comedores de concentraciones de azucar diferentes no fueran diferente que impensado.

## INTRODUCTION

There are 17 species of hummingbirds common on the Pacific slope of the Monteverde area of Costa Rica (Fogden and Fogden 2005). This hummingbird population is diverse despite the fact that it has a limited supply of nectar producing flowers (Tiebout 2000). This species richness has come about because different hummingbird species specialize on different types of flowers or use different foraging behaviors and competitive behaviors. Inter- and intraspecific interactions between hummingbirds can change their community composition (Fogden and Fogden 2005).

Both inter- and intraspecific competition can be influenced by resource value and availability, species-specific foraging behavior, differences in body size, and densities of individuals. Intraspecific competition can also be influenced by mating pressures. Interspecific interactions in hummingbirds are often influenced by the most dominant species in the area. They may limit subordinate species' access to food sources, while dominant individuals may limit their own populations through intraspecific interference at rich food resources (Tiebout 1993).

These dominant hummingbird species are typically classified as territorial. Territorial species are usually medium sized hummingbirds that are very aggressive and often brightly colored (Fogden and Fogden 2005). Their territories usually consist of several flowers that are close enough together to defend. When different species of territorial hummingbirds are found at the same location, the smaller species tend to shift behavior from territorial to subordinate (Lawlor and Maynard Smith 1976).

Difference in resource value, such as the caloric value of nectar, can change hummingbird behaviors. When different resource values are available, birds will usually feed where there are higher quality resources (Pimm et al. 1985). However, optimal foraging theory states that population densities of competing species will influence foraging strategies (Lawlor and Maynard Smith 1976). As the density of hummingbirds increases, inter- and intraspecific competition increases, causing a shift in how birds use the available resources. This would cause subordinate hummingbirds to rely on lower quality resources because more dominant individuals defend the higher quality resources.

Dominant hummingbirds should be more aggressive at resources of greater value and thus affect community composition. We hypothesized that there would be a difference in aggressive behavior between feeders of different sugar concentrations. Therefore, we predicted that higher sugar concentrations will lead to more chases, limiting weaker competitors' access to food sources. Competitive interactions should be less common and intense when territoriality is not as pronounced.

## METHODS AND MATERIALS

### Study Site

The site chosen for our study was on the Santamaría farm in Cañitas, Puntarenas, Costa Rica. Cañitas is a rural community located approximately 2.2 km northwest of Santa Elena. The study site was located along the edge of a forest patch that bordered a coffee farm.

### Natural History of Local Hummingbirds

The four common hummingbirds at our feeders in Cañitas were the Rufous-tailed Hummingbird (*Amazilia* tzacatl), the Striped-tailed Hummingbird (*Eupherusa eximia*), the Steely-vented Hummingbird (*Amazilia saucerrottei*), and the Violet Sabrewing (*Campylopterus hemileucurus*). In Costa Rica, the Rufous-tailed Hummingbird is the most widespread

hummingbird (Fogden and Fogden 2005). Throughout its range, it prefers non-forest habitat such as second growth, coffee plantations, and along forest breaks and gaps (Stiles and Skutch 1989). Both sexes of Rufous-tailed Hummingbirds are aggressive and dominant to hummingbirds of similar size (Fogden and Fogden 2005). Males commonly defend territories. Another common resident to the Monteverde area is the Striped-tailed Hummingbird (Stiles and Skutch 1989). Male Striped-tails occur mainly in the forest canopy, while females prefer the forest understory (Fogden and Fogden 2005).

Steely-Vented Hummingbirds are common in the Monteverde area. There is no sexual dimorphism within the species and both defend territories, though not as effectively as larger hummingbirds. They frequent scrubby woodland, coffee plantations, and gardens, foraging at many flowering trees (Fogden and Fogden). The Violet Sabrewing is among one of the largest and most common hummingbirds in the Monteverde area. It is a high-reward trapliner that prefers understory, edges of mountain forests, or patches of woods in disturbed areas (Stiles and Skutch 1989, Fogden and Fogden 2005). Though rarely territorial at flowers, Violet Sabrewings can easily dominate all other Monteverde hummingbirds at feeders (Fogden and Fogden 2005).

**Procedure**

For this study, four hummingbird feeders were used. Two feeders were filled with a simulated nectar mixture of 20% sugar concentration by volume (approximately 240 g/946.2 ml) and two other feeders were filled with a simulated nectar mixture of 33% sugar concentration by volume (362 g/ 946.2 ml). The four feeders were refilled with an identical sugar concentration every three days to prevent the sugar from degrading. The feeders were alternately placed at a distance of 47 meters ± 1 meter away in order to assure that each feeder could be defended separately from all others. Feeders were set up three days prior to data collection to allow hummingbirds to discover the food sources. Field guides for hummingbirds were used to check accuracy in identification. Binoculars were used in order to study at a distance that would not affect the interactions at the feeder.

Data were collected for eight days at varying times to control for temporal variation. We spent one hour at each of the four feeders, with one day spent together collecting data at all feeders. Sixty total hours were spent in the field. Each feeder was stationed in a tree along the forest edge that was visible from the forest. We recorded the type of hummingbird species, the amount of time spent hovering and feeding, and the type of interaction. Visits were counted if the hummingbird approached the feeder within 15 cm. All interactions were classified as either "chase" or "no chase", (after Dearborn 1998). An interaction was recorded as a "chase" if the hummingbird at the feeder either chased or was chased by another individual, while "no chase" implied no interaction between the hummingbird visiting and another individual. Additionally, we noted which two species interacted. "Far chases" were counted if a chase interaction occurred farther than 15 cm away from the feeder.

**Statistical Analyses**

We used Chi-square analyses to determine if there was a preference by any or all species for one sugar concentration feeder over another, if there was a difference in the frequency of "chase" and "no-chase" interactions at 20 and 33% sugar concentration feeders, and if there was a difference in close and far chase interactions at the two sugar concentration feeders. A parametric t-test was used to compare the mean number of hummingbird visits per hour interval.

## RESULTS

At our study site, four of the 17 species common on the Monteverde Pacific slope were observed: Rufous-tailed Hummingbird (*Amazilia tzacatl*), Stripe-tailed Hummingbird (*Eupherusa eximia*), Steely-vented Hummingbird (*Amazilia saucerrottei*), and Violet Sabrewing (*Campylopterus hemileucurus*). We observed 1732 interactions at the feeders in 60 hours of observations and 1008 chases away from feeders in 51 hours. A total of 1016 visits were observed at the feeders with 20% sugar concentration, while 716 visits at feeders with 33% sugar concentration were observed (Figure 1). The frequency of visits by the four hummingbird species at different sugar concentrations were not different than random (Chi-square test, $\chi^2$ = 273. 67, $p < 0.001$, n = 1732). Rufous-tailed Hummingbirds were more common than expected at the high concentration feeders, while the other species were all less common than expected. The frequency of visitation to the 20% sugar concentration feeder was significantly higher than expected by chance, and vice versa for the 33% sugar concentration feeder.

We compared the number of "no chase" versus "chase" events at the two concentrations of feeders (Figure 2). At different sugar concentrations, there was a significant difference in no chase and chase frequencies. (Chi-square test: $\chi^2 = 24.10$, $p < 0.001$, n = 1735).

The relative abundance of each species at different sugar concentrations was noted. Both feeders show a disproportionately high frequency of visits by the Rufous-tailed Hummingbird, although the 20% feeders show more species diversity (Figure 3). The Rufous-tailed Hummingbird was the most common visitor at each feeder.

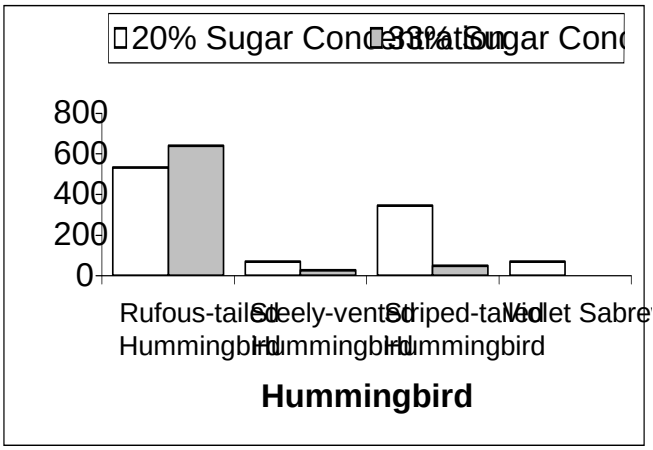



Figure 1. The number of visits by four hummingbird species to feeders of 20 and 33% sugar concentration. The frequency of visits to feeders of the two concentrations was not random. (Chi-square test: $\chi^2 = 273.67$, $p < 0.001$, n = 1732).

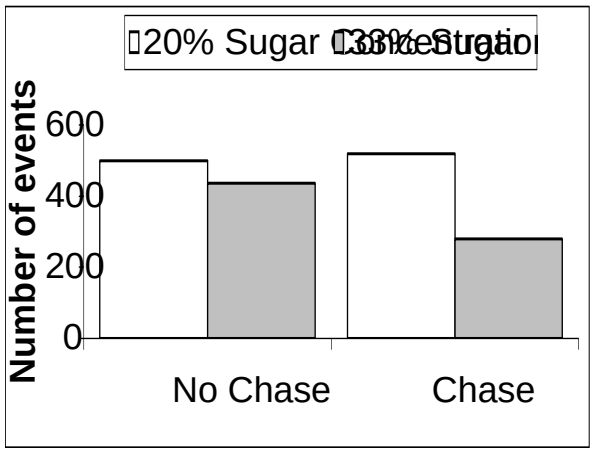



Figure 2. Comparison of hummingbird chases versus no chases at feeders of 20 and 33% sugar concentration. Frequency of "chase" and "no-chase" events at feeders with different sugar concentrations. (Chi-square test: $\chi^2 = 24.10$, $p < 0.001$, n = 1735).

The average number of visits observed per hour interval was 34.0 and 23.8 for 20 and 33% sugar concentration feeders, respectively (Figure 4). There was a significant difference in the average number of visits per hour to each feeder (T-test: t-value = -3.55, $p < 0.001$, n = 60, d.f. = 58).

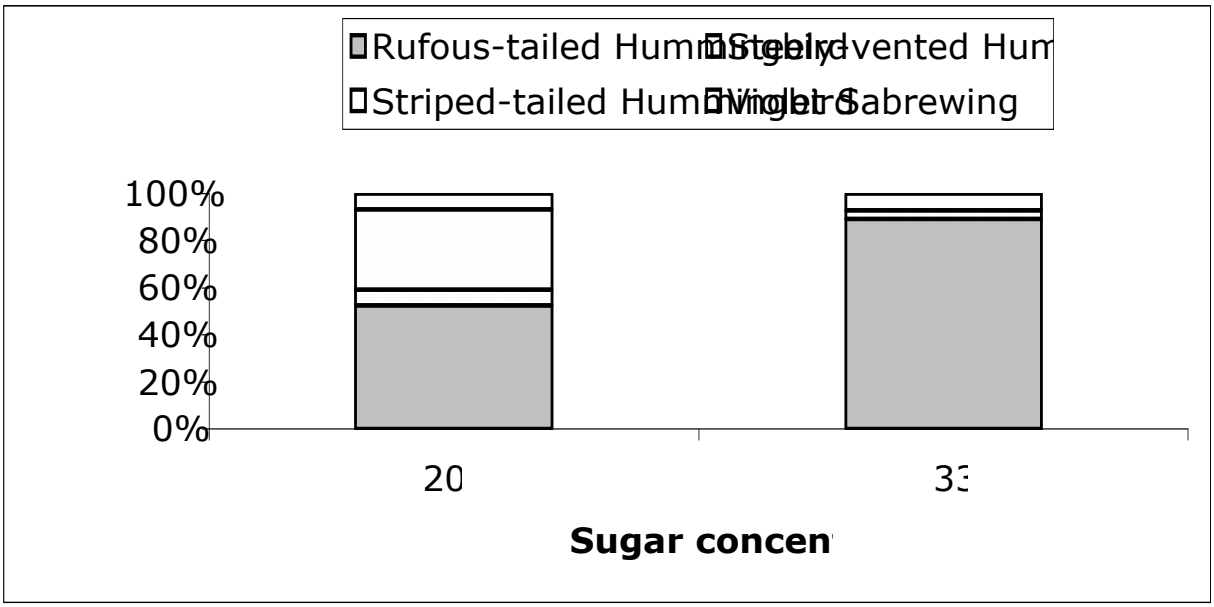
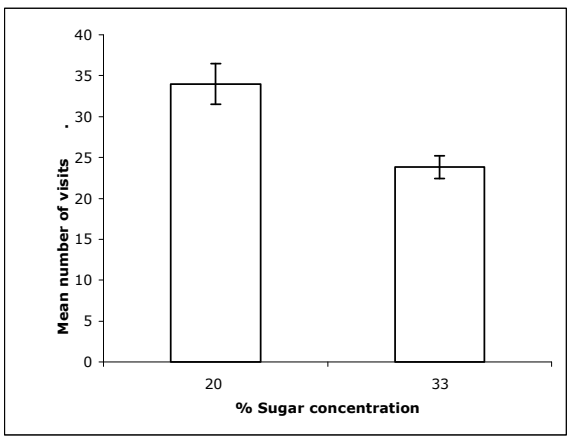



Figure 3. Proportion of visits by different hummingbird species at feeders of 20 and 33% sugar concentration. Rufous-tailed Hummingbird were most common at both feeder types, while there was a larger proportion of Violet Sabrewings, Striped-tailed Hummingbirds, and Steely-vented Hummingbirds at the 20% feeder.



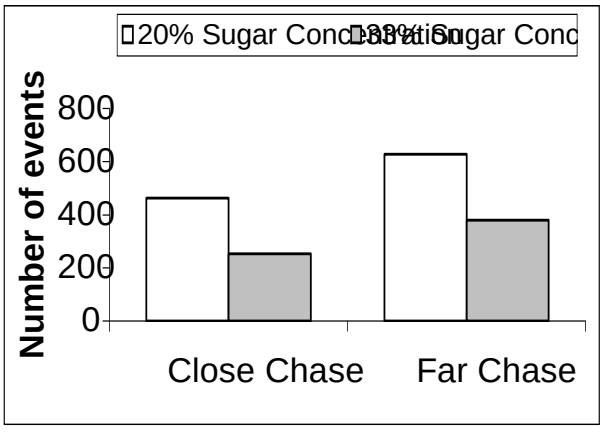



Figure 4. The mean number of hummingbird visits per time interval (one hour) to feeders of 20 and 33 % sugar concentration (± SE). There was a significant difference in the mean number of visits to feeders of different sugar concentrations. (T-test, $t = -3.55$, $p < 0.001$, $n = 60$, d.f. = 58).

Figure 5. A comparison of number of close and far chases at feeders of 20 and 33 % sugar concentrations. There was not a significant difference in close versus far chases at feeders of different sugar concentrations. (Chi-square test: $\chi^2 = 0.93$, p-value = 0.33, n = 1725).

We observed 463 and 254 "close chases" for 20 and 33% sugar concentrations, respectively. There were 628 and 380 "far chases" observed at 20 and 33% sugar concentrations recorded (Figure 5). The frequency of close and far chases at feeders of low and high sugar concentrations was not different than random (chi-square goodness of fit test, $\chi^2 = 0.93$, p-value = 0.33, n = 1725).

## DISCUSSION

Our first hypothesis was that the feeders with higher sugar concentrations, and therefore higher caloric rewards, would have more visits than the lower reward feeder. We found that the opposite was true, in that there were more visits to the lower reward feeder. There were more visits by Rufous-tailed Hummingbirds than other species at both types of feeders, but they were proportionately more abundant at the 33% feeders. We think optimal foraging theory supports our results. Optimal foraging theory suggests that pressures from high densities of a dominant species may cause a subordinate species to avoid higher reward resources and only feed in low reward areas (Pimm et al. 1985, Tiebout 1993). Subordinate species may perceive the lower reward as more beneficial and avoid increased aggressive interactions with the dominant species at the higher reward feeders. This could be an explanation for the lack of diversity at the feeders with higher sugar concentration.

We predicted that, given the option of different sugar levels, there would be a difference in the number of aggressive interactions at low and high sugar concentration feeders. Our study found, contrary to what we hypothesized, that there was a higher frequency of chase interactions at the feeders with 20% sugar concentration than at the higher reward feeders. This could be explained by the possibility that Rufous-tailed Hummingbirds at the 33% sugar concentration feeders are more aggressive and do not allow other individuals access to the resource and hence chase interactions could not be observed. Also, the territorial hummingbirds were often perched nearby, allowing them to readily defend the feeder. Many interactions at the feeders with 20% sugar concentrations involved chases by species other than the Rufous-tailed Hummingbird. This could signify that Rufous-tails at lower reward feeders were not as efficient at defending their territory or not as aggressive when the stakes are lower at defending their territory, allowing individuals of other species to use or defend the resource. These results are also predicted by the optimal foraging theory (Lawlor and Maynard Smith 1976).

We predicted that there would be a higher frequency of far chases than close chases at the higher reward feeder, because it would be beneficial to defend the resource before intruders had a chance to steal the nectar. Our analysis showed that, although there was higher frequency of far chases at the 33% concentration feeder, they were not different from random. Perhaps this could be due to dominant individuals' desire to save energy and remain close to the resource, thereby avoiding theft of the resource during a far chase.

A previous study states that the Steely-vented Hummingbird is territorially aggressive (Young and McDonald 2000), but in our study it took a subordinate role. This subordinate role is probably due to its smaller size relative to other species at our study site. Many times, a territorial bird's decision to defend can be based on the size of the intruder (Dearbor 1998). In our study, the Steely-vented Hummingbird was the smallest species of visitor, thereby severely limiting its ability to defend against other species and giving it a subordinate role in the community.

Previous studies in the Monteverde area focused on territoriality and aggressiveness of hummingbirds. Matheson (2004) found Rufous-tailed Hummingbirds to be the most dominant species in the area, supporting our results that the Rufous-tail was the most aggressive species. The Rufous-tail was the largest territorial species at our study site, giving it an advantage over the other species. Another study reported that the Violet Sabrewing was one of the most aggressive species observed (French 1992). Although this study contradicts our findings, French did not compare aggressiveness between sexes, and only females were observed at our study site. Our results did agree with published accounts of the Violet Sabrewing; that Violet Sabrewings are typically high reward trapliners (Stiles and Skutch 1989, Fogden and Fogden 2005). They were also the least frequent visitor at both 20 and 33% feeders.

One suggestion for future studies could be to measure sugar concentrations by weight instead of volume intially. This would make it easier to compare results with many published articles. Another suggestion is to count far away chases from the beginning of data collection. During our data collection, the identities of species involved in far chases were not recorded. Having this information would make it possible to test at what frequency subordinate species attempt to approach the resource and would be beneficial to future studies. A more pronounced difference in sugar concentrations can be used to determine tendencies in territoriality of resident hummingbird species.

There are several follow-up projects appropriate for the Cañitas area. The topography in Cañitas, as well as throughout the Monteverde region, has strong elevational gradients. At a nearby location, which was more open than our study area, several other hummingbird species were observed, including Plain-capped Starthroats (*Heliomaster constantii*), Coppery-headed Emeralds (*Elvira cupreiceps*), and male Violet Sabrewings as well as all species observed at our study site. This location was less than 300 m away from the study site and only slightly lower in elevation, yet had a different hummingbird community composition. A future study could attempt to determine differences in habitat quality and preferences of local hummingbird species at these locations.

## Acknowledgements

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