Interspecific aggressive behaviors in hummingbird species depending on flower diversity and the level of human disturbance.

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Abstract

Hummingbirds exhibit intense competition for nectar resources, often engaging in aggressive behaviors to defend foraging territories. This study investigated inter- and intraspecific aggression in hummingbird communities at Cloudbridge Nature Reserve, Costa Rica, with a focus on the influence of floral diversity, site disturbance, species identity, and environmental variables such as altitude. Using all-occurrence behavioral observations across 16 sites. Our results showed that while species diversity remained similar across sites, it varied significantly with disturbance levels, pointing to a complex relationship between human activity and hummingbird presence. The most aggressive species were the Snowy-bellied Hummingbird, Violet Sabrewing, and White-throated Mountain-gem. Aggression given depended on species identity but not on flower diversity, weather, sex, or altitude, whereas aggression received increased with altitude, highlighting the role of elevation in competitive dynamics.

Introduction

The hummingbird family (*Trochilidae*) is known to have developed highly unusual abilities in feeding and aerial techniques compared to other bird families. They are small-sized, vividly colored avian species characterized by a rapid hovering flight, which demands substantial energy derived primarily from the nectar they consume (Lotz et al., 2003; Schuchmann, 1999; Rico-Guevara et al., 2021).

Having co-evolved with nectar-producing plants, the 366 extant hummingbird species interact with approximately 7,000 plant species, forming a mutualistic relationship in which they depend on floral nectar to sustain their high metabolic rates, while the plants rely on hummingbirds for pollination (Barreto et al., 2024). This intense energy demand has driven the evolution of advanced spatial memory, enabling hummingbirds to

efficiently recall the location and availability of optimal foraging resources (González-Gómez & Vásquez, 2006; González-Gómez et al., 2011; Tamm & Gass, 1986).

This results in high levels of competition with other pollinators species and specifically intraspecific and interspecific competition between hummingbirds. When entering a feeding territory, hummingbirds define territory and start to feed and will show aggressive behaviors against other hummingbirds coming into their territory, a behavior unusual among birds (Colwell, 1973; Mcguire, 2014; Stiles & Wolf, 1970; Simpson & Richard, 2017).

While competition-derived aggression is a well-documented phenomenon in hummingbirds, underlying factors influencing these behaviors remain poorly understood. One potential factor is the abundance of floral resources, meaning the amount of flowers that are found in one site. Previous studies have produced conflicting results: Florowski et al. (2015) found that aggressive interactions (measured as chases per visit) were more frequent in low-resource sites compared to intermediate- and high-resource sites. In contrast, Rousseau (2014) observed heightened competition in areas with intermediate resource abundance, suggesting a non-linear relationship between resource availability and aggression.

In addition to resource availability, human disturbance may also play a role in shaping aggressive interactions. Jackson (2023) reported that hummingbirds showed a preference for feeding at sites with human activity, which could influence competitive interactions. However, this preference may not be exclusively attributed to human presence, as these sites often share the common characteristic of a high abundance of flowers. Studying the effect of flower abundance regardless of the disturbance of the sites would then be interesting.

Another key factor that may contribute to aggression is population density. The number of individuals present at a site could influence competitive dynamics, with higher densities potentially leading to increased aggressive interactions. Although Rousseau (2014) showed that the number of competitors significantly influenced resource monopolization, with increased competition leading to lower monopolization rates, the relationship between population density and aggression has not been extensively studied in hummingbirds.

The cloud forest of Costa Rica provides an ideal setting for studying

hummingbird behavior due to its high floral and avian diversity. Costa Rica is home to 53 of the world's hummingbird species, making it a biodiversity hotspot for this group (Borgella et al., 2001). The rich variety of flowering plants in these forests offers a unique opportunity to examine how resource availability and competition shape hummingbird interactions. By conducting research in this environment, we can gain valuable insights into the ecological and behavioral dynamics of hummingbirds in a highly diverse ecosystem. A previous study has been done in the Cloudbridge Nature Reserve (Jackson, 2023), focusing on the foraging behavior of hummingbirds. This project will be studying aggressive behaviors in hummingbirds, taking into account flower diversity and the number of individuals present at each observation site.

Some species of hummingbirds are known to be more aggressive than other species (Colwell, 1973; Stiles and Wolf, 1970; Stiles et al., 1990). Male hummingbirds are notably more aggressive, often driving away any intruders that threaten their food sources, including other hummingbirds and even nectar-feeding insects (Pitelka 1942; Stiles & Wolf 1970).

Floral richness and diversity are key indicators of hummingbird abundance, as they provide essential nectar resources that sustain populations (Barney, 2019). Areas with greater plant diversity may support higher hummingbird numbers by offering a continuous and varied nectar supply.

The main objective of this study is then to investigate the dominance hierarchy and abundance of hummingbird species in relation to aggression levels and floral diversity.

This study has three specific objectives. First, it aims to identify which hummingbird species display the highest levels of aggression and which ones are most frequently targeted by aggression. Second, it examines the relationship between the levels of human disturbance and hummingbird abundance on a local scale. Lastly, it explores how different factors such as the altitude impact aggressive interactions among hummingbird species.

Material & methods

1. Study area

This study has been conducted in Cloudbridge Nature Reserve in San Gerardo de Rivas, Costa Rica. This reserve covers approximately 300 hectares of a cloud forest with altitude varying from 1500 to 2600m and temperatures varying between 13,4°C and 24,1°C. It is home to thousands of species of tropical animals and plants. Among them, above 300 species of birds and specifically 53 species of hummingbirds can be found (Borgella et al., 2001). Sixteen sites located on the trails and gardens of the reserve were chosen for this study (Table 2, Fig.1). They were selected based on pre-surveys as locations where hummingbirds were observed feeding on flowers. The site *Rio 2* (Table 1) had to be replaced by *Sentinel* (Table 2) as it had lost all its flowers and hummingbirds were not seen there anymore. Each site has been observed four to six times, depending on different pressures such as the weather and the lack of time to do all observations.

Eight of the sixteen sites are located in human-disturbed places, where there are mostly planted flower species (the gardens of the nature reserve as well as a close garden "*jardin de colibris*" / "hummingbird garden") and eight are in the trails of the nature reserve, where the vegetation is natural.

Table 1: Initial study sites

Sites	**In human-disturbed places**	**In undisturbed places**
	Bird garden	Rio 1
	Memorial garden	***Rio 2***
	Lab site	Waterfall 1
	Classroom site	Waterfall 2
	Visitor car park	Don Victor 1
	Casita Blanca	Don Victor 2
	Welcome Center	Don Victor 3
	Welcome sign	Don Victor / principal

Table 2: Updated study sites

Sites	**In human-disturbed places**	**In undisturbed places**
	Bird garden	Rio 1
	Memorial garden	***Sentinel***
	Lab site	Waterfall 1
	Classroom site	Waterfall 2
	Visitor car park	Don Victor 1
	Casita Blanca	Don Victor 2
	Welcome Center	Don Victor 3
	Welcome sign	Don Victor / principal

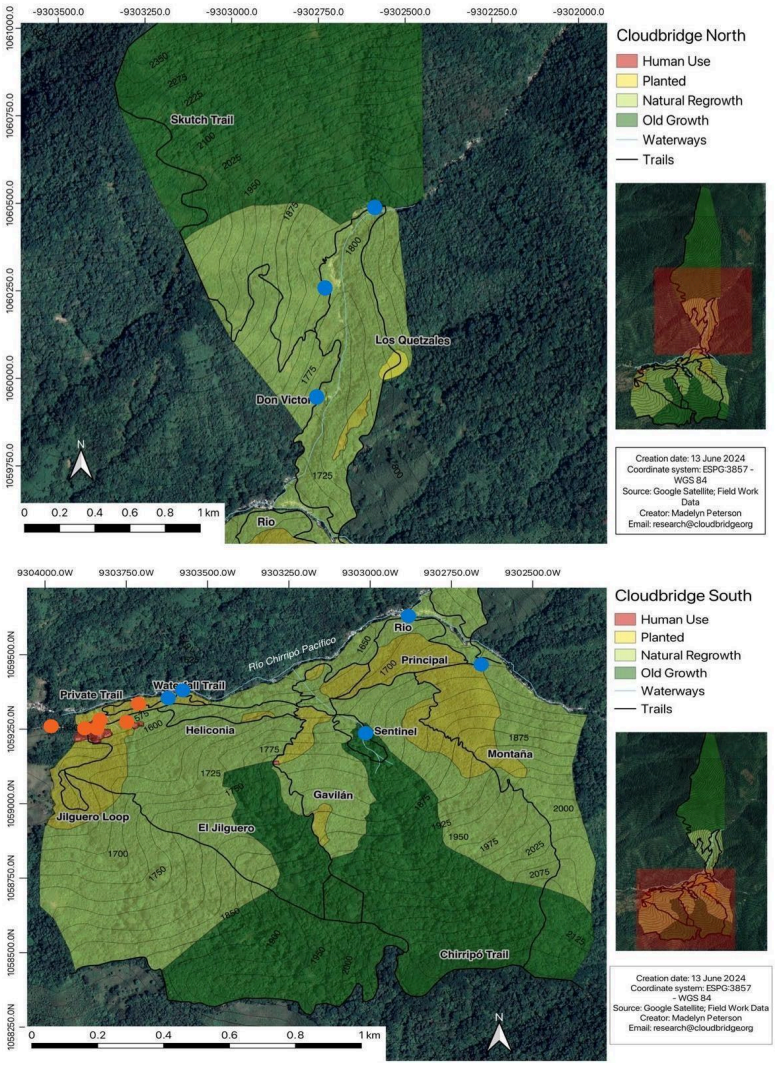

Fig 1: Maps of the updated study sites

2. Behavioral observations

The method used to study hummingbird aggression is an all-occurrence behavioral study, where all observed behaviors (Table 3) and the species performing them are recorded and counted at one site (point counts) over the course of 30 minutes. Four sites are observed each day between 7 and 10.30 am. To prevent biased data, the days the sites were observed was chosen randomly each week and the starting site of the trail changes every week as well.

Aside from the behaviors, other parameters were recorded at the different sites: the species of the hummingbirds observed, the sex of the individual when this one could be identified, the flower diversity (calculated as the amount of different flower species found at one site) and the altitude of the site. The species recorded were also classified by size to construct the SNA.

Table 3: Hummingbird's ethogram (based on Jackson, 2023)

Perching	Sitting stationary (can include scanning local environment)
Feeding	Feeding on nectar from flowers while hovering or perching
Catching insects	Rapid erratic flight in pursuit of insects as alternative food source or to remove from territory
Defending territory	Aggressive behavior to remove other individuals/species from a feeding territory
Being chased	Fleeing territory while being pursued by another individual
Locomotion flying	Flying through a site with no interaction with feeding flowers or other birds (can include vocalizing)

3. Statistical analysis

To analyze the data, Kruskal-Wallis tests were conducted to assess differences in hummingbird species diversity. Additionally, generalized linear mixed models (GLMMs) with a Poisson distribution were employed using R Studio to investigate the factors influencing both the frequency of aggressive behaviors initiated and those received. Predictor variables included hummingbird species,

category of sites and altitude of the sites. All plots were generated using the "ggplot" function in R. The observations were corrected for the times each site has been observed as not all of them were observed for the same amount of time.

Results

1. *Hummingbirds diversity*

Overall, 14 species of hummingbirds and 221 individuals have been encountered in the course of all surveys (Fig.2). The most encountered species was the white-throated mountain-gem (*Lampornis castaneoventris*, 35 individuals) and 64 individuals have been unidentified.

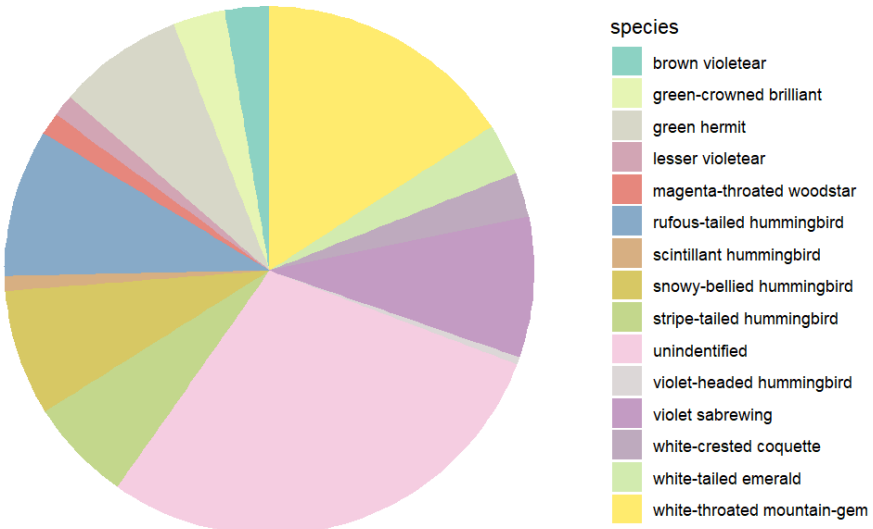

Fig.2:
Hummingbird's species distribution among all surveys.

The number of hummingbird species was unequally distributed per site (Fig.3). There were the most hummingbirds in the site "bird garden" than in any other site. This site was also the one with the most species between the more disturbed sites and the site waterfall 2 had the most species among the less-disturbed sites (Fig.3). However, there are no significant differences in the hummingbird diversity per site (df = 15, p-value = 0.4514, Fig.3). There was significant differences between the hummingbirds' diversity per category of sites (df = 1, p-value = 0.02282, Fig.4).

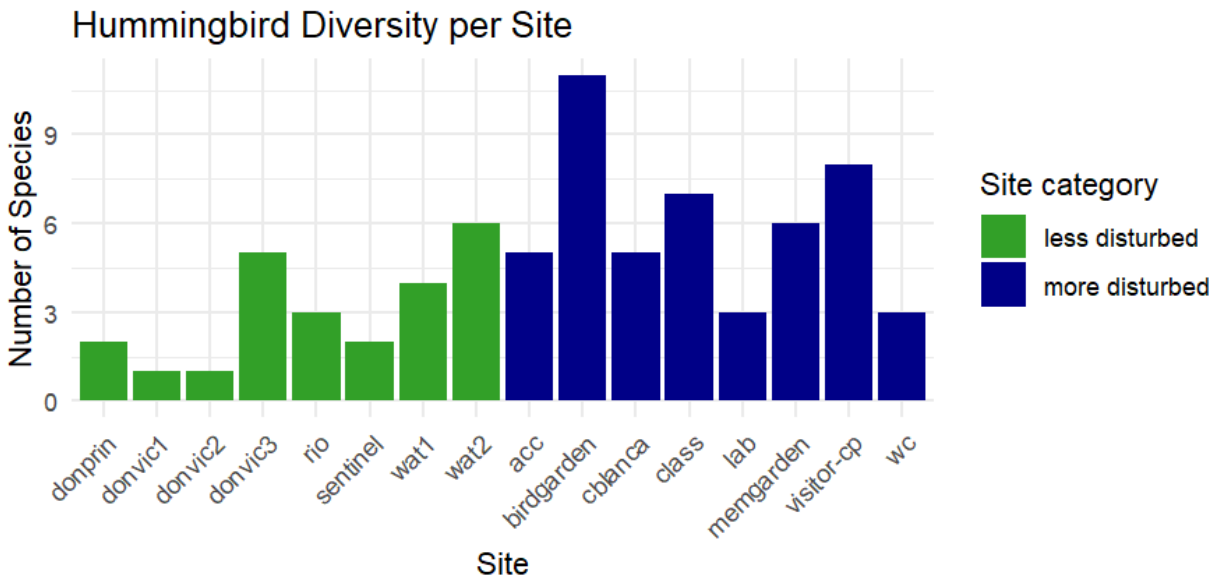

Fig.3: Hummingbirds diversity per site

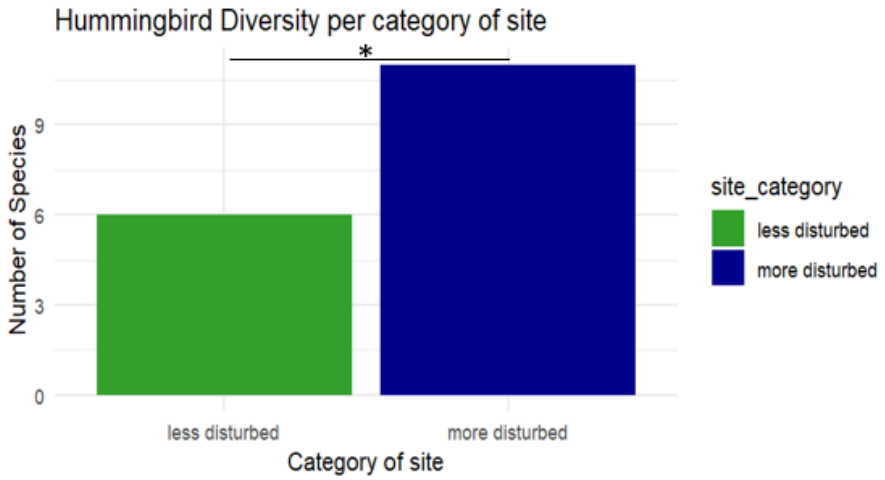

Fig.4: Hummingbirds diversity per category of site

2. *Aggressivity in hummingbirds*

- Social Network Analysis (SNA):

The Social Network Analysis (Fig.5) shows that the rufous-tailed hummingbird (*Amazilia tzacatl*) is highly central and dominant as it has many outgoing arrows, interacts with multiple species and thick edges connecting that suggest frequent aggressive interactions. Unidentified individuals also show connectivity, indicating important but unclassified individuals in the aggressivity network. Three species have not engaged in any aggressive or noticeable interactions during the observation period: the magenta-throated woodstar (*Philodice bryantae)*, the scintillant hummingbird (*Selasphorus scintilla*) and the violet-headed hummingbird (*Klais guimeti)*.

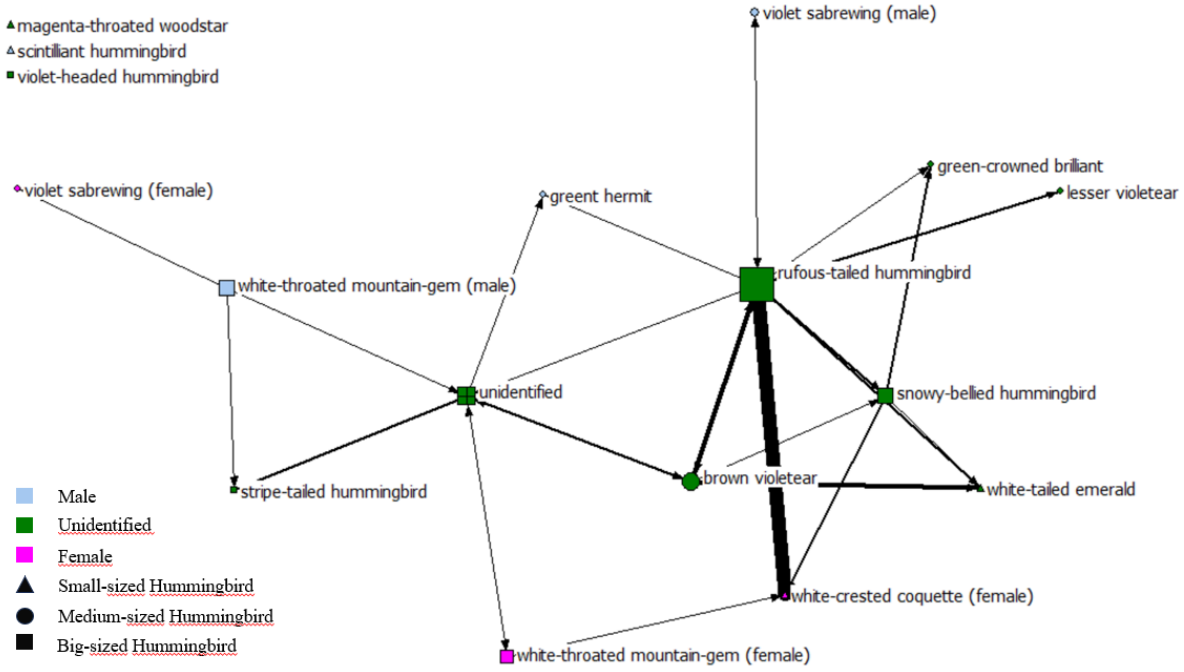

Fig. 5: Social network analysis of the aggression interaction between the hummingbirds species.

- *Aggression given:*

The quantity of aggression given differed significantly depending on the species of the hummingbirds ($p = 1.23e-05$, Table 3) did not differ significantly depending on the flower diversity in the different sites, the altitude and the sex of individuals (Table 3). There was no correlation between the different numeric variables in the model (Fig. 6).

Table 3: Results of the drop1 test on the model of aggression given.

	Df	AIC	P-value
Altitude	1	278.62	0.14719
Flower diversity	1	279.66	0.07628
Weather	3	275.46	0.40083
Sex	3	273.73	0.75048
Bird species	14	298.70	1.23e-05***

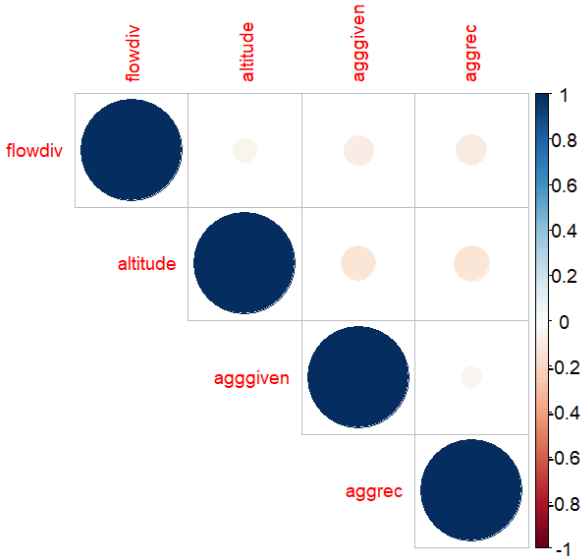

Fig. 6: Correlation matrix between the variables ("flowdiv" = flower diversity, "agggiven" = the amount of aggression given, "aggrec" = the amount of aggression received). The scale represents the correlation coefficients going from -1 (perfect negative correlation) and +1 (perfect positive correlation).

The model containing the species of hummingbirds (AIC = 275.7111) was a better fit than the null model (AIC = 320.0435) and the species *Saucerottia edward* (snowy-bellied hummingbird, p= 0.013852), *Campylopterus hemileucurus* (violet sabrewing, p = 0.001625) and *Lampornis castaneoventris* (white-throated mountain-gem, p = 8.93e-05) had a significant impact on the amount of aggression given.

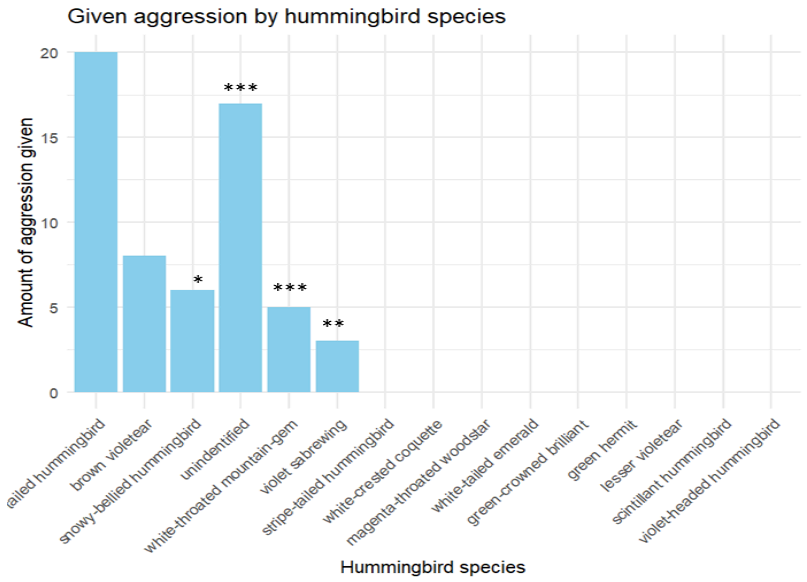

Fig. 7: Amount of aggression given by the different hummingbirds species (x = The species of hummingbirds, y = the amount of aggression given (counts)).

- *Aggression received:*

The altitude had an effect on the amount of aggression a hummingbird individual received (p = 0.01885, Table 4). Altitude appears to influence hummingbird behavior, with the level of aggression received varying across species. For instance, aggression decreased at higher altitudes for species like the snowy-bellied hummingbird and unidentified individuals, while it increased for others such as the violet sabrewing and white-throated mountain-gem (Fig. 8).

	Df	AIC	P-value
Altitude	1	294.30	0.01855*
Flower diversity	1	291.08	0.12981
Weather	3	287.68	0.40796
Sex	3	289.37	0.20430
Bird species	14	283.70	0.10377

Table 4: Results of the drop1 test on the model of aggression received.

However, the model containing both “altitude” and “birdspecies” was a better fit (AIC = 287.5963) than the full model (AIC = 290.7821), the model only containing altitude (AIC = 294.6941) and the null model (AIC = 300.1477).

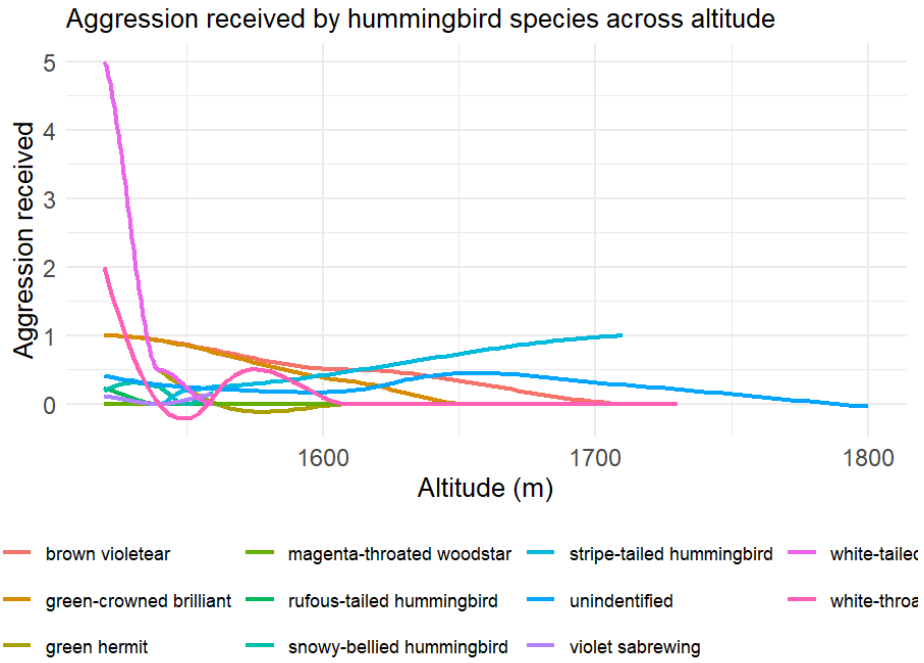

Fig. 8: Aggression received by hummingbird species across altitude (x = altitude (m) and y = the amount of aggression received by species of hummingbirds).

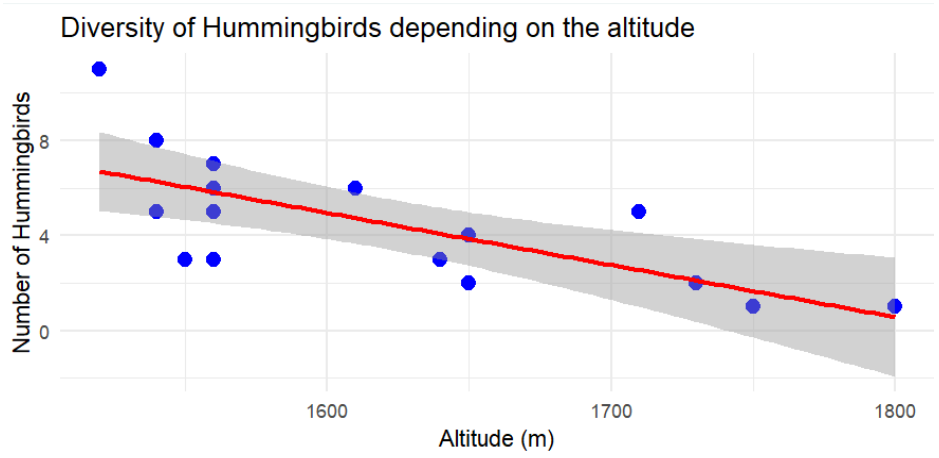

Fig. 9: Amount of Hummingbirds depending on the altitude (m).

Discussion

1. Hummingbirds' diversity

No difference was seen in hummingbirds species' diversity across sites. However, there was a difference in diversity across categories of sites (Fig.4). Hummingbirds are likely more accustomed to human presence in areas with frequent human activity, and therefore may exhibit reduced fear in the presence of observers. However, in some cases, the opposite is true ; species can be less inclined to stay in undisturbed, natural feeding sites or territories when exposed to human presence (Mendiola-Islas et al., 2023). The lack of diversity difference across sites may also be attributed to species turnover, as certain species are exclusive to less-disturbed sites (scintillant hummingbird (*Selasphorus scintilla)*), while others are found only in more-disturbed areas (rufous-tailed hummingbird (*Amazilia tzacatl*)) and some in both (green hermit, violet sabrewing (*Campylopterus hemileucurus*), white-throated mountain-gem (*Lampornis castaneoventris*)).

While factors like flower richness and canopy cover would offer valuable insights into hummingbird diversity, they were beyond the scope of this particular study.

2. Aggression in hummingbirds

a) Social Network Analysis

The rufous-tailed hummingbird has proven to be the most aggressive species when counting the total amount of aggressive interaction (Fig.5). The absence of aggressive interactions involving the three missing species may be attributed to several factors. The main hypothesis would be that this is due to shy or subordinate behaviors; these hummingbirds might avoid confrontations or areas dominated by more aggressive species. However, the main reasons are that these hummingbirds have only been observed sporadically (one time for the violet-headed hummingbird, twice for the magenta-throated woodstar) or in sites where there were fewer overall species observed in the first place. That was the case for the scintillant hummingbird, who was always observed alone and in a single site ("sentinel").

b) Aggression given

Contrary to what was expected , flower diversity—defined as the number of different flower species at a site—did not significantly influence hummingbird aggressivity levels (Table 3). This suggests that hummingbird territorial behavior may be more strongly driven by the quantity or density of nectar resources rather than species richness alone. Sites with high flower species diversity can still exhibit low nectar availability, reducing the incentive for territorial defense. Moreover, changes in floral resource availability may alter the dominance hierarchy among Hummingbirds, indicating a potential avenue for future research (Márquez-Luna et al., 2019). Preferences for specific floral resources may be influenced by floral traits such as display size (e.g., number of flowers per plant or inflorescence), corolla shape and color, and nectar attributes like volume and sugar concentration (Meléndez-Ackerman et al. 1997).

Some hummingbird species, such as the rufous-tailed hummingbird, are known to defend nectar-rich patches regardless of floral diversity. This suggests that environmental factors like canopy cover, number of flowers, flower height, and site openness may play a more critical role in shaping aggressive interactions by influencing resource visibility, defensibility, and ease of movement. Notably, the snowy-bellied hummingbird, violet sabrewing, and white-throated mountain-gem were the primary contributors to aggressive behavior (Fig.7), acting as frequent initiators of aggressive encounters. This finding is somewhat unexpected, as the rufous-tailed hummingbird —widely regarded as highly territorial—did not rank among the most aggressive species in this context (Fig.7), despite predictions based on previous observations and the SNA (Fig. 5). Consistent with prior studies, the Violet Sabrewing was identified as the most aggressive species at human-disturbed sites (Mundy & Laurel, 2008; Tsay & Whitney, 2009). Similarly, the White-throated Mountain-gem has previously exhibited aggression toward White-tailed Emerald and Snowy-bellied Hummingbirds at Cloudbridge Nature Reserve, while the snowy-bellied hummingbird has been observed chasing off the Scintillant Hummingbird, the White-tailed Emerald, and the Stripe-tailed Hummingbird (Rabone & Staunton, 2015).

c) Aggression received

Hummingbird aggression is not uniformly distributed across elevations (Fig. 8), and species-specific patterns suggest that vulnerability or dominance may shift with altitude. For instance, the Snowy-bellied Hummingbird received less aggression at higher elevations, which may indicate reduced competition or the absence of dominant competitors in those environments. On the contrary, the Violet Sabrewing and White-throated Mountain-gem experienced increased aggression at higher altitudes, possibly because these species are typically more dominant at lower elevations and face stronger competition from highland-adapted species when moving upslope. These patterns align with ecological expectations that interference competition may intensify at higher elevations due to increased energetic demands and reduced resource availability (Feinsinger et al., 1979). Moreover, competition is likely to be most intense among species with similar morphologies, as they rely on overlapping nectar sources within these resource-limited habitats (Feinsinger et al., 1979). However, the amount of hummingbirds also decreased with the altitude (Fig.9) and this could explain more the decrease of aggression for concerned species more than competition issues.

3. Limits of the study

This study is conducted over a single period spanning six weeks, which is a relatively short duration for a behavioral study as it does not account for the uniform distribution of flowers throughout the entire year, nor the hummingbirds' life cycle.

Some behaviors and individuals can be missed due to observational limitations as only one observer was present for most of the surveys. Also, since the individuals are not marked, the same hummingbird could be counted more than once at a single site.

Moreover, the inability to identify some individuals resulted in missing data, which may have affected the recorded levels of aggression given and received by certain species. Individuals categorized as "unidentified"—those that could not be reliably assigned to a species—also exhibited high levels of aggression. This

suggests that some of these unidentified individuals may have belonged to dominant or highly aggressive species that went unrecognized during observations, potentially influencing the accuracy of species-specific aggression patterns. Several additional factors that were not assessed in this study could have further explained variation in aggressive behavior, including patch size, flower species composition, nectar abundance, wingspan, and overall body size of the hummingbirds. While such traits have been linked to dominance in hummingbirds in previous studies (Stiles and Wolf 1970; Dearborn 1998; López-Segoviano et al. 2017), our Social Network Analysis (SNA) suggests that larger body size does not necessarily predict dominance. In fact, other research has shown that smaller species are also capable of establishing and defending foraging territories against larger species (Wolf et al. 1976; Márquez-Luna et al.). These findings highlight the complexity of factors influencing hummingbird aggression and territoriality and point to the need for further research that integrates different factors.

Conclusion

While no significant differences in hummingbirds species composition were observed across study sites, there was significantly more hummingbird species in more disturbed sites than in less disturbed ones.

The species Snowy-bellied Hummingbird, Violet Sabrewing and White-throated Mountain-gem exhibited the highest levels of territoriality. Furthermore, altitude was identified as a significant factor influencing the frequency of aggression received by individuals. Further research is needed to explore additional ecological and social factors that may contribute to aggressive interactions in hummingbird communities.

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