Comparison of Flower Feeding Behavior of Two Neotropical Hummingbird Species

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Hummingbirds, which are largely nectarivorous, often compete for food sources with other pollinators, leading to the establishment of different foraging strategies and social dominance hierarchies. I studied hummingbird feeding behavior at Camaquiri Conservation Initiative in the Caribbean lowlands of Costa Rica. The most abundant hummingbirds at this site were Blue-chested and Rufous-tailed hummingbirds; all data I collected were from these two species. Both species frequent porterweed shrubs but have different feeding strategies—traplining and territoriality, respectively. Hummingbirds made 1,300 stops at a flower or cluster of flowers, for which I recorded 1. the duration of the stop and 2. the flower position on the plant (upper half or lower half). Feeding time varied by species: on average, Rufous-tailed Hummingbirds fed at a flower cluster for 19% longer than Blue-chested Hummingbirds. Both species of hummingbirds preferred feeding at higher flowers, and flower height did not affect feeding time for Rufous-tailed Hummingbirds, although Blue-chested Hummingbirds displayed longer feeding times at the less-visited lower flowers. These results suggest that Rufous-tailed individuals exhibit social dominance as the larger and more territorial species. Such dominance relationships may influence outcomes of interspecific competition, place species into unique ecological niches, and have broader implications for species diversity and structure in ecological communities.

COMPETITION FOR FOOD RESOURCES influences feeding behavior in ecologically similar species, such that they establish niches to obtain limited but sought-after resources (1,2). When multiple species rely on a particular resource, individuals experience competitive pressure from both conspecifics and heterospecifics (3). Dominant species have priority of access to shared resources, which can result from successful displays of aggression, such as chasing (1).

All hummingbirds are predominately nectarivorous, and thus hummingbird species occupying the same habitat will seek similar food sources and can exhibit competitive behaviors. As nectar consumers, hummingbirds also play an ecological role as pollinators. As they visit flowers to consume nectar, they pick up pollen grains that can be transferred to other plants of the same species as they forage (4). Pollinators are crucial in the reproduction of many plants, making them important in almost all terrestrial ecosystems, including tropical ecosystems that have high plant species diversity (5). An estimated 88% of angiosperms rely on animal pollinators for sexual reproduction, including approximately 70% of major global crops (6). Landscape disturbances may negatively impact the distribution and diversity of pollinators like hummingbirds, such as by increasing interspecific competition, or impede movement of pollinators, both of which can reduce pollination success (7).

Different foraging behaviors and dominance statuses—which are influenced by both individual traits and characteristics of available food sources—impact interactions between hummingbird species in competition for resources (2). Two main foraging strategies used by hummingbirds are territoriality and traplining (2). Territorial hummingbirds defend a particular group of flowers as their feeding territory, whereas trapliners visit groups of flowers following a regular and repeatable route (2).

Blue-chested Hummingbirds (*Amazilia amabilis*) inhabit forest edge areas, often foraging individually at low flowers (8). They feed on nectar by either following a circuit, like trapliners, or defending floral territories (8).

Rufous-tailed Hummingbirds (*Amazilia tzacatl*) also forage at the forest edge, solely using the territorial strategy (9). This territoriality results in aggressive behavior toward both conspecifics and other nectarivores. Rufous-tailed Hummingbirds tend to chase away birds and insects that approach the flowering plants or human-made feeders in its territory rather than tolerating the presence of other feeding individuals (9).

Rufous-tailed Hummingbirds are known to demonstrate such interspecific aggression toward Blue-chested Hummingbirds (10). Rufous-tailed Hummingbirds are larger than Blue-chested Hummingbirds, with a mean mass for males of 5.1 g and 4.1 g, respectively (10). Dearborn suggests that this may explain the subordinate role of Blue-chested Hummingbirds: they tend to flee when chased due to the potential costs associated with escalating the conflict with the larger Rufous-tailed Hummingbirds (10).

In this study, I examined the feeding behavior of these two species, particularly 1. how long the birds spent feeding at each flower cluster and 2. whether the hummingbirds preferred high versus low flowers on focal shrubs. I predicted that the more aggressive species, the Rufous-tailed Hummingbirds, would be more likely to feed at the higher flowers and would spend more time at each cluster than the Blue-chested Hummingbirds, because their status as the dominant species would afford them the opportunity to feed more openly and without risk of being chased by the less dominant species.

METHODS

STUDY SITE AND SPECIES: I conducted this study at the Camaquiri Conservation Initiative (CCI), in the La Rita district, Pococí County, Limón Province, Costa Rica. Data collection took place 7-9 January 2020. The most abundant species of hummingbird I observed here were Blue-chested Hummingbirds, which I identified by their straight, black bills and bronze tails, males' bright blue chests, and females' whiter chests with iridescent blue spots, and Rufous-tailed Hummingbirds, which I identified by their green chests, rufous-colored tails, and reddish beaks with black tips. I observed Bronze-tailed Plumeleteers (*Chalybura urochrysia*) on a few occasions, but this was by far the least common of the three observed species; I therefore did not include them in this study.

Almost every observation of hummingbird feeding behavior took place at blue porterweed (*Stachytarpheta frantzii*) or pink porterweed (*S. mutabilis*) shrubs, except for two samples in which a Blue-chested Hummingbird fed at an orange heliconia flower.

OBSERVATIONAL STUDY: To observe hummingbird feeding behavior, I stood ~ 5 - 10 m away from a patch of porterweed shrubs, such that I could quickly identify hummingbird movement without disturbing their normal feeding behavior. Upon identifying the presence of a hummingbird feeding at a flower cluster, I started a voice recording using the function on my cell phone to note the start and stop point of the hummingbird's feeding at each cluster. To indicate the start, I said "high" or "low," depending on whether the flower cluster was within the uppermost 50% of flowers on the shrub, or closer to the ground, in the lower 50%. I said "stop" as soon as the bird left this flower cluster. I repeated this process—noting "high" or "low" to mark the start and noting "stop" to mark the end of the feeding visit—for all stops at flower clusters. I followed the hummingbird so that it remained in my line of sight as it moved to different shrubs, while continuing to remain ≥ 5 m from the subject hummingbird such that I could make accurate observations without causing the birds to flee or stop feeding due to my presence. I ended a sample after the bird flew out of sight or into a tree. I used binoculars when necessary to confirm species identification. I recorded stops throughout various periods of time in the morning, afternoon, and at dusk, when the birds appeared to be most active. I collected data during sunny, cloudy, and light rain conditions, but not during periods of heavy rain, during which hummingbird activity greatly declined. The 3-day study period yielded 62 samples for Blue-chested Hummingbirds and 38 samples for Rufous-tailed Hummingbirds.

DATA ANALYSIS: I scored recordings using a stopwatch to obtain the time in seconds spent at each flower cluster, going through each recording two or more times to ensure accurate scoring. I noted species and whether each stop was "high" or "low" for each time recorded. I tested for relationships between species, flower position, and time spent feeding at each cluster using JMP v14. I used a nonparametric Wilcoxon test to analyze the relationship between feeding times and species because the data did not follow a normal distribution: the data for each species had a right skew due to there being a wide range of longer stops, while I was unable to record stops shorter than 0.4 s.

RESULTS

FEEDING TIME AND SPECIES: I collected data from 867 Blue-chested Hummingbird flower cluster visits over the 62 samples, and 433 Rufous-tailed Hummingbird visits over the 38 samples. The length of a stop at a flower cluster was 18.6% higher for Rufous-tailed over Blue-chested Hummingbirds (Fig. 1; Wilcoxon $Z = 7.305$, $p < 0.0001$).

FEEDING TIME BY SPECIES AND FLOWER POSITION: There was no interaction between species identity and whether the visit was at a high/low flower ($F_{1, 1296} = 3.1$, $p = 0.078$). After eliminating this interaction, species did affect feeding time (see above). Flower position (high/low) did not affect feeding time (both species combined, Fig. 1; $F_{1, 1297} = 0.12$, $p = 0.27$).

FEEDING TIME AND FLOWER POSITION: While flower position had no effect on feeding time across both species combined, flower position did affect feeding time for Blue-chested Hummingbirds alone (Fig. 1; two-tailed $t_{865} = 2.0$, $p = 0.049$): these hummingbirds, on average, spent 7.6% more time at a single visit to a cluster of low flowers (N = 227 visits) than at a cluster of high flowers (N = 640 visits). Rufous-tailed Hummingbirds did not exhibit a comparable difference ($t_{431} = -0.75$, $p = 0.45$).

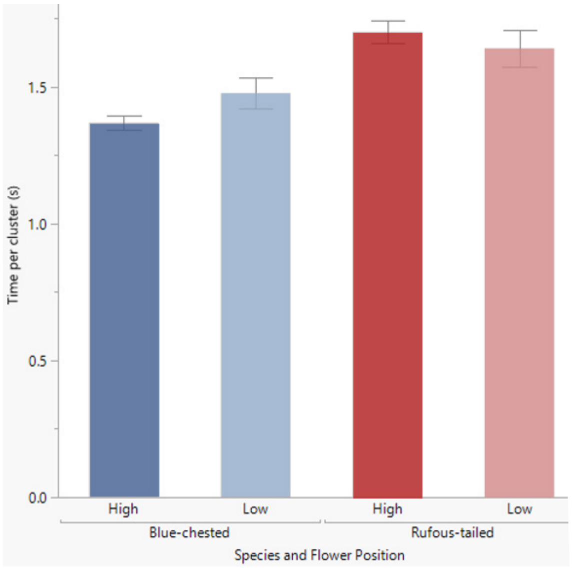

Figure 1. Mean time per cluster (± SE) for each species visiting high and low flower positions. Combining stops at high and low flowers, Rufous-tailed Hummingbirds fed at a flower cluster for longer (mean 1.7 s ± 0.034 SE) compared to Blue-chested Hummingbirds (mean 1.4 s ± 0.024 SE). Flower position has no effect on feeding time for Rufous-tailed Hummingbirds, while on average Blue-chested Hummingbirds fed for a longer amount of time at low flowers than at high flowers.

FLOWER POSITION PREFERENCE: Out of 1300 visits, birds chose the high flowers 73% of the time, differing from the 50%:50% pattern expected by chance (likelihood ratio $\chi 2 = 285.71$, df = 1, $p < 0.001$). Rufous-tailed Hummingbirds exhibited a preference toward high flowers (71.4% of visits to high and 28.6% to low flowers, N = 433 visits; likelihood ratio $\chi 2 = 81.64$, df = 1, $p < 0.001$), as did Blue-chested Hummingbirds (73.8% of visits to high and 26.2% to low flowers, N=867 visits; likelihood ratio $\chi 2 = 204.95$, df = 1, $p < 0.001$). The magnitude of preference for the higher flowers was indistinguishable between the species (likelihood ratio $\chi 2 = 0.88$, df = 1, $p = 0.35$).

DISCUSSION

FEEDING TIMES: Rufous-tailed Hummingbirds are territorial and defend a particular group of flowers as their feeding territory, while trapliners like Blue-chested Hummingbirds tend to visit groups of flowers following a regular and repeatable route (2). These different feeding strategies may cause Rufous-tailed Hummingbirds to act as the more aggressive species. During this study, both Rufous-tailed Hummingbirds and conspecifics chased Blue-chested individuals away from porterweed shrubs, while there were no instances of a Blue-chested Hummingbird chasing away a Rufous-tailed Hummingbird. While many feeding stops naturally ended when a bird flew to an adjacent flower to feed, or landed on a perch, other stops were cut short by chasing.

As the larger species, Rufous-tailed Hummingbirds are favored in the 'cost of engagement' hypothesis, which predicts that the rate of intruders being chased varies inversely with intruder body size (10). Rufous-tailed Hummingbirds face little risk in chasing Blue-chested Hummingbirds, while Blue-chested Hummingbirds may not find it energetically worthwhile to defend their feeding location against the larger and territorial dominant species. This territorial dynamic could conceivably influence the feeding times in one of two ways—either the dominant species would have shorter feeding times as they are concerned with abandoning feeding to chase away intruders, or the less dominant species would have shorter feeding times due to being chased away, or due to fear that if they stay in one spot for too long, they would be chased. In this way, territoriality could lead to reduced feeding times for either species. However, the results of this study suggest that individuals of the more dominant species, Rufous-tailed Hummingbirds, spend more time on average feeding at each flower cluster than the Blue-chested Hummingbirds, lending support to the latter hypothesis.

FLOWER POSITION: A study of hummingbirds at a flowering tree in the Guanacaste region of Costa Rica found that different feeding height preferences could lead to a partitioning of hummingbird feeding areas between species, noting that larger species of hummingbirds tend to drive out smaller species (11). The study found that of trees in bloom, hummingbirds' feeding preference was toward the taller trees (11). Another study found that hummingbirds prefer higher nectar sources, such that sucrose concentrations were not their sole concern in choosing feeding sites (12). While in my study, the porterweed shrubs and heliconia flowers visited were much smaller in height than flowering trees and poles used in the cited studies, both species exhibited a preference toward the higher flowers. Therefore, the prediction that the more aggressive and larger species (Rufous-tailed Hummingbird) would be more likely to feed at the higher flowers than the less aggressive and smaller species was not supported by the data, as both species preferred higher flowers over lower flowers. This may be due to factors such as foliage density and visibility, which affect a bird's ability to view and defend the area while feeding (11).

While, like Rufous-tailed individuals, Blue-chested Hummingbirds may prefer the higher flowers for ease of access and visibility factors, they tended to feed for longer at the lower flower clusters. This may be because at lower flowers, they are less visible to Rufous-tailed or competing Blue-chested hummingbirds and would therefore be less likely to be involved in a confrontation. In areas where visibility is obstructed, such as due to higher foliage density, intruders are more easily able to access a defended resource, which may explain this longer feeding time at lower flowers: in this case, the less dominant Blue-chested Hummingbirds may be seen as intruders in the territory of Rufous-tailed Hummingbirds (13). As the dominant species, Rufous-tailed Hummingbirds did not show differences in feeding time between high versus low flowers.

LIMITATIONS AND FUTURE DIRECTIONS: Some observation bias may be involved. For example, I may have interpreted extremely short feeding visits as a hummingbird simply flying by a flower, without stopping to feed. The shortest feeding visit I was able to record was 0.4 s ($N = 12$ flower cluster stops). There may have been shorter visits that I was not able to record, thus causing a higher average feeding time for each species.

Additionally, the large difference between observed visits at high versus low flowers across the 1300 total flower visits (73% high, 27% low) may be influenced by visibility constraints. In most cases I was able to see hummingbirds on any side of a shrub when they were feeding in the top 50% of flowers due to low leaf density. It was difficult to see hummingbirds on the side of the shrub opposite the observer when they fed at the lower 50%. While I tried to move my observation position to account for this and record as many feeding stops as possible, there may have been more stops that I missed at low flowers than at high flowers.

Rico-Guevara and Mickley (14) note that observing animal behavior can be difficult due to human sensory limitations and time intensiveness of certain ecological studies, and that a system of high-speed video cameras proved helpful in observing fast movements of hummingbirds. Therefore, a potential improvement to address the issues of observation bias in this study could be to film using cameras and score footage to determine stop length and flower position. Cameras could be set up on all sides of the shrubs of interest such that there would be no observation bias for flower position. Further, footage could be slowed down to check for stops of < 0.4 s. Another possibility is to have multiple observers, mirroring each other on either side of a patch of shrubs, to ensure low stops are not missed.

A further limitation was the inability to identify hummingbirds as individuals, so feeding behavior could only be analyzed on a species level. Thus, this study did not account for potential differences in feeding behavior or levels of dominance between individuals of the same species, or account for factors such as age and sex. It is also uncertain how many individuals of each of the two species contributed toward the data for all flower stops.

Because I did not identify hummingbirds as individuals, I cannot determine whether the notable difference in sample sizes between the two hummingbird species (867 Blue-chested Hummingbird flower cluster visits over 62 samples, and 433 Rufous-tailed Hummingbird visits over 38 samples) reflects abundance differences between the species in the study area. However, it is possible that there were fewer Rufous-tailed Hummingbirds in the study area because of their highly territorial nature: they may defend more strictly defined territories with less overlap between conspecifics (9).

Another factor I noted is that the Rufous-tailed individuals appeared to be more strongly defensive of flowers on one side of the path, while Blue-chested Hummingbirds preferred the shrubs that the Rufous-tailed Hummingbirds visited on a less frequent basis. Future studies looking into social interactions and quantifying territorial behavior could help to further explain the results obtained in this study. Analysis of the effects of weather and time of day on feeding behavior and territoriality could be another worthwhile future direction.

This study of feeding behavior in species using the same flowers as their primary energy source can have broader implications in examining interspecific competition, which can affect species diversity in an ecological community (15). Examining competition becomes increasingly relevant; habitat loss and fragmentation are ongoing phenomena that have the potential to push species together that otherwise would not be sharing or competing for certain resources (16). Deforestation and its consequences for pollinator species diversity and competition can have broader effects on an ecosystem by impacting plant species reliant on animal pollination. For example, deforestation and landscape changes are known to influence hummingbird movement patterns, and can therefore impact pollen movement (7).

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Dr. Robert Curry is a Professor in Villanova's Department of Biology (Ph.D. Michigan, 1987). Since 1991, he has taught courses on ecology, conservation biology, animal behavior, and tropical ecology, as well as a genealogy course for non-science majors. His research focuses on behavioral and evolutionary ecology, especially regarding hybridization in chickadees (songbirds). Other studies concern a uniquely herbivorous spider and island-endemic Neotropical birds. Dr. Curry has served as President of the Wilson Ornithological Society and on the Ornithological Council's Board of Directors. In 2019, he received Villanova's Outstanding Faculty Mentor Teaching Award and the Wilson Society's Margaret Morse Nice Medal.

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