Hummingbird Foraging Flight and Energy Usage:

A Study of Flight Forms and Time Allocation on the Island of Dominica

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Abstract

Hummingbird flight morphology and energetics is a topic of interest for many scientists yet the allocation of time between forms of flight is little studied. This study attempts to find possible connections or trends between hummingbird species and time allocations during feeding. The study took place on the island of Dominica and focused on the Green-throated Carib, Purple-throated Carib, and Antillean Crested Hummingbird, with additional observations on the non-hummingbird nectar feeding Bananaquit. I expected to find that all hummingbird species would allocate more time to hovering and linear flight than perching as a side effect of their territorial behavior. The data from the Green-throated Carib and Antillean Crested Hummingbird supported this hypothesis but the Purple-throated Carib spent more time perching and hovering than in linear flight. I also expected to find that the larger the species, the more time would be allocated to hovering. The data did not support this hypothesis and, in fact, suggested the opposite was true.

Introduction

Many studies have been conducted concerning hummingbird flight and morphology. This is due to the Trochilidae family's unique ability among avian fauna to hover (Altshuler and Dudley 2002). While this skill is common among insects, no other vertebrate of such a size has this ability. One long studied aspect of interest in hummingbird locomotion is the vast amount of energy necessary for hovering flight (Eduardo 1998). As altitude increases, the air density, oxygen partial pressure, and air temperature all decrease making flight very energetically demanding at high elevations (Altshuler and Dudley 2002). Therefore, hovering is also one of the most energetically expensive types of all animal movement (Altshuler et al. 2004). While the

mechanisms for hummingbird energy production and consumption have often been explored, the differences in energy usage among hummingbird species are rarely studied. This study attempts to compare the flight time allocation, and therefore energy usage, of 3 common Dominican hummingbird species, the Green-throated Carib (*Eulampis holosericeus*), the Purple-throated Carib (*Eulampis jugularis*), and the Antillean Crested Hummingbird (*Orthorhyncus cristatus*), as well as another common nectar feeder, the Bananaquit (*Coereba flaveola*) (James 2005). Knowing that hovering is generally more energetically expensive than linear flight and perching is less expensive, the time each bird (or species) allocates to each of these forms of flight can be used to determine how their energy is likely being utilized.

The island of Dominica presents a sufficient location for such a comparative study because of its concentration of multiple Trochilidae species in one habitat (James 2005). Since these species compete within the same environment, they must also operate under the same situational requirements. Dominica also provides a particularly unaltered site including little human interference with the hummingbirds because they have been protected by Dominican law since the 1914 Wild Birds Ordinance (James 2005). The edge of the veranda at the Archbold Tropical Research and Education Center in Springfield, Dominica proved to be a suitable location with a previously hung chain providing a place to hang the feeders and the presence of nearby plants that were observed to be frequented by hummingbirds, including *Morinda citrifolia* from the Rubiaceae family.

Methods and Materials

The most important materials required for this study were two First Nature 16 oz. hummingbird feeders, a water source, and sugar. The hummingbird feeders needed to be identical in model and

include perches. Any water source would do as long as it was freshwater and met drinking standards. Any type of white sugar was acceptable and a general amount of 3 grams was used, though extra was recommended in case of miscalculation or incident. Other necessary items included: a water boiling device, a 250 mL measuring cylinder, two 4-liter plastic pitchers, a 100 mm funnel, masking tape, a permanent marker, 20 lb. monofilament fishing line and scissors (or hooks) for hanging, an Atago 0~32% Refractometer, a Cronus Pro Survivor stopwatch, a watch (or second stopwatch), a Canon XL1 Digital Video Camcorder with 16x Zoom Lens and Stereo microphone, tripod, and miniDV cassette tape.

For the sugar water mixtures, a liter of water was brought to boil for each concentration then poured into one of the two pitchers. Next, a measured amount of 500 mL sugar was added to one container and stirred until it was dissolved. A measured amount of 400 mL was added and dissolved into the second container. Another liter of cold water was then added to each concentration to speed up the cooling process and create the desired concentrations. Using the masking tape and marker, the two feeders were labeled “1/5” and “1/6” for their respective concentrations. Once room temperature, the mixtures were poured into their previously labeled feeders using a funnel to minimize loss. A refractometer was used to verify the actual concentrations which were approximately 18.7% and 15.2%.

As soon as the feeders were fully assembled, they were hung about 0.5-1.0 meters apart in an open area along the veranda wall that allowed for plenty of light and the opportunity to videotape or personally observe the hummingbirds without interfering in the collected data.

Figure 1: Photo of Feeder Placement

For the data sheets, a simple chart was created in Excel. The date, location, and weather conditions for each day were recorded at the top of the chart. For each instance of hummingbird or Bananaquit attendance at the feeders, the time of day, feeder(s) visited, species present, flight times, and any general notes were recorded. The flight times were separated into four categories: hovering flight, linear flight, perching (no flight), and total flight time.

On the first day, a surveyor sat nearby with a data sheet and stopwatch ready to time the hummingbirds' flight patterns. The stopwatch was started when a target bird came into view near the feeders. The stopwatch could be stopped when the bird changed modes of flight and started again when it reverted to its original flight form, as long as the surveyor kept a consistent count with a watch or second stopwatch of the time spent in the other form of flight. Alternately, the stopwatch's "split" function could be used to mark when flight mode was changed and then the

surveyor could later subtract the difference between split times to get times for each mode of flight.

Due to the difficulties of using the stopwatch accurately with such short visits and fast movements of the hummingbirds, the second set of data was collected using the Digital Video Camcorder. It was placed out on the tripod, level with the feeders, approximately 0.75 meters away and set to record for about 1 hour. The video was then loaded onto the computer and edited using Windows Movie Maker. The time of each bird's appearance was easily marked down to the second. The video of each occurrence was played separately and a stopwatch was used to record the amount of time spent in each flight form. This allowed for more accuracy by cutting down on opportunities for human error.

Results and Discussion

Overall, time allocation for the three types of flight showed perching as consisting of about half the total feeding time for both days, with Day 1 approximately 55% and Day 2 equaling about 59% (Figure 4). The birds spent approximately 1/3 of their time perching, showing 35% for Day 1 and 31% for Day 2 (Figure 4). Overall, the birds spent 10% of their time in linear flight for both days (Figure 4). However, this average is greatly affected by the Bananaquit data, which consisted of only perching and lasted for much longer periods, as seen in Figures 2 and 3.

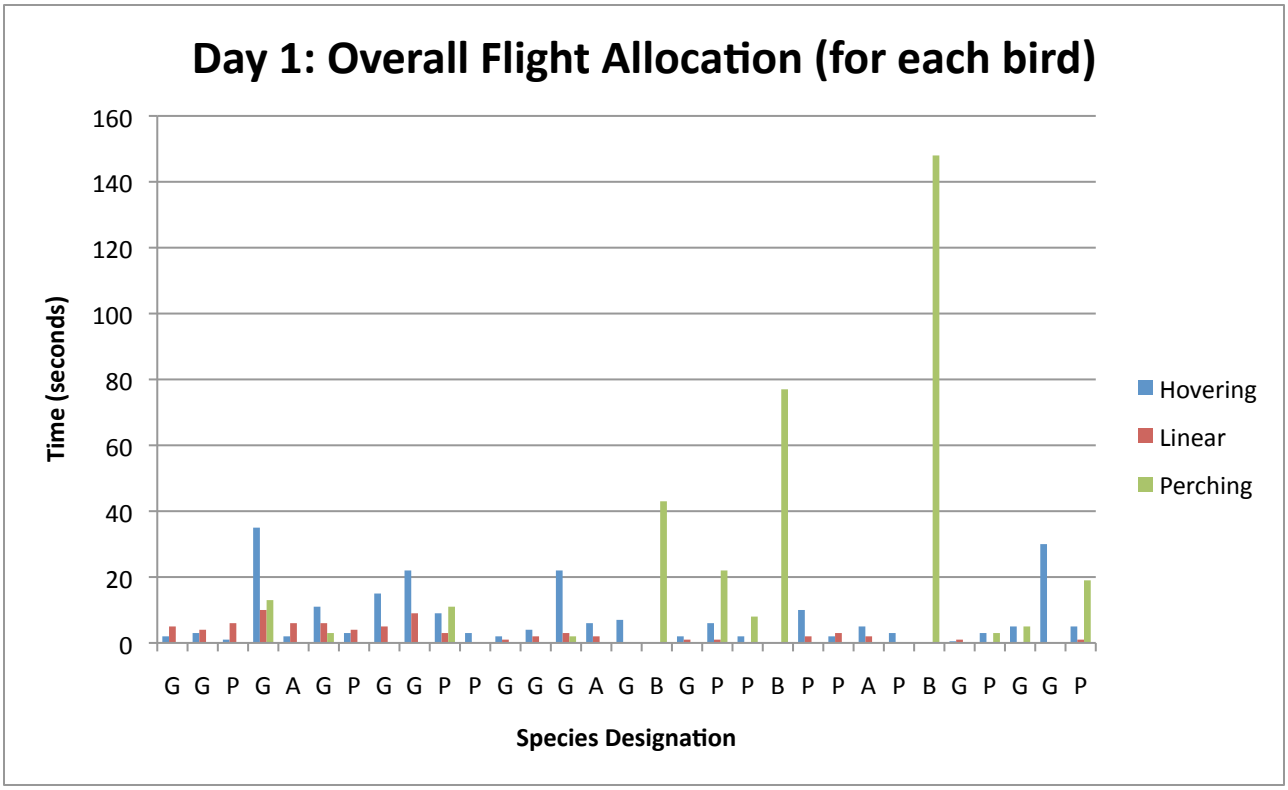

Figure 2: Bar Graph of all Day 1 (6/04/2010) data collected. Species Key: G - Green-throated Carib, P - Purple-throated Carib, A - Antillean Crested Hummingbird, and B - Bananaquit.

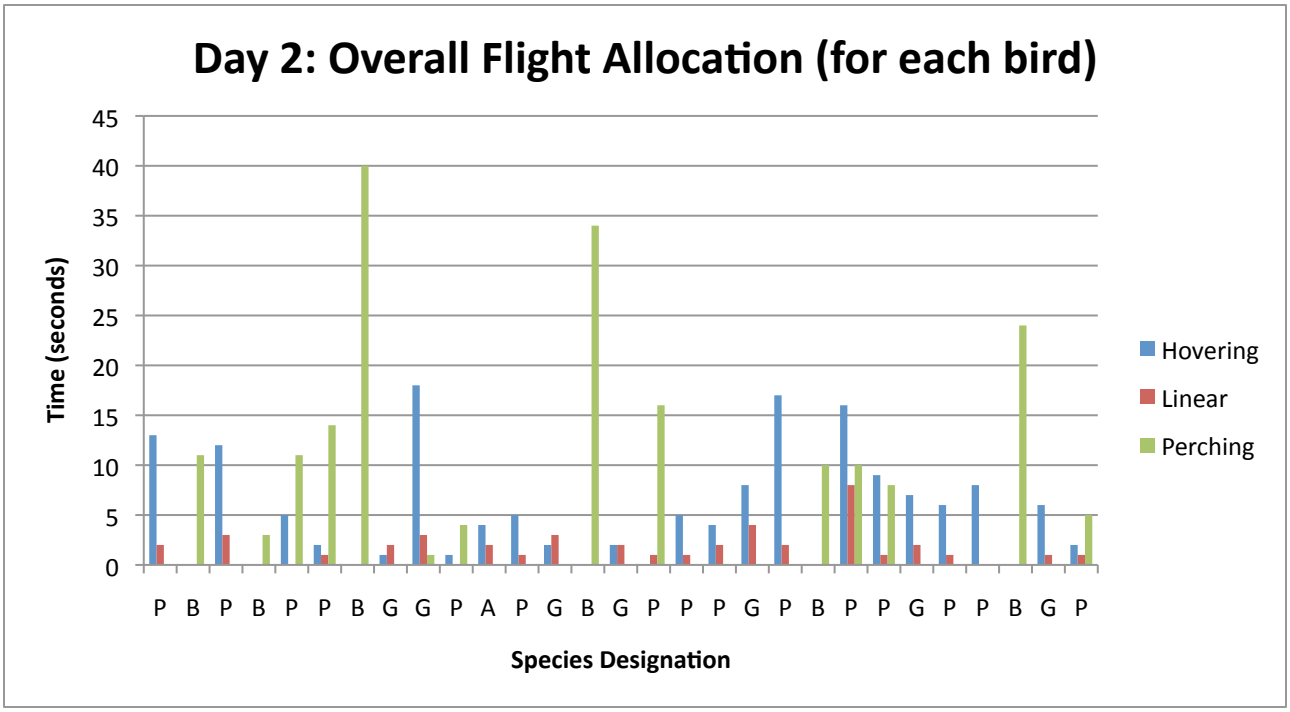

Figure 3: Bar graph of all Day 2 (6/06/2010) data collected. Species Key: G - Green-throated Carib, P - Purple-throated Carib, A - Antillean Crested Hummingbird, and B - Bananaquit.

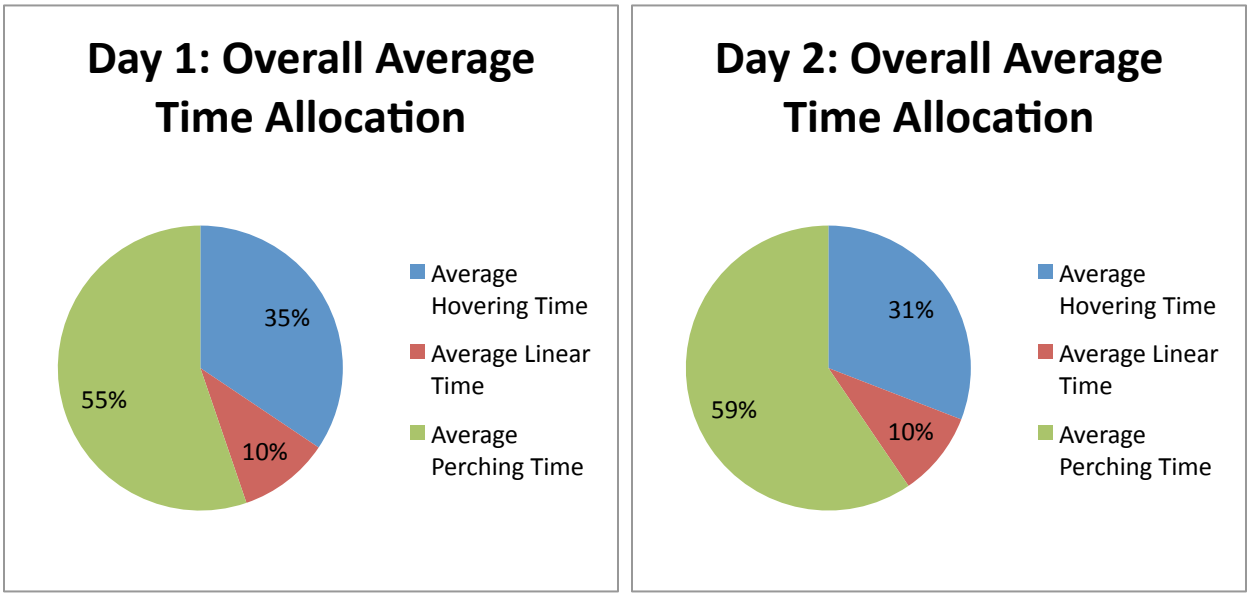

Figure 4: Pie Charts of Average Time Allocations for all species on Day 1 and Day 2.

In order to better analyze and compare the data, time allocation charts have been separated out by species. This allows for a very visual representation of how each species divides its feeding time, and therefore, how it spends its energy.

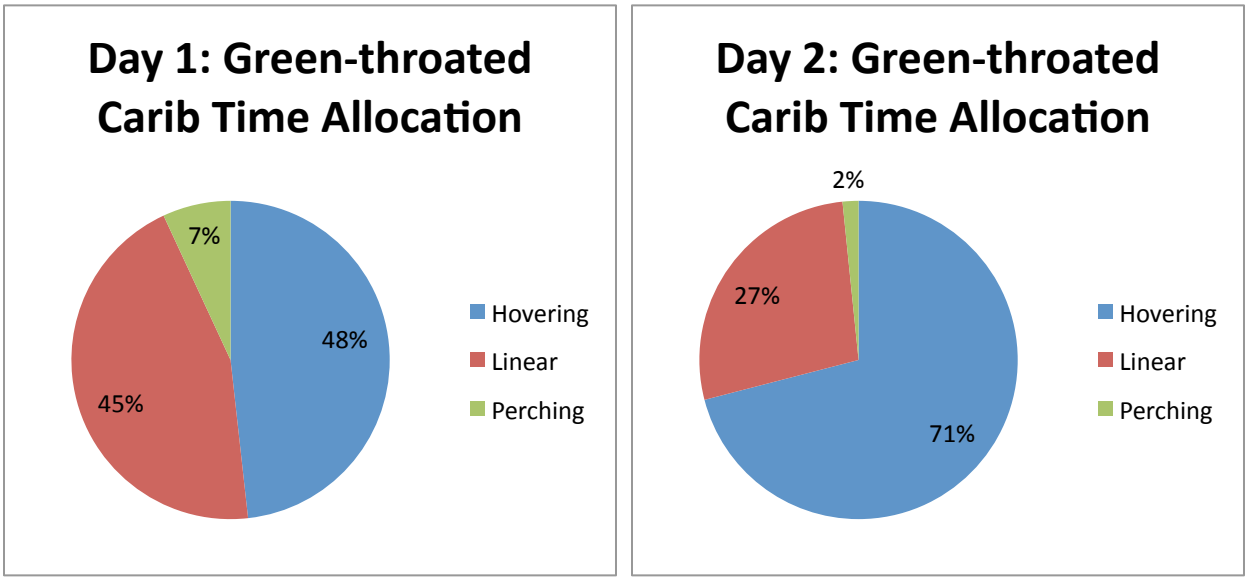

Figure 5: Pie Charts of Average Time Allocations for the Green-throated Carib on Day 1 and Day 2.

The Green-throated Carib was the only species to show a difference between its Day 1 and Day 2 data (Figure 5). The data showed a 23% increase in average hovering flight on Day 2 and decreased portions of linear flight, from 7% to 2%, and perching, from 45% to 27% (Figure 5). In general, the Green-throated Carib spends the majority of its time hovering, the rest in linear flight, and rarely perches to feed.

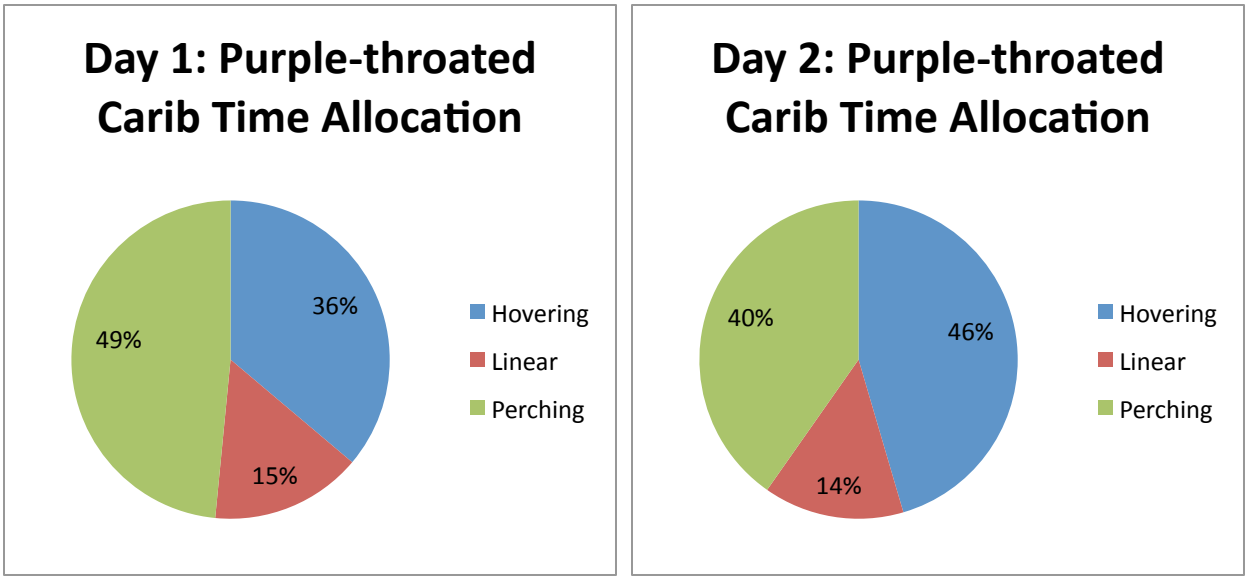

Figure 6: Pie Charts of Average Time Allocations for the Purple-throated Carib on Day 1 and Day 2.

The data from the Purple-throated Carib showed little change between Day 1 and Day 2 (Figure 6). It also showed the most balanced time allocation of the four species, with the Purple-throated Carib splitting most of its time between hovering and perching with about 14-15% of it spent in linear flight (Figure 6). On Day 1, a slight majority of flight time was allotted to perching, at 49%, and on Day 2, a small majority was given to hovering, at 46%.

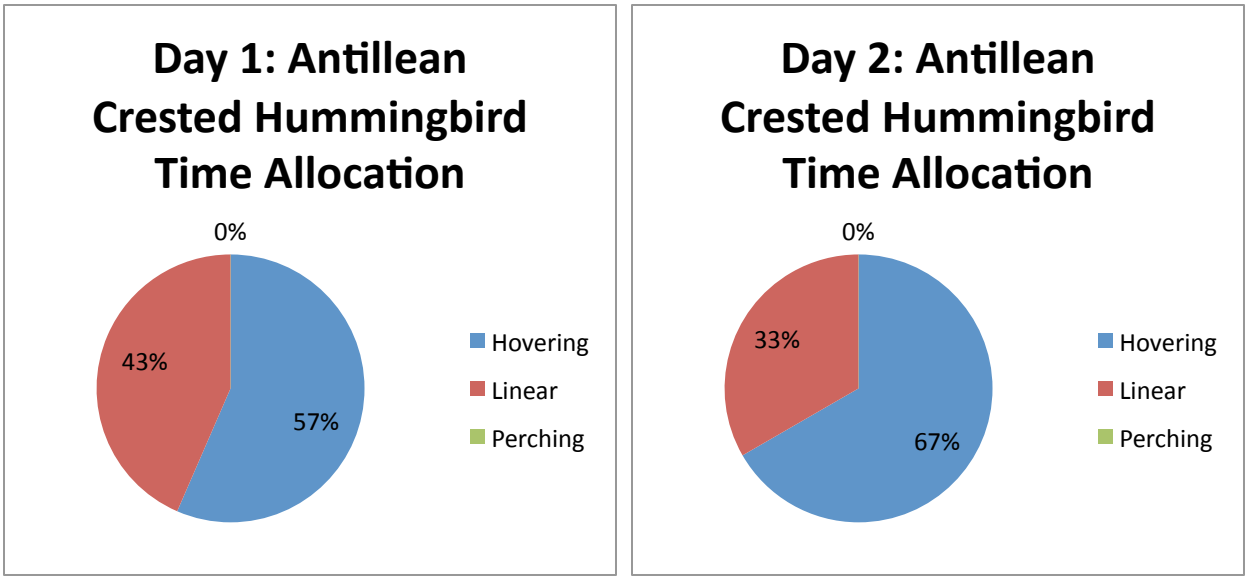

Figure 7: Pie Charts of Average Time Allocations for the Antillean Crested Hummingbird on Day 1 and Day 2.

Though the Antillean Crested Hummingbird never fed at either feeder, some data were still recorded thanks to their fondness for the neighboring *Morinda* plant. This species was never observed perching, whether on the feeder or plant, thus the data reflects this with a consistent 0% of time allocated to perching (Figure 7). What data were gathered showed a majority, 57% on Day 1 and 67% on Day 2, of time spent hovering and the rest used in linear flight (Figure 7).

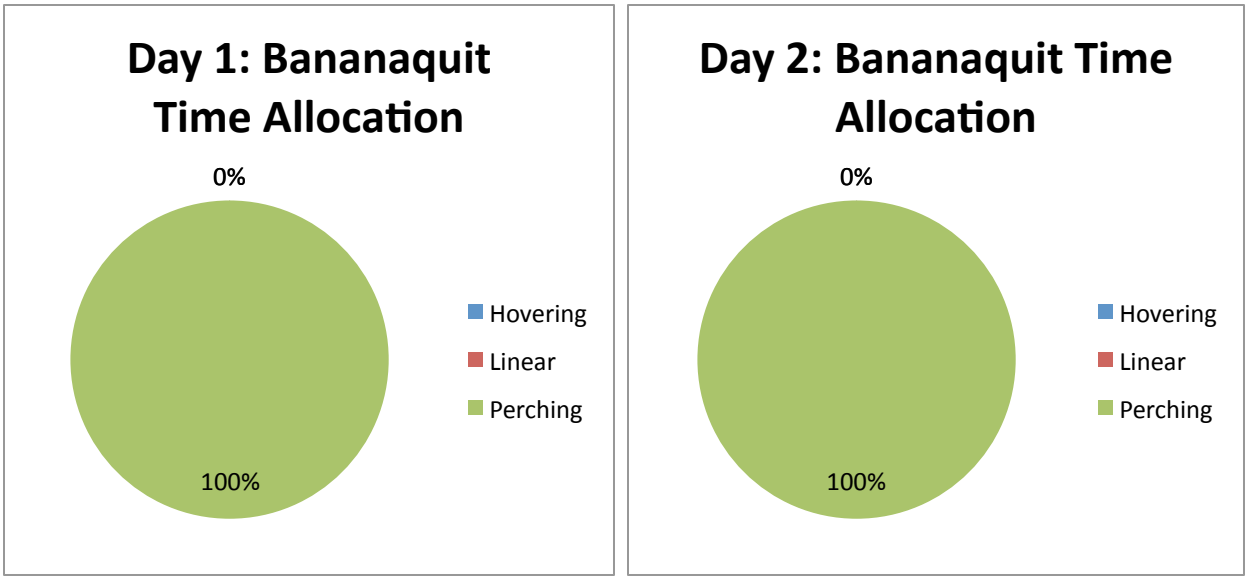

Figure 8: Pie Charts of Average Time Allocations for the Bananaquit on Day 1 and Day 2.

Presenting time allocation of the Bananaquit was relatively simple. The Bananaquit did not hover because it could not due to its physical limitations. It also never spent time in linear flight near the feeders because it immediately perched upon interest in feeding. Therefore, the data showed 100% of its time was allocated to perching during feeding (Figure 8).

Species	Day 1	Day 2	All Days
Green-throated Carib	14	7	21
Purple-throated Carib	11	15	26
Antillean Crested Hummingbird	3	1	4
Bananaquit	3	6	9
All Species	31	29	60

Figure 9: Chart of Population Counts by Species and Day.

A total of 60 feeding occurrences were recorded. A total of 21 incidents involved the Green-throated Carib, 14 on Day 1 and 7 on Day 2. Another 26 incidents involved Purple-throated Caribs, 11 on Day 1 and 15 on Day 2. The Antillean Crested Hummingbird was observed 4 total times, 3 on Day 1 and 1 on Day 2. Lastly, the Bananaquit was recorded a total of 9 times, 3 on Day 1 and 6 on Day 2 (Figure 9).

Conclusions

Comparing the different species reveals that the Green-throated Carib spent the most time hovering while the Purple-throated Carib spent relatively equal amounts of time perching and hovering. The Antillean Crested Hummingbird also allotted most of its time to hovering but, unlike the Green-throated Carib, it spent no time perching. Using the Bananaquit as a control for Passerines, the data seems to suggest that the Purple-throated Carib has the closest relationship, of the three hummingbird species, to other bird families in its use of flight type. The two largest and heaviest species, the Bananaquit and Purple-throated Carib, also perch the most. Not all hummingbird species allocated more time to hovering and linear flight than perching. The Purple-throated Carib spent more time perching and hovering than in linear flight. It was also found that the smaller the species, the larger the time that was allocated to hovering. The absence of the Antillean Crested Hummingbird at the feeders could be explained by its small size, possibly as a response to the risk of predators since it was observed as feeding mostly under cover of the plant. Its lack of perching could also be due to predator avoidance or to the ease with which it can carry its lighter body mass. So, difference in species flight preference may be attributed to differences in body mass though more research would be necessary to explore this hypothesis. Further research attempting to discover a connection between allocation of flight

time and body mass would be beneficial to understanding hummingbird energetics. Though this study was originally set up to also include data collected on species dominance, it was soon apparent that not enough information could be accurately gained with such a low competition level and with so little time. It would make a good follow-up study to investigate dominance in connection with flight time allocation and energy usage.

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