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Placement Student's Final Report*

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*Abridged from original. Contains only Scientific Report portion.

SCIENTIFIC REPORT

THE EFFECT OF AN ARTIFICIAL FEEDER ON HUMMINGBIRD BEHAVIOUR

ABSTRACT

Like their fellow nectarivores, Hummingbirds try to maximize the ratio of energy obtained to energy expended; they try to consume as much nectar with as little movement as they can (Feinsinger, 1978; Hainsworth & Wolf, 1972). The way in which they optimize their consumption is through their ecologically defined roles, they behave in such a way to increase their chances of obtaining food; they often match the length of their bill to the length of the flower. Montgomerie & Gass (1981) noted that Hummingbirds abundance appears to be limited by the availability of nectar. In this study the presence of the artificial feeder provides a constant supply of food while it is up, which could cause a change in the Hummingbirds behaviour for example are maurders (bare in and feed) seen to convert to trapliners (visit multiple flowers), or territorialists (defenders) to become filchers (thieves)?

Artificial feeders can affect hummingbirds foraging behaviour and abundance, but despite its potential importance, few previous studies have focused on the consequences of nectar feeders giving contradictory results (Feinsinger, 1978; Sonne et al., 2015). In a study by Arizmendi et al., (2007) the presence of a nectar feeder reduced hummingbird visitation to nearby plants in their study in Mexico. However in Brockmeyer and Schaefer's study (2012) the number of visits to the flowers around the feeder increased when the feeder was present. This studies main focus is to determine how the presence of an artificial feeder affects the hummingbird's behaviour specifically feeding, perching and aggression. To do this the hummingbirds interactions with the flowers within the plot and the artificial feeder were observed so that trends could be determined.

KEYWORDS

Costa Rica, Hummingbird, Artificial feeder, Behaviour, Feeding, Perching, Aggression

INTRODUCTION

Hummingbirds belong to the second largest, strictly New World avian family. The family has over 320 species, with many of the species being found in the tropics 5 degrees north, and south of the equator (Stiles and Skutch, 1989). Fifty-four species of hummingbirds can be found in Costa Rica (Skutch, 1973), with 27 species being observed at Cloudbridge Nature Reserve (CNR, 2017).

Hummingbirds have a number of highly specialized evolutionary adaptations for feeding on nectar (Garrigues & Dean, 2007). Ninety percent of hummingbird diets as a whole consist of nectar with the remaining 10% provided by small insects. Hummingbirds consume around one and a half times their body weight in nectar which provides easily convertible energy to fulfil the high metabolic requirements of a hummingbird, whereas the insects provide protein (Rabone & Staunton, 2015).

Hummingbirds can be divided into two groups via their morphology and behaviour (Fogden & Fogden, 2006). The subfamily *Phaethorninae* contains hummingbirds with long, curved bills such as the Green Hermits. The second

group, the *Trochilinae*, contains hummingbirds with relatively short, straight bills. In general, the length of the bill dictates which species of flowers they feed from, but there are many exceptions to this rule.

In 1978, Peter Feinsinger and Robert Colwell classified hummingbirds according to their feeding behaviours (Feinsinger & Colwell, 1978). They can be split into 3 feeding behaviours; territorial, trapliners (high and low reward) and territory parasites (marauders and filchers) (Rabone & Staunton, 2015).

Territorialists are aggressive hummingbirds that will defend a defined feeding territory made up of dense clumps of flowers against invaders of the same, or different, species (Feinsinger & Colwell, 1978). These tend to be medium sized hummingbirds with bright plumage (Feinsinger & Colwell, 1978; Fogden & Fogden, 2006).

Trapliners are hummingbirds that follow a repeating feeding circuit among successive flowering plants (Feinsinger & Colwell, 1978). High-reward trapliners such as Green Hermits visit flowers that produce high levels of nectar. The flowers are too widely dispersed for the hummingbirds to defend, so instead the hummingbirds repeat the same circuit throughout the day (Feinsinger & Colwell, 1978; Fogden & Fogden, 2006). Low-reward trapliners feed on small flowers that are not being defended, either due to their low quality or because they are too scattered. Low-reward trapliners tend to be smaller hummingbirds. As nectar concentration declines throughout the day, any of the feeding behaviour classes can act as low-reward trapliners (Feinsinger & Colwell, 1978; Fogden & Fogden, 2006).

Hummingbirds can also be classed as territory parasites. Within this class, the biggest of the birds are classified as marauders. Due to their size, they are able to force their way into territories and feed from the flowers, ignoring attempts of defenders to drive them out. Marauder species could defend their own territories, but the energetic costs are higher than invading others' territories (Feinsinger & Colwell, 1978; Fogden & Fogden, 2006). The other type of territory parasites are filchers. These are small hummingbirds that wait until the territorial hummingbirds are off defending their patch and use this opportunity to sneak in to feed. Another technique filchers use is to feed on areas that the territorialist cannot see, or which are not heavily used. Filchers are often persistent and will often return over and over after being chased away (Feinsinger & Colwell, 1978; Fogden & Fogden, 2006).

Most hummingbirds are pugnacious and intolerant to other hummingbirds, regardless of species and sex (Stiles and Skutch, 1989). This study aims to assess if the presence of an artificial feeding source will affect the hummingbirds' behaviour, particularly aggression, feeding and perching. Specifically, four sub questions were answered:

1. Does the frequency of feeding visits increase when the artificial feeder is present?
2. Does the duration of feeding visits increase when the artificial feeder is present?
3. Does the duration of perching increase when the artificial feeder is present?
4. Does the presence of the artificial feeder have an influence on aggression?

STUDY AREA

The study was conducted in south-central Costa Rica in Cloudbridge Nature Reserve on the Pacific slope of the Talamanca mountain range along the western edge of Chirripó National Park near San Gerardo de Rivas. The reserve itself consists of 225ha of land and ranges from 1524 to 2530m in altitude. The study area was a 4m circular plot marked out by yellow flagging tape as it was easily seen but did not affect the hummingbirds in the memorial garden (a planted area of endemic flowering species) in cloudbridge at an elevation of 1550m. The study site was chosen because it contains 7 species of flowers that hummingbirds can feed from (Figures 1 & 2).



Figure 1: Study site and flowers contained in it.







<div>1. Lantana camara</div> <div></div>	<div>2. Bomarea costaricensis</div> <div></div>	<div>3. Tillandsioideae vriesea</div> <div></div>	<div>4. Heliconia wagneria</div> <div></div>
<div>5. Heliconia bihai</div> <div></div>	<div>6. Impatiens walleriana</div> <div></div>	<div>7. Stachytarpheta frantzii</div> <div></div>	

Figure 2: List of flower species in study site

METHODS

A 7-day baseline study was carried out from April 26th to May 2nd, 2017 to determine if the area contained a wide diversity of flowering plants and that various hummingbird species chose to visit to feed before the introduction of the artificial feeder (Rabone & Staunton, 2015). The wide variety of flowers in the designated 4m plot allowed the hummingbirds to express natural feeding preferences when multiple resources were available simultaneously (Peterson & Rehaid, 1984). From this interaction, the range of flowers visited in natural conditions can be determined (Benadi et al, 2014).

A pilot study with the artificial feeder up was conducted on May 4th to confirm that when the artificial feeder is present at least some of the hummingbirds would use the feeder and to give the birds a chance to become accustomed to it. The focal study was conducted from May 5th to June 7th, 2017. Both the preliminary test and the focal study were carried out in the rainy season which lasts from May to November (Maglianesi, Bohning-Gaese and Schleuning, 2014). The commercial artificial feeder was set up on a tree in the centre of the plot. The artificial feeder held 1000ml of sugar water solution and had 3 plastic flower outlets where the hummingbirds could access the feeder solution. The feeder solution was made up of 1:4 cups of sugar to boiling water.

The artificial feeder could hold enough sugar water to give a constant supply for four days so the feeder did not need to be refilled, meaning there was minim disruption to the study plot. It was then removed for five days (four days of observation with the fifth day as a break between sets). The 8 days of observation (4 with the feeder and 4 without) was classed as a set. My study was made up of 4 sets, giving me 15 days of observation of the feeder both absent and present, for a total of 30 days of observation.

The artificial feeder was set up for only four days at a time to prevent the growth of *Stachybotrys chartarum*. *S. chartarum* is a black mould that causes a fungal infection that makes the hummingbird's tongue swell, making it impossible for the bird to feed (Maglianesi, Bohning-Gaese and Schleuning, 2014). To prevent this, the artificial feeder was taken down after four days and soaked for 15-minutes in a dilute solution of 1:10 bleach to water.

Data was collected through observation. The study plot was watched for 30 minutes, three times a day (6:00am, 8:30am and 11:00am), for a total of 90 minutes. Throughout this 90 minute period, anytime a hummingbird was witnessed carrying out one of the specified behaviours, the start and end times were noted, as well as the species of hummingbird. The three behaviours observed were feeding, perching and aggression (Appendix 1).

A feeding instance was recorded when the bird was observed probing either flowers or the feeder within the plot (the feeding source was also recorded). The feeding instance lasts as long as the bird was visiting a feeding source within the plot, and ended when the bird leaves the plot or begins another behaviour within the plot.

A perching instance was recorded if the bird was sighted sitting on a branch within the study plot. If the bird moved from one branch to another, but continued perching, this was still classed as the same instance. In an aggressive instance, a hummingbird is either the aggressor or the aggressee. A hummingbird was recorded as an aggressor when they displayed any of these aggressive behaviours: loud, fast-paced chirping; changing posture to display gorget (in males); flaring the tail; hovering in front of intruder, then flying high before diving at the intruder; or chasing the intruder out of the dominant hummingbird's territory. The hummingbird was recorded as an aggressee if it is victim to any of these behaviours, for example if it was the hummingbird being perused. Although both the aggressor and the aggressee were identified, analysis was only carried out on the aggressor.

After testing the data sets for normality, it was determined that in general they were non-normally distributed. Due to this, the non-parametric Mann-Whitney U test was used. The difference in the median value for when the artificial feeder was absent or present was tested for significance at a 0.05 confidence level. This was done for species presence, perching duration, feeding duration and feeding frequency. The numbers of aggressive instances were standardized to a percentage of behaviours observed in order to account for differences in hummingbird presence between when the feeder was present or absence, allowing more accurate comparison. For example when the feeder was absent a hummingbird was only present 6 times, aggressive 2 out of 10 behaviour observations (20%) and when the artificial feeder was present the hummingbird was present 30 times, aggressive 2 out of 60 observations (3%). Both had 2 aggressive observations but the frequency of aggression dropped when the feeder was present. Aggression was analysed using a two-proportion test to determine whether the percentages of aggressor instances differ significantly between when the artificial feeder was present or absent.

RESULTS

In this study, 9 species of hummingbirds were observed with at least one species that displayed one of the typical feeding behaviours (Table 1). The typical feeding behaviour/ecological role was gleaned from the literature wherever possible. In cases where there was no defined behaviour, a determination was made from the observations in the baseline study. 3495 instances of hummingbird feeding was recorded, 1565 of perching and 1244 instances of hummingbirds being aggressors.

Table 1: Species observed throughout study, size and ecological role.

Common name	Scientific name	Size	Ecological Role
Violet Sabrewing	<i>Campylopterus hemileucurus</i>	15cm	Marauder ¹
Green Hermit	<i>Phaethornis guy</i>	15cm	High-reward Trap-liner ¹
Green-crowned Brilliant	<i>Heliodoxa jacula</i>	13 cm	Marauder *
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	10cm	Territorial
Stripe-tailed Hummingbird	<i>Eupherusa eximia</i>	10cm	Territorial (♂) Low-reward Trapliner (♀) ²
Snowy-bellied Hummingbird	<i>Amazilia edward</i>	10 cm	Low-reward Trap-liner *
White-throated Mountain-gem	<i>Lampornis castaneiventris</i>	10 cm	Territorial (♂) Low-reward Trapliner (♀) ¹
White-tailed Emerald	<i>Elvira chionura</i>	8 cm	Filcher *
Scintillant Hummingbird	<i>Selasphorus scintilla</i>	8 cm	Filcher ²

*based on observations during baseline study

¹ (Fogden & Fogden, 2006), ² (Fogden et al., 2014)

BASELINE STUDY RESULTS

Through observations, the Green-crowned Brilliant was defined as a marauder as it one of the bigger species found in Costa Rica. The flower it preferred to feed on was rarely visited by other species, so did not have to challenge any other species. The Snowy-bellied Hummingbird was defined as a low-reward trap-liner as it was observed visiting the multiple flowers of the *Stachytarpheta frantzii* in the study plot, often repeating the same route. The White-tailed Emerald was defined as a filcher due to its small size and was also observed feeding when the territory defender was absent. As well, it would often feed then leave the area. Out of the 9 species observed, only 3 of them were observed perching which could imply an increase in territorial behaviour. The Violet Sabrewing and Scintillant Hummingbird were observed solely feeding. The White-throated Mountain-gem had the greatest proportion of aggressive behaviours of all the hummingbirds (Figure 3).

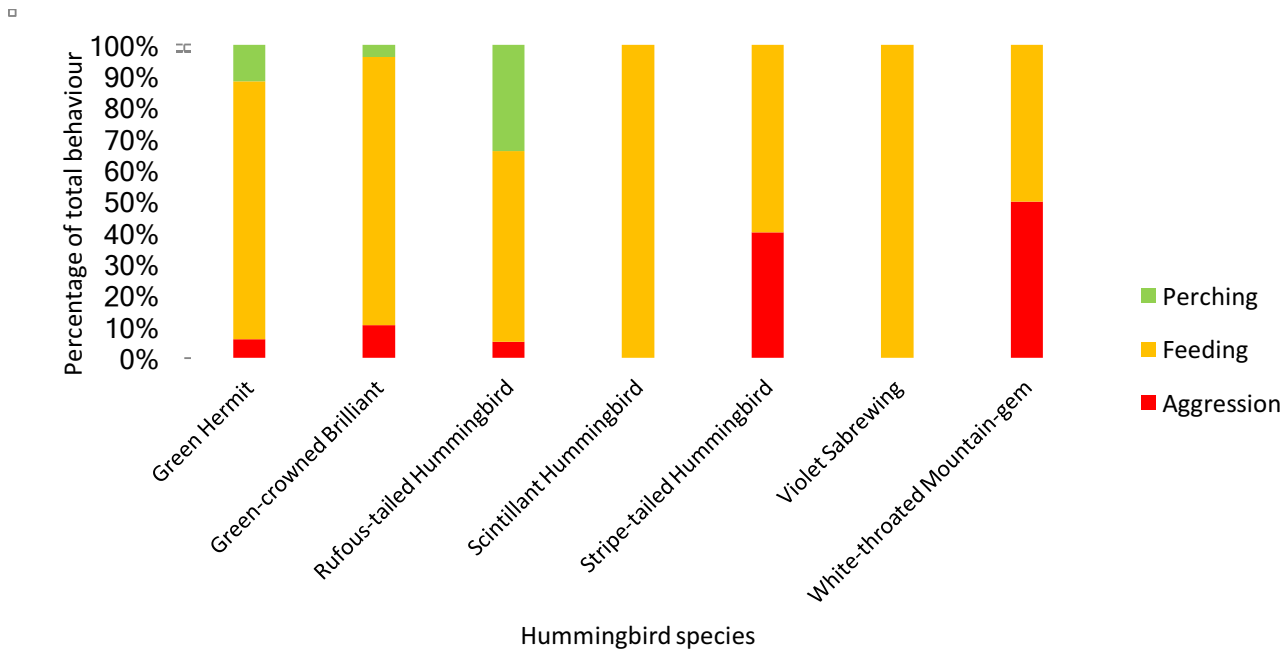


Figure 3: Proportion of hummingbird behavioural events in the baseline study.

FOCAL STUDY RESULTS

Daily Visits

The Violet Sabrewing was the only species that had a significant difference (P-value 0.0000) with median number of daily visits (Table 2) increasing from 47 when the feeder was absent to 866 when the feeder was present. The Snowy-bellied Hummingbird was intermittently present throughout the study; it would visit some days, but not others. The Green Hermit was infrequently observed; it would visit most days but only a few times.

Table 2: Median number of daily visits to site observed when artificial feeder present or absent.

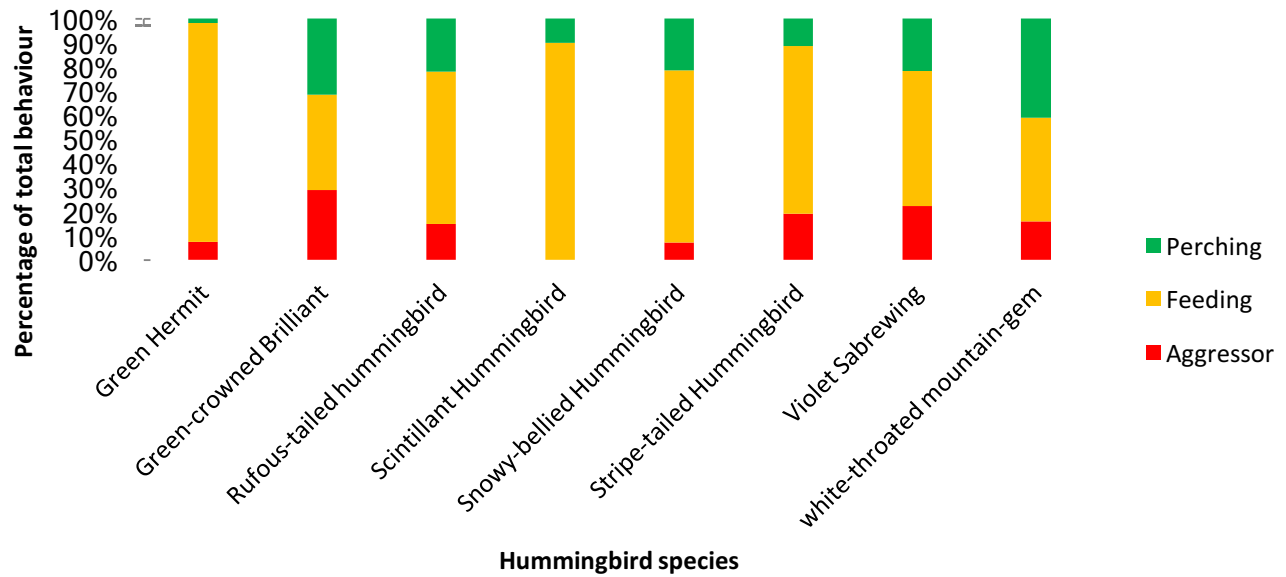
Species	Present			Absent			P-Value
	Median (count)	Range (count)	n	Median (counts)	Range (counts)	n	
Green-Crowned Brilliant	1625	824 - 12202	60106	1509	587 - 9448	38286	0.2371
Green Hermit	45	0 - 186	716	16	0 - 94	521	0.5438
Rufus-tailed Hummingbird	124.0	0 - 3193	10712	157	0 - 4337	11386	0.6764
Snowy-bellied Hummingbird	0	0 - 191	440	0	0 - 2288	5083	0.3615
Stripe-tailed Hummingbird	1336	77 - 3192	20252	430	85 - 1579	8300	0.0745
Violet Sabrewing	866	211 - 3937	18807	47	0 - 224	1000	0.0000
White-throated Mountain-gem	544	0 - 9270	30463	716	0 - 8260	35477	0.9336
Overall	770.0	0 - 12202	146571	229	0 - 9448	95141	0.0659

Overall Behaviour

For the Green Hermit, the main difference between the presence or absence of the feeder was that, when the feeder was present, this was the only instance the Green Hermit was observed perching (Figure 5). When the feeder was present the Green-crowned Brilliant's proportion of aggression increased by 10.67% but its feeding decreased by 13.49%. The Rufous-tailed Hummingbird also had an increase in aggression (5.56%) but only a small decrease in feeding (2.85%). Similarly the Stripe-tailed Hummingbird had an increase in aggression (5.56%) but also perching (7.59%) causing a decrease in feeding when the artificial feeder was present (13.16%). The Scintillant Hummingbird was not observed being aggressive when the artificial feeder was absent or present but when the artificial feeder was present feeding increased by 15% causing perching to decrease by the same amount. The Snowy-bellied Hummingbird showed a decrease in aggression (2.46%) and perching (4.17%) when the artificial feeder was present but the proportion of feeding increased (6.63%). The Violet Sabrewing's biggest change in proportion was a decrease of 5.7% in feeding with aggression increasing by 3.79% and perching by 1.38%. The White-throated Mountain-gem's proportion of aggression almost doubled when the artificial feeder was present, going from 8.15% to 16.06%, the proportion spent perching also increased by 5.74% causing feeding to decrease by 13.66.

□

A. Present



□

B. Absent

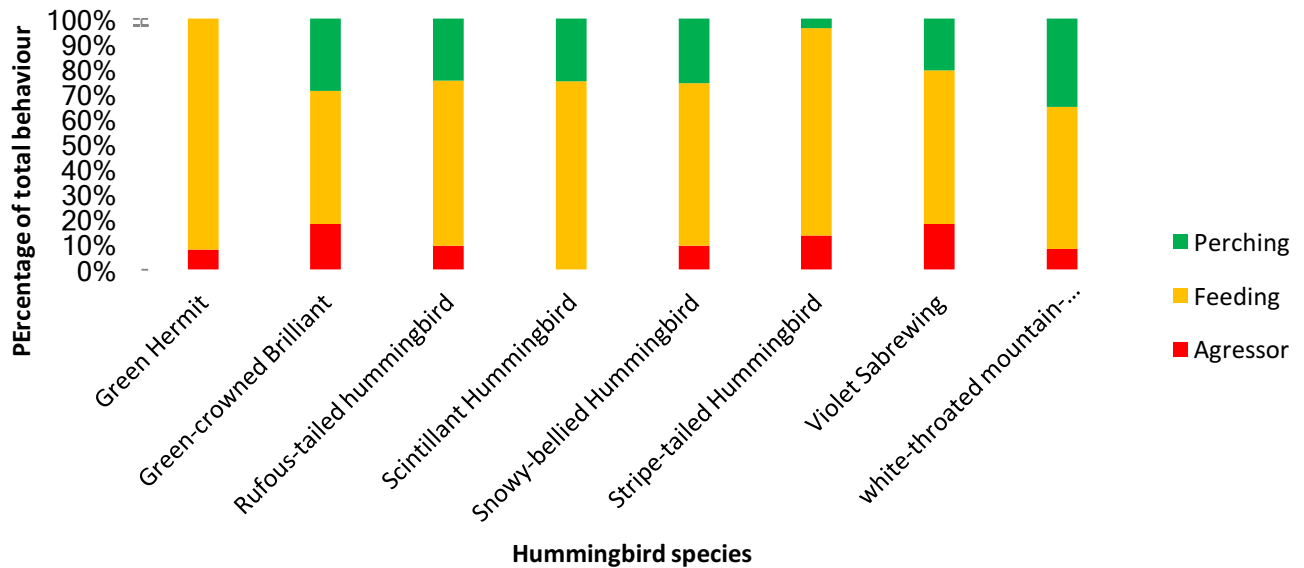


Figure 4: Comparison of proportion of hummingbird behaviours when feeder is A. Present and B. Absent.

Perching

Only two hummingbird species showed a significant difference in the median time spent perching (Table 3). Both the Green-crowned Brilliant and Rufous-tailed Hummingbird's perching time increased significantly when the feeder was absent (P-values 0.0001, 0.0035, respectively).

Table 3: Median time spent perching when artificial feeder present or absent.

Species	Present			Absent			P-Value
	Median (sec)	Range (sec)	n	Median (sec)	Range (sec)	n	
Green-Crowned Brilliant	24	1 - 1211	543	45	4 - 937	133	0.0001
Rufous-tailed Hummingbird	25	3 - 461	78	41.5	7 - 514	50	0.0035
Snowy-bellied Hummingbird	21	6 - 37	3	20	2 - 252	34	0.6160
Stripe-tailed Hummingbird	21	2 - 329	111	20	4 - 53	8	0.6165
Violet Sabrewing	17	3 - 601	162	15	3 - 104	16	0.3442
White-throated Mountain-gem	31	2 - 898	249	39	5 - 1277	177	0.1402
Overall	24	1 - 1211	1146	37.5	2 - 1277	400	0.0000

Feeding

The median time spent feeding was significantly different for all but the Green Hermit and the Snowy-bellied Hummingbird (Table 4). Of the 5 species that had a significant difference, the Violet Sabrewing was the only species that significantly increased when the artificial feeder was present (0.0032). For the rest, the time spent feeding increased when the feeder was absent.

Table 4: Median time spent feeding when artificial feeder present or absent.

Species	Present			Absent			P-Value
	Median (sec)	Range (sec)	n	Median (sec)	Range (sec)	n	
Green-Crowned Brilliant	12	0 - 3607	787	59.5	2 - 893	253	0.0000
Green Hermit	14	1 - 50	43	12.5	1 - 67	33	0.4378
Rufous-tailed Hummingbird	17	1 - 1205	224	192	5 - 197	130	0.0000
Snowy-bellied Hummingbird	38	12 - 114	9	29	5 - 204	80	0.9899
Stripe-tailed Hummingbird	16	1 - 575	662	28	2 - 234	223	0.0000
Violet Sabrewing	14	1 - 3610	411	9	1 - 52	47	0.0032
White-throated Mountain-gem	21	2 - 266	280	32	0 - 689	287	0.0000
Overall	15	0 - 3610	2422	32	0 - 893	382	0.0000

Daily Feeding Visits

The median number of daily feeding visits significantly increased when the feeder was present for the Green-crowned Brilliant, Violet Sabrewing, and Stripe-tailed Hummingbird (P-value 0.0000, 0.0000, and 0.0310, respectively).

Table 5: Median number of daily feeding visits when artificial feeder present or absent

Species	Present			Absent			P-Value
	Median (count)	Range (count)	n	Median (count)	Range (count)	n	
Green-Crowned Brilliant	44	24 - 82	788	14	5 - 39	254	0.0000
Green Hermit	3	0 - 7	44	2	0 - 8	34	0.2102
Rufous-tailed Hummingbird	5	0 - 50	131	2	0 - 38	225	0.2628
Snowy-bellied Hummingbird	0	0 - 4	81	0	0 - 39	10	0.2805
Stripe-tailed Hummingbird	41	3 - 96	224	14	2 - 30	663	0.0310
Violet Sabrewing	30	8 - 52	412	3	0 - 7	49	0.0000
White-throated Mountain-gem	17	0 - 55	281	19	0 - 53	286	0.8349
Overall	162	115 - 234	2432	71	44 - 104	1064	0.0000

Aggression

The presence of the artificial feeder significantly increased the proportion of aggressive behaviour in Green-crowned Brilliant, Stripe-tailed Hummingbird and White-throated Mountain-gem (P-values 0.000, 0.036 and 0.000, respectively) (Table 6). The Scintillant Hummingbird was not observed enough times for analysis.

Table 6: Proportion of aggressive behaviours compared with other behaviours.

Species	Artificial feeder	Aggressive events (%)	n	P-value
Green Hermit	Absent	7.89	38	0.931
	Present	7.41	54	
Green-crowned Brilliant	Absent	18.20	478	0.000
	Present	28.87	2144	
Rufous-tailed Hummingbird	Absent	9.41	202	0.0600
	Present	14.97	354	
Scintillant Hummingbird *	Absent			
	Present			
Snowy-bellied Hummingbird	Absent	9.60	125	0.765
	Present	7.14	14	
Stripe-tailed Hummingbird	Absent	13.48	267	0.036
	Present	19.04	961	
Violet Sabrewing	Absent	18.07	83	0.360
	Present	22.46	757	
White-throated mountain-gem	Absent	8.15	503	0.000
	Present	16.06	772	

*no instances of aggression observed

DISCUSSION

BASELINE STUDY

In the baseline study, the hummingbirds' feeding behaviours were observed without the influence of the artificial feeder to observe their natural ecological role (Table 1) (Fogden & Fogden, 2006). All of the hummingbird species, with the exception of the Rufous-tailed hummingbird, displayed the predicted role as found in the literature (Table 1). The Green Hermit was observed feeding the majority of the time. This is in line with its standard behaviour as a high-reward trap-liner as it moves around an area visiting various flowers with high nectar concentration (Fogden & Fogden, 2006). The study area contained one high-reward flower and the hermit was observed visiting it regularly. However, it would then leave the area in search of other high-reward flowers, as a result only spending a small amount of time perching in the study plot to digest its food (Fogden & Fogden, 2006). Although not a territorial bird, the hermit was observed to be the aggressor once, when another bird was feeding from its preferred flower.

Both the Green-crowned brilliant and Violet Sabrewing are defined as marauders (Table 1) (Fogden & Fogden, 2006). All of the Violet Sabrewing's observed behaviours and the majority of the Green-crowned Brilliant's behaviours were feeding (85.53%) (Figure 3). The Green-crowned Brilliant was also observed perching (3.95%) to digest; and was aggressive 10.53% of the time. Although the Green-crowned Brilliant is not a territorial bird, hummingbirds in general are known to have a low tolerance for other birds which could account for these aggressive instances. It could also be due to the Green-crown Brilliant's size. The other marauder, the Violet Sabrewing, is a bigger bird so smaller birds will often move out of its way (Table 1). However, this may not have been the case for the Green-crowned Brilliant who, as a smaller bird than the Violet Sabrewing, had to be aggressive to make the other birds vacate.

The Scintillant Hummingbird's standard behaviour is filching (Table 1). On each occasion it was observed, the Scintillant was feeding. The lack of perching could be due to the hummingbird wanting to feed and exit the area as swiftly as possible as to not get caught by the territory defender. Due to the Scintillant's small size of 8cm (Table 1) it is not a successful aggressor against other species and prefers flight rather than fight.

The proportion of behaviour observed in the Stripe-tailed Hummingbird and the White-throated Mountain-gem could be due to the difference in behaviour between the two sexes (Figure 3). In the literature the males of the two species are said to be territorial so are known to be aggressive with the females being low-reward trapliners. As the sex of the birds was not recorded during the observation period, further investigation would be needed to confirm this.

The Rufous-tailed Hummingbird was the only bird observed to deviate from its standard ecological role as a territorialists, defined in literature. Both sexes of the Rufous-tailed are known to be aggressive and dominant over other species, however this was not the case in the baseline study. It was only aggressive 5.15% of the time, which is a very small amount (Figure 1). The majority of their total behaviour was feeding though low-reward traplining.

FOCAL STUDY

Daily visits

For all the hummingbird species except the Violet Sabrewing, there is no significant difference in the number of daily visits when the artificial feeder was absent or present (Table 2). The reason for this could be that the main motivation for a hummingbird to visit a site is to feed, they do not move into a site to be aggressive or to perch, these behaviours are byproducts of feeding. Hummingbirds are known to become used to the presence of a feeder, returning each day in the hopes of finding it again. For this reason, the bird will visit a site and if the artificial feeder is absent, the bird will feed on the surrounding flowers. Many birds in this study were observed flying to where the feeder should be as if looking for it. The Violet Sabrewing is the only bird that significantly fed more when the feeder was present. This could be due to the low number of suitable flowers in the plot, which meant that when the feeder was absent, the Violet Sabrewing had little reason to stay in the plot or to visit as frequently.

Feeding frequency and duration

Due to the hummingbirds' typical small body size, a lot of energy is used in homeostasis (Skutch, 1973). They obtain most of their calories from nectar high in easily metabolized monosaccharides and disaccharides (1973; Hainsworth & Wolf 1972). In the wild, hummingbirds consume approximately 1 and a half times their body weight in nectar (Rabone & Staunton, 2015). In Walter Scheithauers' 1967 study on captive hummingbirds, the birds were seen to consume 60 – 70% of their body weight, but this could be due to the nectar solution provided having a higher sugar concentration than found naturally in flowers.

In the current study, both the feeding frequency and feeding duration were observed (Table 4 & Table 5). The Violet Sabrewing was the only species to have displayed a significant increase when the artificial feeder was present for both feeding duration and feeding frequency (P-values 0.0032, 0.0000, consecutively). This could be linked to the Violet Sabrewing ecological role as a marauder (Table 1). The study site contained limited flowers for the bird to feed on, but once the feeder was introduced they visited more often and fed for longer. The duration of the feeding occurrence could also be longer than other species, as the Violet Sabrewing is one of the bigger hummingbird species so is not easily driven out and requires more food.

The Green-crowned Brilliant and the Stripe-tailed Hummingbird both experienced a significant difference in feeding duration and feeding frequency (P-value 0.0000, 0.0000 & 0.0000, 0.0310, consecutively) (Table 4 & Table 5). However, unlike the Violet Sabrewing, a significant increase in feeding duration was shown when the artificial feeder was absent. When the artificial feeder was absent both birds may have resorted to low-reward traplining, meaning they visited flowers of a lower quality so had to feed longer to meet their energy requirements. Both species showed a significant increase in feeding visits (P-value 0.0000 & 0.0310, consecutively) when the feeder was present. This could be that there were only brief opportunities for the birds to feed from the artificial feeder as the Violet Sabrewing monopolized the feeder, meaning other birds could only feed a little at a time, but often. Even though both the Violet Sabrewing and the Green-crowned Brilliant are marauders, the Violet Sabrewing is 2cm bigger which could explain their success as hierarchical dominance is related to body size (Justino, Maruyama & Oliveira, 2012) (Table 1).

There was also a significant increase in the feeding duration when the artificial feeder was absent in the White-throated Mountain-gem and the Rufous-tailed Hummingbird (P-value 0.0000, 0.0000 consecutively) (Table 4). This could be due to the sucrose concentration in the artificial feeder being higher than that found from their typical natural sources. The birds that visited the artificial feeder would be able to get higher energy food from the feeder

so fed for less time. To meet the same energy requirements from the flowers a hummingbird would have to visit many individuals increasing its feeding time. The Rufous-tailed Hummingbird was observed feeding from the *Tillandsioideae vriesea*, the flower the Green Hermit preferred in the plot as the corolla is long and curved ((Maglianesi, Bohning-Gaese and Schleuning, 2014). It is unusual for the Rufous-tailed Hummingbird to feed on this flower due to the morphological constraints of having a shorter bill. This could be due to the Green Hermit's visiting so infrequently that the nectar volume in the flower exceeded the nectar chamber causing it to be accessible to hummingbirds that do not have a long bill like the hermit's, such as the Rufous-tailed Hummingbird (Stephens & Krebs 1986). This could have an effect on the Rufous-tailed feeding duration as the *T. vriesea* were more difficult to feed from than the *Stachytarpheta frantzii* it was observed feeding regularly on.

Of the 4 species that displayed a significant increase in feeding duration when the artificial feeder was absent, 3 of them were territorialists (Table 1 & Table 4). This could be due to the significant increase in the Violet Sabrewing's feeding frequency when the feeder is present. When the Violet Sabrewing was around, the territorialists were unable to defend the artificial feeder meaning they had to revert back to the natural feeding source of the flowers which is time consuming. The lower feeding duration when the feeder was present may be due to the sabrewing interrupting their feeding which didn't happen as much when the feeder was absent.

The Green Hermit showed no significant difference in feeding frequency or duration (P-value 0.2102, 0.4378 consecutively) (Table 4 & Table 5). This is likely to be caused by the fact that the hummingbird almost exclusively fed from *Tillandsioideae vriesea*, and it was only observed feeding from the artificial feeder once, meaning the feeder's presence had little impact on its behaviour. A difference in sugar concentrations between *T. vriesea* and the artificial feeder could also explain the lack of instances of the Green Hermit feeding from the artificial feeder as they favour flowers with high nectar concentrations (Stiles & Freeman, 1993). The hermit was observed feeding once from the artificial feeder which could have been the bird tasting the sugar water, but ultimately preferring the nectar from the flower. In 1979 Wiklund, Eriksson and Lundberg proposed that the Green Hermit's elongated mouthparts give the bird an opportunity to exploit nectar resources from long curved flower types (Feinsinger, 1976). This could explain why the Green Hermit was observed feeding from *T. vriesea*. Also due to the Green Hermit's feeding style the *T. vriesea* in the study plot is likely to be one of many flowers visited, although the patterns and sequences hermits make remains unknown (Gill, 1988).

Perching

The duration of the Green-crowned Brilliant's perching bouts significantly increased when the feeder was absent (P-value 0.001) (Table 3). The cause of this could be a change in the Green-crowned Brilliant's ecological role. Although it is typically a marauder (Table 1), when the artificial feeder was absent the bird was observed to perch more, which suggests the bird was attempting to defend the territory. When the artificial feeder is absent the Violet Sabrewing visits less often so the Green-crowned brilliant becomes the biggest bird present so would have a better chance at defending the territory. A characteristic of Green-crowned Brilliants feeding style is too perch rather than hover when feeding so it could be that as feeding durations increased so does perching bouts (Garrigues & Dean, 2007).

The Rufous-tailed Hummingbird showed a significant increase in perching duration when the feeder was absent (P-value 0.0035) (Table 3). This could be caused by the Rufous-tailed Hummingbird trying to claim the territory. In a study by Stephens & Krebs 1986, artificial feeders containing 14% sucrose solution were put in potential territories in mid May and by late May each of the feeders was defended by a Rufous-tailed Hummingbird. This shows how Rufous-tailed Hummingbirds are naturally territorial, but in the current study they were unable to defend the feeder due to larger birds like the Violet Sabrewing visiting. Although the Green-crowned Brilliant also showed

territorial behaviour, it is 2cm smaller than the Violet Sabrewing meaning the Rufous-tailed Hummingbird had a slightly increased chance of maintaining a territory when the Green-crowned Brilliant was present. This increase could also be caused by the significant increase in feeding when the artificial feeder was absent so the bird needs to spend more time perching to digest.

The Green Hermit is data deficient for perching duration as it was only observed perching once so was excluded from analysis as there were too few perching bouts observed. It is not in the Green Hermit's nature to perch until it has sufficient food, which, due to its size (Table 1), can take some time. In a study by Gill (1988), Hermits regularly visited 10 or more sites. So, in the current study, when the Green Hermit was observed feeding, it was just one of many high reward flowers it would visit before perching.

The remaining hummingbird species showed no significant difference in perching duration (Table 3). This does not mean that the length of perching did not increase, it just means that the bird was likely to have perched in a safe area out of the study plot as the study plot was visited by many birds with some trying to defend it.

The Snowy-bellied Hummingbird showed no significant difference in feeding duration or frequency, which could explain the lack of change in its perching duration (Table 4, Table 5 & Table 3). They visited to feed for a similar number of times and fed for a similar length of time so it makes sense that the perching duration is similar as they have not taken in any extra food.

Aggression

In the literature, hummingbirds are noted as being an aggressive family. In a study by Stang, Klinkhamer and Van Der Meijden, (2006) aggression was observed as hummingbirds would chase away potential competitors who were attempting to feed from the aggressors preferred flowers (Table 6). This could be an indicator for direct competition for nectar resources either natural (from flowers) or artificial (from the feeder). The presence of the artificial feeder provided an unlimited food source allowing for niche overlapping, but this also meant that multiple species were utilizing a single food source which gave cause for aggression (Stang, Klinkhamer and Van Der Meijden, 2006).

The Green-crowned Brilliant, White-throated Mountain-gem, Stripe-tailed Hummingbird and Rufous-tailed Hummingbird all showed a significant increase in aggression when the artificial feeder was present (P-value 0.0000, 0.0000, 0.036 and 0.060, consecutively) (Table 6). The Green-crowned Brilliant, in an attempt to try and defend the artificial feeder, increased aggressor instances as it tried to prevent other species from using the feeder. This is further evidence of the Green-crowned Brilliant moving away from being a marauder and towards being a territorialists as it tried to gain food security. The bird sees the artificial feeder as a constant, reliable, high-quality food source, and is willing to waste energy on attempting to defend it. The other three hummingbirds, the White-throated Mountain-gem, Stripe-tailed and Rufous-tailed Hummingbird are known to be aggressive species and the presence of the artificial feeder only enhanced this. Hummingbirds commonly show aggressive behaviour around resource rich patches (Justino, Maruyama & Oliveira, 2012) and the artificial feeder was very resource rich.

The Violet Sabrewing showed no significant difference in aggression as its feeding technique is that of an aggressive one (P-value 0.360) (Table 6). The fact that the Green Hermit and Snowy-bellied Hummingbird showed no significant difference in aggression could be down to their ecological roles. The Snowy-bellied Hummingbird is a filcher so tends to evade rather than persecute. The few occasions it was aggressive were not influenced by the artificial feeder's presence. The rare occasions the Green Hermit was aggressive was to defend its flower from the Rufous-tailed Hummingbird. The Rufous-tailed Hummingbird was observed attempting to feed from the flower, which the Green Hermit was not tolerant towards, so ran the Rufous-tailed Hummingbird out. High-reward

Trapliners such as the Green Hermit prefer to invest time and energy in visiting flowers, sometimes to no success, rather than being aggressors and chasing away possible competitors (Gill, 1988). Also according to a study by Gill (1988) the intensity of competition trapliners such as Green Hermits varies day to day which could explain the infrequency in aggression as there may not always be need for it. On one day there could be competition, then on the next day nothing, which is reflected in the number of times the Green Hermit was observed to be an aggressor in this study.

Limitations

One of the major limitations to this study is the weather. The circumstances in the rainforest vary unpredictably and uncontrollably from day to day (Gill, 1988). It is for this reason that three periods of observation were taken each day so that if any big anomalies occurred they could be discounted. This study was only carried out in the rainy season due to time constraints, but for a more detailed understanding of the effect artificial feeders can have on hummingbird behaviour it should be carried out in the dry season too.

During this study, there was inadequate observations of the Scintillant Hummingbirds behaviours causing it to be excluded from any analysis meaning it could not be determined whether or not the artificial feeder had an effect on that species.

Something that could have been done to strengthen the research would have been to mist net the natural community. Mist netting the birds that visited the plot would have allowed the abundance of the individual species to be evaluated (Ralph et al, 1993). The individuals that were captured would be tagged with a suitable method such as an aluminum numbered band or sprayed with a non harmful paint (Stephens & Krebs, 1986) and identified to species level according to Stiles and Skutch (1989). This would allow for identification of individual birds when observed in the study plot so an ethogram for each individual bird could be created and analysed. However, even though Cloudbridge Nature Reserve is privately owned it still has to abide by MINAE (Costa Rican Environmental agency) regulations and permits are required to handle animals which could not be obtained due to timing.

The use of video equipment could have verified the accuracy of the observations and is recommended for any further studies. In this study, all observations were carried out manually by eye. This meant that the same researcher had to be present the whole study period in an attempted to standardize errors in identification. There is a possibility of human error in this study as the hummingbirds are very quick so it is possible that behaviours could have been missed or species misidentified, but using a camera would reduce this. However, a suitable camera was unavailable.

Further studies could be executed at suitable intervals using artificial feeders, with flower outlets of different lengths and curvature similar to those used in Maglianesi, Bohning-Gaese and Schleuning's, 2014 study. This could assess how morphological constraints could also affect behaviour. For example if the feeder with flower outlets longer than the hummingbird's bill were present would the hummingbird still try to visit it? Would the hummingbird still try to defend it even if it reaches a length it can no longer feed from? A single artificial feeder with multiple outlets of varying sizes could also be used to see if aggression will increase or whether niche overlap would occur, with smaller birds using the smaller outlets and larger birds using the larger ones simultaneously, or whether the larger birds who are able to feed from all the outlets monopolise on this and defend it.

CONCLUSION

The results varied between species, with some species unaffected and others showing significant differences in their behaviour when the feeder was present or absent. The effect of the feeder's presence depends on the ecological roles of the hummingbirds. Although the artificial feeder did not cause the Violet Sabrewing to change its ecological role of a maurder, the feeder did have a positive effect on its feeding behaviour as feeding duration and feeding frequency significantly increased with its presence (P-value 0.0032, 0.0000).

The presence of the artificial feeder caused the Green-crowned Brilliant to move away from being a maurder and towards being a territorilist in attempt to secure enough food through defending flower patches.

The Rufous-tailed Hummingbird was affected by the artificial feeder's presence as it was incapable of establishing territories so was unable to act in its defined ecological role of a territorilist. It instead had to revert to being a low-reward traplener.

The presence of the artificial feeder did significantly increase the White-throated Mountain-gem's feeding duration (P-value 0.0000). However this was not enough of a change as it appears both sexes stuck to their ecological roles of males being aggressive and females low reward traplainers (although sex was not recorded there was an obvious difference in morphological characteristics between the two sexes).

It is unclear if the artificial feeder had an effect on the Stripe-tailed Hummingbird. In males their ecological roles are territorialists with females being low-reward traplainers. The significant increase in aggression (P-value 0.036) could be females becoming more aggressive territorialists or it could just be males moving into the plot so more aggression was seen as they are territorialists.

The Snowy-bellied Hummingbird was completely unaffected by the artificial feeder's presence and remained a low-reward traplener. The artificial feeder also had no effect on the Green Hermit; it remained in its defined role as a high-reward traplener concentrating on visiting high reward flowers instead of the feeder.

However the effects of the feeder are also determined by what other Hummingbirds are present in study plot for example the feeder encouraged the Rufous-tailed Hummingbird into the study plot, it then attempted to feed from *T. vriesea* causing the Green Hermit to be an aggressor. The presence of the feeder also encouraged Violet Sabrewing's to visit the study plot. Their presence had an effect on the other hummingbirds as in many cases it prevented other birds from feeding from the feeder or becoming victims to the Violet Sabrewing's aggression.

In three of the species the presence of the feeder significantly increased the number of daily feeding visits but in the remaining 5 species significantly decreasing the time spent feeding. Due to the feeder solution being made of 1:3 sugar to water it is likely that the feeder was providing a higher quality food source than the surrounding flowers allowing the birds to feed less to achieve the same energy requirements reducing feeding time. The feeder only affected the perching behaviour of 2 territorial species, with median perching time decreasing when the feeder was present. Perching is one of the techniques hummingbird use to help defend an area as they are present in the patch, which in itself is a deterrent to possible visitors. The drop in perching may be due to the presence of larger hummingbirds in the study area when the feeder was present driving out the smaller birds. Finally, three hummingbirds saw an increase in the proportion of aggressive behaviours displayed when the feeder was present. Hummingbirds are generally known to be pugnacious toward other hummingbirds, regardless of gender of species, and the presence of the feeder increased this. It caused some birds to attempt to defend the feeder from other hummingbirds, increasing the aggressive displays seen.

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APPENDIX 1

Data collection parameters

Session

Each set lasted 4 days; observation days were numbered 1 to 4 then repeated for the next set

Date (dd.mm.)

Date the observation was carried out

Feeder A/P

Absence or presence of feeder was recorded.

Duration (h:mm) – length of observational period

Species

Species of Hummingbird

Behaviour

Feeding, Perching or Aggression

Behaviour start and end time (h:mm:ss)

The time the behaviour started and either finished, changed into another or moved out of the study area.

Feeding source

Species of flower or artificial feeder.