CLOUDBRIDGE
NATURE RESERVE

Hummingbird Diets in a Mountain Cloud Forest Reserve

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White-throated Mountain-gem (*Lampornis castaneoventris*)

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1 INTRODUCTION

The Trochilidae family is the second largest avian family, and is strictly found in the New world (Stiles and Skutch, 1994). It comprises over 320 hummingbird species, 54 of which live in Costa Rica (Stiles and Skutch, 1994). Hummingbirds are known for their feeding on nectar, which comprises 90% of their diet, with the remaining 10% made up of arthropods which provides them with vital protein (Fiensinger and Colwell, 1978). The number of arthropods consumed increases during breeding when higher protein levels are needed (Poulin *et al*.,1994). To a lesser extent, they are also known to utilize other sugar sources, such as tree sap, honeydew, fruit, and pollen (Reichoff and Reichoff, 1973; Miller and Nero, 1983; Schuchmann, 1999; Ruschi, 2014; Partida-Lara, 2018).

There are two main groups of hummingbirds, *Phaethorninae* and *Trochilinae* (Fogden and Fogden, 2006). *Phaethorninae* hummingbirds (hermits) tend to have curved, long bills that help them feed from ornithophilous plants (pollinated by birds) that are specialized toward hummingbird pollination. These plants provide a rich nectar reward, but require the hermits' specific bill shape to reach the nectar (Feinsinger & Colwell, 1978). The other hummingbird group, *Trochilinae*, often have shorter and straighter bills, and feed from a greater variety of generalist flowers, which tend to be less rich in nectar (Fiensinger *et al*., 1986). These flowers are a shared resource with other pollinators, such as insects and bats (Martén-Rodríguez *et al*., 2009). However, there are variations in morphology – the Violet Sabrewing (*Campylopterus hemileucurus*) is part of *Trochilinae*, but has a bill that closely resembles a hermit.

There is limited research on the diet of hummingbirds in cloud forests within Costa Rica, of which most has been conducted at Monteverde in the north-west (Fiensinger, 1978; Feinsinger *et al.,* 1987; Carroll and Moore 1993). There has been no previous research in the Talamanca mountain range.

Twenty-eight hummingbird species have been recorded within Cloudbridge Nature Reserve, and are regularly recorded year-round at all point count locations (Cloudbridge Nature Reserve, unpublished data). This indicates that there is a sufficient and regular supply of food which they can readily exploit throughout all seasons. Thus, this leads to this study's research question:

'What plants do hummingbirds feed from at Cloudbridge Nature Reserve?'

2 STUDY LOCATION

This study took place in the Talamanca mountains at Cloudbridge Nature Reserve (Cloudbridge), San Gerardo de Rivas, Perez Zeledon Province, Costa Rica (9.471778° latitude, -83.578141° longitude), between 1650 – 1800 m asl. The land is bordered on its western edge by the Chirripó National Park, which at the border is mainly primary forest. The land was initially deforested for pastureland, and is now made up of 283 hectares of primary, planted and naturally regenerated forest. Part of the nature reserve is a small residential area that has ornamental and non-native plant species. The mean average temperature during May is 17-19 °C, while the average rainfall is 360 mm (Powell 2019, AYA 2018).

3 MATERIALS & METHODS

3.1 STUDY SITE

Study sites were identified by reviewing past 'point count' data, and seeing where hummingbirds have been recorded most frequently around Cloudbridge over the last three years during the same months of our study - April, May, and June. This was done in order to maximise the amount of observations that could be recorded. If sites did not yield any observations after two visits, then they were dropped and another site was used instead. Old growth sites were not included, as this study aimed to look at regenerating areas. The sites are listed in Table 1 and shown on a map in Figure 1.

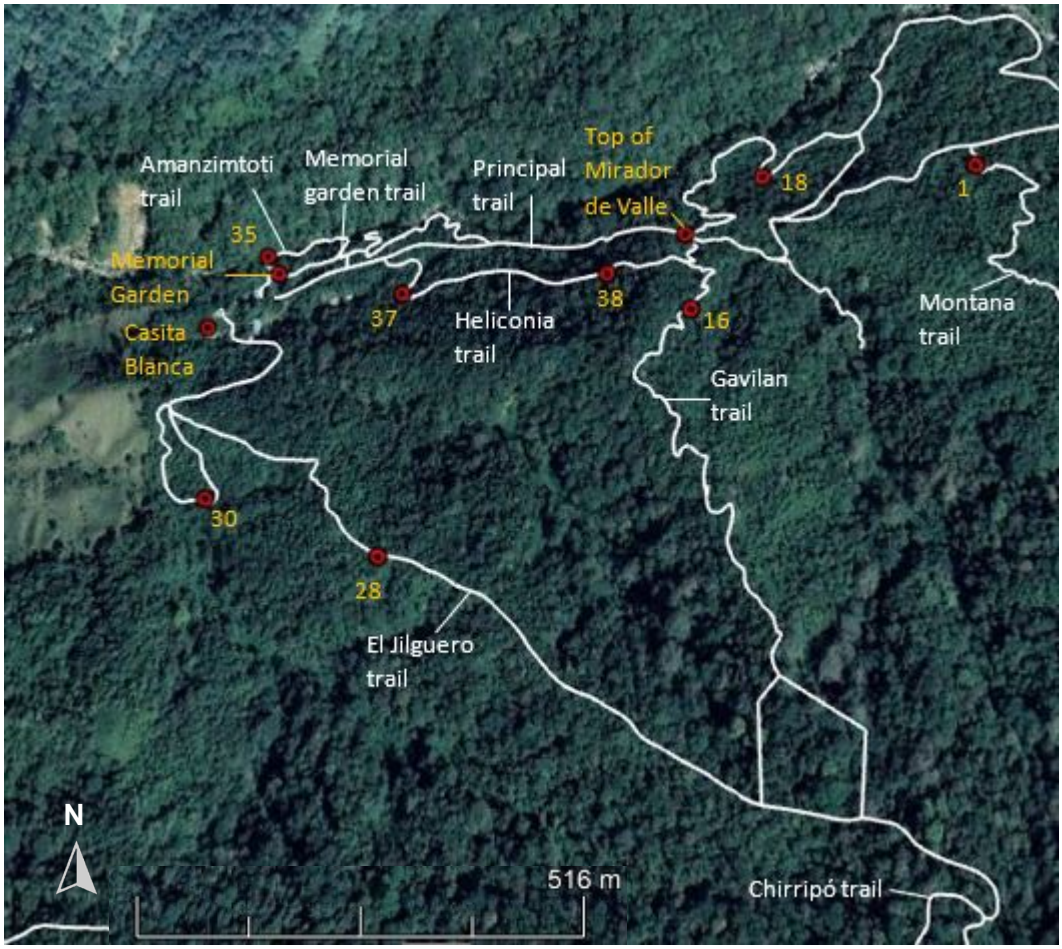

Figure 1: Map of site showing the different trails and observation point count areas.

Table 1: Study site details.

Site	Latitude	Longitude	Elevation (m)	Habitat Type	Trail
Casita Blanca	9.471762°	-83.578382°	1566	G	Road
Memorial Garden	9.472433°	-83.577500°	1575	G	Memorial Garden
1	9.473409º	-83.568988º	1730	P	Montana
16	9.471758º	-83.572306º	1735	P/NR<30	Gavilan
18	9.473445º	-83.571454º	1650	P/NR<30	Rio
28	9.468912º	-83.575908º	1760	NR<30	El Jilguero
30	9.469620º	-83.578210º	1640	P	El Jilguero
35	9.472635º	-83.577640º	1566	NR<30	Amanzimtoti
37	9.472122°	-83.575886°	1627	NR<30	Heliconia
38	9.472242°	-83.573312°	1674	NR<30	Heliconia

Habitat Types: P= Planted, NR = Natural Regeneration, O = Old Growth, G = Garden

3.2 DATA RECORDING

The hummingbird survey was conducted between 30th of April and the 21st of May.

Observation periods lasted between 60-90 minutes. The following data was collected during observations:

1) Species name & sex (Male, Female, Juvenile, Unknown)
2) Time (seconds) spent feeding on a plant and time spent perching.

   The time would stop when the hummingbird was lost from view. If a hummingbird both perched and fed within a single observation this was noted as such. For example, if a hummingbird first fed, then perched, then fed again, and was then lost from view, it would be noted as fed 1 (time), perch 1 (time), fed 2 (time). A simple stopwatch smartphone application was used to record time.

3) After a feeding or perching observation, it was noted whether the hummingbird Flew (for an unknown reason), was Chased (by another bird), or Pursued another bird. Additionally, the other bird species in the interaction was recorded if possible.
4) A note of any other bird species were within two meters of the hummingbird during feeding or perching.
5) A description of the plant fed upon, and photographs.
6) Any other notes thought relevant to the study.

Only the first bird seen would be recorded; for instance, if a bird was being recorded feeding and another one turns up and starts feeding too, it would be ignored.

Bird species were identified using the Garrigues & Deans (2014) field guide.

4 DATA ANALYSIS

Plant species were identified to the lowest possible taxonomic classification using a mixture of field guides (Zuchowski, 2005; Gargiullo *et al.*, 2008), the Cloudbridge plant species list (CNR, 2017), and the National Herbarium of Costa Rica (Joaquin Sanchez, pers. comm).

The proportions of the different food plants used by individual species, excluding the two ornamental sites, were calculated. A feeding observation is defined as a species seen feeding on a plant at a location within an observation period – repeat visits were discarded. Feeding observed along trails was also included.

5 RESULTS

Approximately 1385 minutes were spent collecting data. A total of 13 hummingbird species were seen during the study, 3 of these were only seen within the ornamental areas, 3 were only seen in the regeneration areas, while the remaining 7 were seen in both. The sexes of Rufous-tailed hummingbird (*Amazilia tzacatl*), Snowy-bellied Hummingbird (*Amazilia Edward*), and Purple-crowned Fairy (*Heliothryx barroti*) were not recorded, but for all other species, both sexes were recorded. Hummingbirds were seen to feed on a total of 13 plants. Four plant species were only in the ornamental areas, 6 were only in the regeneration areas, while the remaining 3 were seen in both. Hummingbirds fed upon flowers of 12 plants, and on the fruit of 1 (*Saurauia montana*) (Table. 2). Pictures of plants are provided in Appendix 1 and 2.

Scintillant Hummingbird (*Selasphorus scintilla*) was reported 14 times, Volcano Hummingbird (*Selasphorus flammula*) 3 times, and *Selaphorous* sp. 5 times – so for subsequent analysis, they are grouped together under *Selaphorous* sp.. The number of feeding observations was variable, the lowest being a single observation (Purple-crowned Fairy), and the highest being 22 (*Selaphorus sp.*). Many were recorded only feeding on a single plant species, while 2 (Stripe-tailed Hummingbird (*Eupherusa eximia*) and White-throated Mountain-gem (*Lampornis castaneoventris*)) were seen feeding on 5 plant species (Figure 2).

The way in which the data has been analysed does not account for rarity of feeding events, as a single species of plant may have been visited multiple times within an observation, and another plant species would only have to be visited once for them both to be counted as a feeding observation. This means that our results under-represent which plants the hummingbirds regularly fed upon, while overstating the rarer plants.

Insect catching was observed a total of 19 times throughout the study period. White-throated Mountain-gem had the most instances of insect hawking, with 13 sperate feeding sessions, while the other 6 instances were by Stripe-tailed Hummingbird, Green Hermit (*Phaethornis guy*), and Snowy-bellied Hummingbird.

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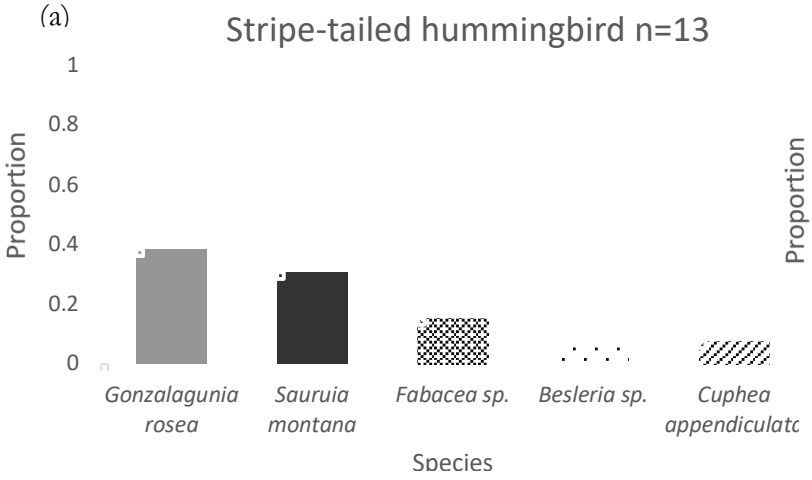
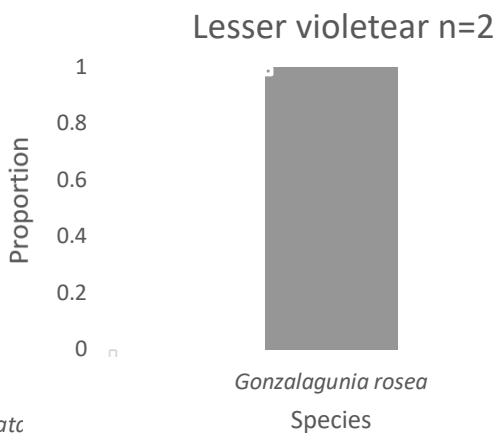
Table 2: Plant types hummingbirds fed upon at each study location.

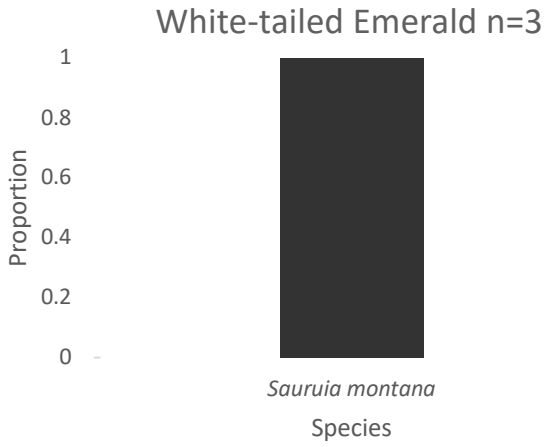
Location →	Casita Blanca					Memorial Garden					1		16		18	28				30			35						37				38	On trail observations				
Plant → / Birds ↓	LC	SF	HEL	WW	G2	G2	HEL	SF	GR	CA	GR	CAP	GR	HEL	HEL	SM	GR	PL	HEL	GR	Y	HEL	BF	HEL	PL	GR	RT	EG	GR	SM	PL	HEL	GR	SM	EG	HEL	GR	CAP
WTE						X																												X				
STRIPE	X										X					X				X	X		X						X					X				X
RU	X	X																																				
SABRE			X				X															X																
LVE																													X									
GCB	X			X											X									X												X			
FAIRY																																		X				
VH	X	X																																				
WMG	X	X			X			X	X	X		X	X				X	X		X			X		X				X	X	X			X	X			
GHERM			X				X							X	X				X			X		X			X	X				X			X			X
VOL	X	X																																			X	
SCIN	X	X							X		X		X				X			X						X			X				X				X	
SNO	X	X																																				

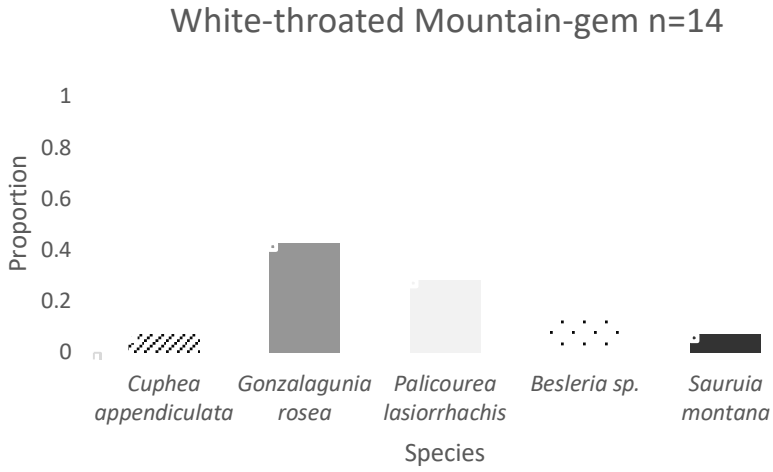
For hummingbirds: WTE = White-tailed Emerald, STRIPE = Stripe-tailed Hummingbird, RU = Rufous-tailed Hummingbird, SABRE = Violet Saberwing, LVE = Lesser Violetear, GCB = Green-crowned Brilliant, FAIRY = Purple-crowned Fairy, VH = Violet-headed Hummingbird, WMG = White-throated Mountain-gem, GHERM = Green Hermit, VOL = Volcano Hummingbird, SCIN = Scintillant Hummingbird, SNO = Snowy-bellied Hummingbird. For Plants, identified to lowest taxonomical class: LC = *Lantana camara.,* SF = *Stachytarpheta frantzii*, HEL = *Heliconia* sp., WW = *Werckelea sp.,* G2 = Unknown tree, GR = *Gonzalagunia rosea*, CA = *Citrus aurantium*, SM = *Saurauia montana*, PL = *Palicourea lasiorrhachis*, Y= *Fabaceae* sp., BF= *Besleria sp.,* EG = *Erythrina sp.,* CAP= *Cuphea appendiculata*

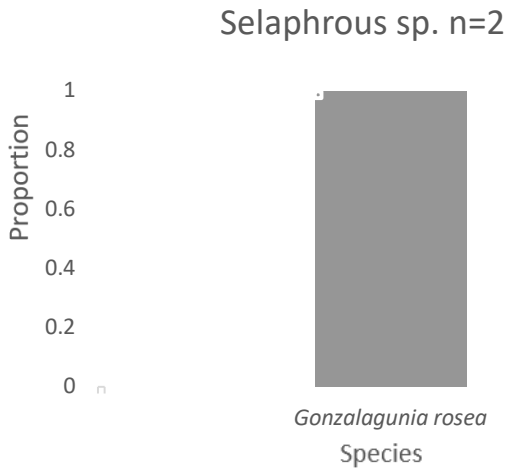
(a)

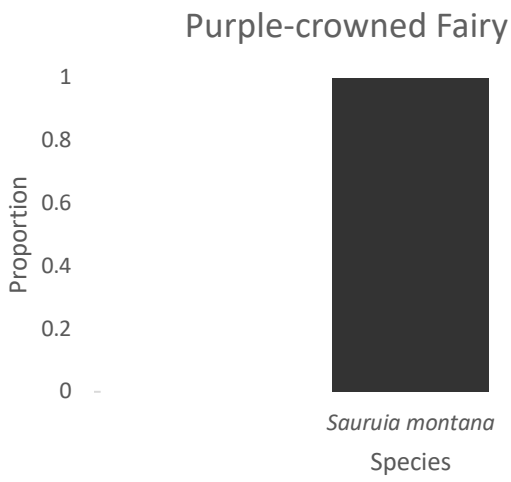

Stripe-tailed hummingbird n=13
Proportion
1
0.8
0.6
0.4
0.2
0
Gonzalagunia rosea
Sauruia montana
Fabacea sp.
Besleria sp.
Cuphea appendiculatc
Species


Lesser violetear n=2
Proportion
1
0.8
0.6
0.4
0.2
0
Gonzalagunia rosea
Species


White-tailed Emerald n=3
Proportion
1
0.8
0.6
0.4
0.2
0
Sauruia montana
Species


White-throated Mountain-gem n=14
Proportion
1
0.8
0.6
0.4
0.2
0
Cuphea appendiculata
Gonzalagunia rosea
Palicourea lasiorrhachis
Besleria sp.
Sauruia montana
Species


Selaphrous sp. n=22
Proportion
1
0.8
0.6
0.4
0.2
0
Gonzalagunia rosea
Species


Purple-crowned Fairy n=1
Proportion
1
0.8
0.6
0.4
0.2
0
Sauruia montana
Species

(b)

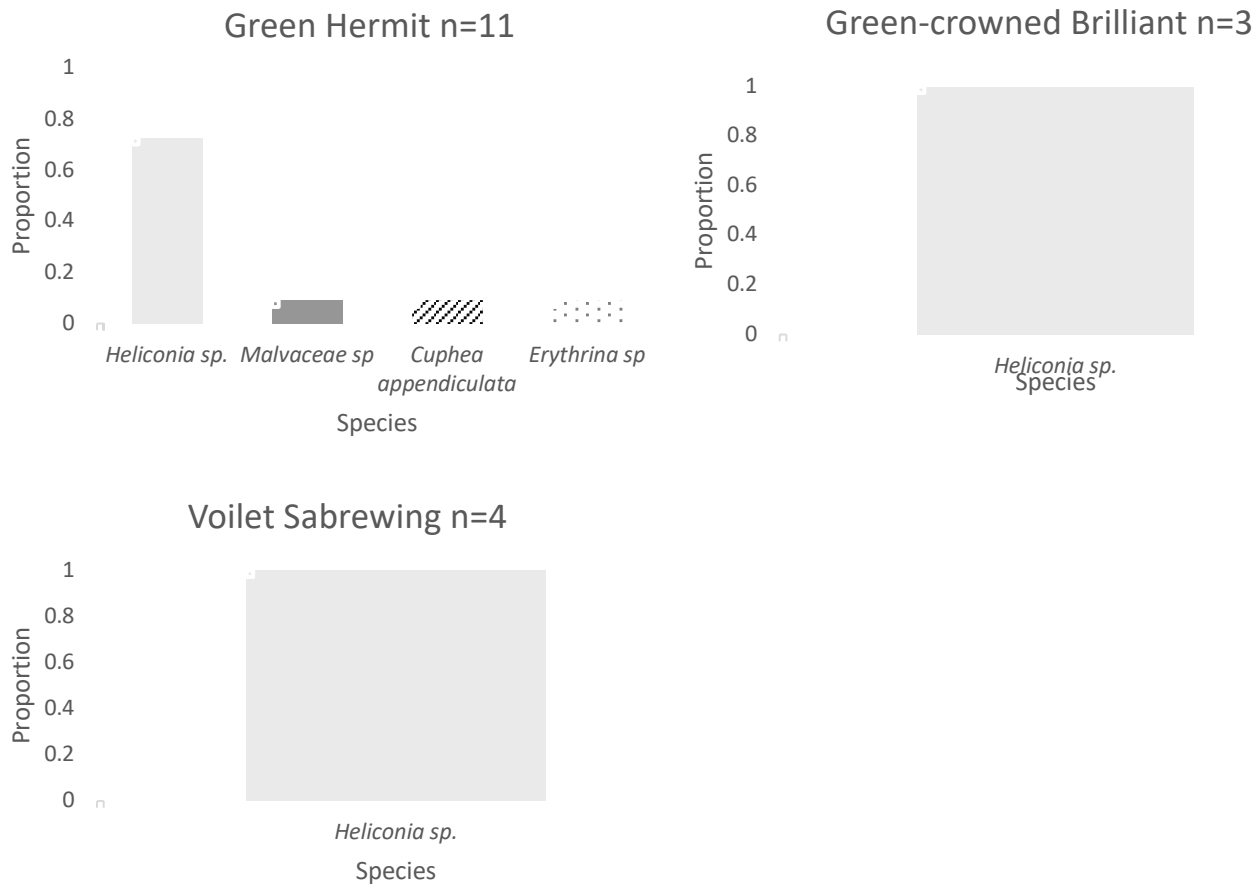


Figure 2: Plants fed upon by hummingbird species as proportion of total feeding observations. A feeding observation is defined by a species seen feeding on a plant at a location within an observation period- repeat visits are discarded. Feeding observed along trails is also included. Hummingbirds are grouped as (a) canopy species, and (b) understory species.

6 DISCUSSION

6.1 UNDERSTORY FORAGING

Within the forest, 2 species (Green-crowned Brilliant (*Heliodoxa jacula)* and Violet Sabrewing) exclusively fed on various *Heliconia sp*. (Appendix 1a), while *Heliconia sp*. made up 73% of Green Hermit feeding observations (Figure 2). These 3 species are 'high reward trapliners' travelling long distances between feeding locations (Feinsinger and Colwell, 1978), as a result, Heliconia increases its pollen load when visited by these species, thus spreading the pollen over a wider area (Betts *et al*., 2015). Heliconia is an ornithilous species, exclusively pollinated by hummingbirds (Stiles, 1975; Temeles and Kress, 2003). Bill morphology influences the efficiency at which

hummingbirds can extract nectar from ornithilous plants (Wolf *et al*., 1972; Temeles *et al*., 2009; Betts *et al*., 2015). Fitting the shape of the corolla best, long curve-billed hummingbirds such as the Green hermit and Violet Saberwing are the most efficient at extracting nectar from Heliconia (Betts *et al*., 2015) – Green-crowned Brilliants have long straight bills so can still extract nectar to a lesser extent, but enough to make it an efficient foraging strategy. While these hummingbirds where regularly observed using the native species of heliconia in the forest, in the Memorial garden where there are lots of ornamental Heliconias, only the Green Hermit was observed feeding, and then only on a single occasion. This lack of feeding could be for various reasons. Firstly, the fact that the Heliconias are ornamental and often not native, usually means that they are bred for aesthetics and not for nectar, therefore having less of an energy gain for the hummingbirds (Feinsinger and Colwell, 1978). The Heliconias present at this site were also very exposed; in the forest they are part of the ground vegetation and have higher vegetation around them, providing more cover. It is possible that the hummingbirds do not feel as safe feeding from the Heliconias out in the open.

While the Green-crowned Brilliant was seen to only feed on *Heliconia* sp. within the forested areas, it was seen feeding on a *Werckleа woodsonii* (Appendix 1b) within the ornamental garden. This is a tree with large yellow flowers; to feed, a Green-crowned Brilliant would perch on top of a flower and then pierce through the base to access the nectar.

There was a small stream running through observation point 35 (Figure 1). A *Besleria* sp. (Appendix 2b) grew abundantly in this area, seemingly being associated with the saturated soil conditions. This area was also devoid of vegetation growing higher than the *Besleria* sp., giving the appearance of a monoculture. Both White-throated Mountain-gem and Stripe-tailed Hummingbird were seen foraging on the nectar from the small orange flowers. At a different location, these hummingbird species, with the addition of Green Hermit, were seen to forage on the flowers of *Cuphea appendiculata* (Appendix 2h) on a single occasion. Within the canopy, on single occasions, Green Hermits were also seen to feed from the flowers of a Malvaceae species (Appendix 2e) and a Erythrina species. This shows that, despite its specialised bill and interactions with Heliconia, it will forage on alternative food sources.

6.2 CANOPY FORAGING

White-throated Mountain-gem and Stripe-tailed Hummingbird were observed feeding on the greatest variety of flowers (5) (Figure 2). White-throated Mountain-gem was observed to be very territorial, often found in the same place over multiple days, feeding on the same plants, and chasing off any subordinate hummingbirds. Within one 90-minute survey, they were also noted only to be catching insects, without feeding on any flowers. *Gonzalagunia rosea* (Appendix 2d) made up the majority of White-throated Mountain-gem feeding observations (43%). They were also commonly seen foraging on *Palicourea lasiorrhachis* (Appendix 2g), making up 29% of observations. *P. lasiorrhachis* has small yellow flowers, is widespread around Cloudbridge, and appeared to start flowering towards the end of data collection, so may make up a larger proportion of the hummingbirds' diet as the season continues. *G. rosea* made up the 38% of Stripe-tailed Hummingbird feeding observations, while *S. montana* (Appendix 2c) fruit comprised 31%. The significance of this frugivorus behavior is outlined below (Section 6.2.2). A *Fabaceae* sp. (Appendix 2f) also comprised a small proportion of feeding observations.

All other short straight billed species that were seen foraging within the forest were either foraging upon *G. rosea* or *S. montana* fruit (Figure 2).

6.2.1 GONZALAGUNIA ROSEA

The most used species of plant was *Gonzalagunia rosea,* a flowering tree, containing bunches of small pink flowers. This was used by a wide range of generalist hummingbird species (Table 2). The two species of the genus *Selasphorous*, Scintillant Hummingbird and Volcano Hummingbird, were seen feeding solely on *G. rosea* when not in the ornamental gardens. This flowering tree is common and found on all trails throughout Cloudbridge. While

G. rosea was consistently used throughout almost all sites of the reserve, no feeding was observed at point 18 on the Rio trail during the surveys, despite there being reasonably sized trees present with lots of flowers. Hummingbird species that were expected to feed upon *G.rosea* were regularly recorded during general bird point counts at Point 18, so it is likely that the hummingbirds were just not present during our observation period, rather than totally absent from the site. Hummingbirds have been recorded to regularly feed from *G. rosea* within Monteverde Cloud Forest (Feinsinger *et al.,* 1987). Despite their regular association, hummingbirds, do not pick up much pollen from the flowers of *G. rosea*, and are hence poor pollinators – this is more likely done by invertebrates (Feinsinger *et al.,* 1987).

6.2.2 FRUGIVORY OF *SAURAUIA MONTANA*

Four hummingbird species were observed feeding from the fruits of *Saurauia montana* (The Snot Tree); Purple-crowned Fairy, Stripe-tailed Hummingbird, White-tailed Emerald (*Elvira chionura*) and White-throated Mountain-gem. This is the first record of frugivory in hummingbirds within Costa Rica, and the greatest number of species observed feeding on the same fruit.

Hummingbirds have only rarely been recorded feeding from fruit; the most frequently recorded (five species) is from the fruit of cacti (Lack, 1976; Bosque, 1984; Silvius, 1995; Wendelken and Martin, 1988; Vázquez-Castillo *et al.,* 2019). Poulin *et al.* (1994) inspected the stomach contents of the Coppery-rumped Hummingbird (*Amazilia tobaci*) and the Buffy Hummingbird (*Leucippus fallax*); they found seeds from 1 and 3 species, respectively, but the species were not identified. There are only two other instances of hummingbirds consuming non-cactus fruit. One study in Brazil recorded the Blue-chinned Sapphire (*Chlorestes notata*) actively piercing and consuming the fruit of the non-native Jamaica Cherry fruit (*Mutingia calabura*) (Ruschi, 2014). The Green-throated Mountain-gem (*Lampornis viridipallens*) was recorded feeding upon a *Saurauia* species (*S. scabrida*), in a montane cloud forest in Mexico (Partida-Lara *et al.,* 2018). As our findings are a similar behavior to what has been observed with species of the same genus, this suggests this behavior may be more common than previously thought.

6.2.2.1 SITE: 28

At site 28, Stripe-tailed Hummingbirds were solely feeding upon the *S. montana* fruit during most of the observation periods, even though there was *G. rosea* present, a flower that this hummingbird species was frequently noted feeding upon (Figure 2). This suggests a preference for the fruit, which could be because of higher sucrose levels; further studies are needed to confirm this. During the last week of the survey, a group of White-faced Capuchins (*Cebus capucinus*) were seen eating the fruits and after this the Stripe-tailed Hummingbird was no longer observed feeding at the trees, presumably because there was no ripe fruit left.

6.2.2.2 SITE: TOP OF MIRADOR DE VALLE

At the observation point at the top of Mirador de Valle, four species of hummingbird were found to be feeding at a *S. montana* tree on several different occasions. Stripe-tailed Hummingbird, White-tailed Emerald, and White-throated Mountain-gem were observed multiple times, whereas Purple-crowned Fairy was observed just once. Towards the end of the study period, this tree was also stripped of fruit by other birds and mammals. Common Chlorospingus (*Chlorospingus flavopectus*) was once seen feeding on the fruits of this particular tree, and a White-nosed Coati (*Nasua narica*) was also seen eating the fruit of a nearby *S. montana* tree. Thereafter, the visits by hummingbirds decreased.

6.2.2.3 SCINTILLANT HUMMINGBIRD *SELASPHORUS SCINTILLA*

As a generalist species, Scintillant Hummingbirds were expected to take advantage of the fruits, like the other short, straight-billed species. They were frequently observed feeding on *G. rosea* within close proximity of *S. montana* trees

at site 28 and at the top of Mirador de Valle, but never feeding on *S. montana* fruits. One conclusion is that as a subordinate to most other hummingbird species, they did not consider it worth the risk if there were other hummingbird arounds. However, it was seen when there were no other hummingbirds feeding on the fruits, and still did not feed from them itself. Currently it is unknown why the Scintillant Hummingbird excluded this resource.

6.3 ORNAMENTAL GARDENS

Three hummingbird species were only seen in the ornamental gardens (Table 2). For the Rufous-tailed Hummingbird, this is not surprising, as they are typically found in cleared areas (Stiles and Skutch, 1994). Furthermore, both the Snowy-bellied and the Violet-headed (*Klais guimeti*) Hummingbirds are both at the higher ends of their altitudinal occurrences in Cloudbridge, so their presence at Cloudbridge may be due to the large food quantity within the ornamental gardens (Stiles and Skutch, 1994), which is at the lowest point of the reserve. The Violet-headed Hummingbird showed a strong preference for *Lantana camara* (Appendix 1c), while the Snowy-bellied hummingbird preferred *Stachytarpheta frantzii* (Appendix 1a).

6.4 DATA COLLECTION

Recording times of feeding events was subject to vast human error, and with some variables uncontrolled, subsequent analysis was excluded. Firstly, the sizes of plants, along with the number of flowers they produced was very varied between locations. For this reason, making comparisons of feeding times between locations would result in misrepresentative data. In addition, a feeding hummingbird may have been lost from view, and then reappeared – in such cases it was unclear if this was a new feeding individual, or the same one coming back into view. This meant that recorded total feeding time may not have been the same as the actual feeding time. This could be improved by selecting a small area of a flowering plant to observe, in order to standardise results across multiple locations.

7 CONCLUSION & RECOMMENDATIONS

The diversity of plant species that are regularly fed upon by hummingbirds within Cloudbridge is relatively low. Our results over-represent rare feeding events, while under-represent common ones, but clearly shows what plant species hummingbirds feed upon within the reserve. There appears to be two main groups of feeding hummingbirds, the understory species, which specialise on *Heliconia* sp., and the canopy species, which feed on a broader diet. *G. rosea* is a widespread plant within Cloudbridge and provides abundant nectar for most of the hummingbirds.

It is important to look into hummingbird's diet at other times of the year, as it is very likely to change and may yield very different results. Future studies could look more specifically into how the different hummingbirds interact with *G. rosea*. Cloudbridge is also a perfect site to collect more data regarding frugivory of *S. montana*, especially as this is such a rare event. To further explore the diversity of plants utilised by hummingbirds within Cloudbridge, walking surveys could be conducted. This would cover a greater area of the reserve, potentially revealing other food sources.

8 ACKNOWLEDGEMENTS

We would like to thank Cloudbridge Nature Reserve for allowing us to conduct our study here, in particular Jennifer Powell for her assistance and guidance throughout the study. We would also like to thank Jonathan Slifkin for assisting with surveys and providing photographs of some of the hummingbirds.

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Appendix

APPENDIX 1 – ORNAMENTAL PLANT SPECIES

a) *Stachytarpheta frantzii,* b) *Wercklea woodsonii,* c) *Lantana camara,* d) *Citrus aurantium,* and e) Unknown.

Appendix

APPENDIX 2 – FOREST PLANT SPECIES

a) *Heliconia* sp., b) *Besleria* sp., c) *Saurauia montana,* d*) Gonzalagunia rosea,* e) *Malvaceae* sp., f) *Fabaceae* sp., g) *Palicourea lasiorrhachis,* and h) *Cuphea appendiculata.*