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Diet Preference, Competition and Learning in a Cloud Forest Hummingbird Community

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ABSTRACT

The purpose of this study was to determine hummingbird preference between protein and higher sugar concentrations, and how any preference affects competition and memory. We hung three sets of three feeders in triangular patterns and observed hummingbird visits and interactions. We also, noted solitary feedings on the days directly following both site establishment and feeder rotation. Our results showed that there was an overall preference for the feeder with higher sugar concentration, that larger species and newcomers were generally dominant and that birds did not take longer to learn the values of established leaders that had been rotated than feeders whose contents were unknown. We concluded that larger, more aggressive birds had a stronger preference for the feeder with the highest sugar concentration, smaller birds tended to take more dips per feeding, birds with curved beaks showed less interest in the feeder with fruit flies present, it is easier for a newcomer to dominate a feeder and to maintain control of it after an interaction and spatial location of feeders is the most important memory cue.

RESUMEN

El propósito de este proyecto fue determinar si los colibríes tienen una preferencia entre la proteína y una concentración de azúcar más alta y como la preferencia afecta la competencia y la memoria de los colibríes. Nosotros suspendimos tres juegos de tres comederos de forma triangular y observamos los colibríes. Nosotros notamos también la alimentación solitaria en los cinco días directamente después del establecimiento de un sitio y la rotación de los comederos. Nuestros resultados mostraron que hubo una preferencia por los comederos con las concentraciones de azúcar más alta. Además las especies grandes y colibríes recién llegados fueron generalmente dominantes. A los colibríes les tomo mas tiempo aprender los valores de los comederos con contenido desconocido que los comederos establecidos que fueron rotados. Nosotros concluimos que los colibríes mas grandes v mas agresivos tuvieron una preferencia mas fuerte por los comederos con una concentración de azúcar mas alta. Los colibríes más pequeños tendieron a tomar mas bebidas por visita. Los colibríes con picos encorvados mostraron menos interés en el comedero con moscas de fruta presentes por la proteína. Es mas facil para un colibrí recién llegado dominar un comedero y mantener el mando de un comedero después de una interacción y la situación de los comederos es la más importante que la memoria de los colibríes.

INTRODUCTION

Background

Their high energy requirements necessitate that hummingbirds expend the bulk of their feeding time searching for and consuming sugars, however, it is also known that all species of hummingbirds require additional nutrition, fulfilled in natural settings by foraging for arthropods (Long 1997; Stiles & Skutch 1989). Hummingbirds have been intensively studied both in captivity and in the field to determine the extent and the

nature of their competitive interactions (Feinsinger 1976; Hazlett et al. 1979; Melcher et al. 1983; Tiebout 1992; Trombulak 1979). Studies point to aggressive inter- and ultra-specific competition for both sugar and protein. Other studies have focused on the learning abilities of hummingbirds (Trombulak 1979) or their learning mechanisms (Gayle & Clifton 1993; Hurley 1996; Hurley & Healey 1996). The consensus among such studies seems to be that the spatial location of a resource is more important to hummingbird memory than are visual cues.

The tropical cloud forest of Monteverde, Costa Rica presents a unique opportunity to study large hummingbird communities in their natural settings. This species-rich area is known to support at least 30 different hummingbird species (Fogden 1993).

Study Design and Predictions

This study investigated preference for different resources of seven species of hummingbirds reported in lower montane wet forest in Monteverde, Costa Rica by Fogden (1993). In three separate sites, three feeders were hung in the shape of an equidistant triangle and differed from each other both qualitatively and quantitatively. One of the feeders had fruit hung from it to attract fruit flies. The presence of fruit flies provided a constant protein source at the feeder, allowing birds to fulfill their sugar and protein requirements at the same time. This feeder was expected to be more attractive to straight-billed species than to species with strongly decurved bills because curved bill morphologies can preclude efficient fly catching (Stiles 1995). One of the feeders had a higher concentration of sugar. We predicted that across all species there would be a general preference for the feeder with the highest sugar concentration. We expected that species with straight bills (*Heliodoxa*, *Lampornis*, *Eupherusa*, and *Calliphlox*) would prefer the feeder with the fruit flies as much as the feeder with the higher sugar concentration. We thought that the average length of feedings would be greater for all species at the feeder with the highest sugar concentration.

This study also attempted to quantify the competitive interactions between males of the four most common species at our study sites. We examined the role that circumstance has on dominance by noting the resident and newcomer in each interaction. We expected the birds that Stiles and Skutch (1989) label as very aggressive (*Lampornis* and *Eupherusa*) would be dominant in inter-specific competition. We thought that birds arriving at a feeder first (residents) would hold no competitive advantage over those arriving subsequently (newcomers). We did not expect a significant difference in frequency of winners between residents and newcomers. Finally, we expected that competitive interactions would occur with greatest frequency at the feeder with the highest sugar concentration.

We hypothesized that the feeding frequencies at newly erected sites would come to resemble the solitary feeding frequencies at well-established sites faster than frequencies at sites where feeder positions had just been rotated. This expectation was a

result of both preliminary results and studies, which suggest that spatial patterns are the most important factors for hummingbird memory (Gayle & Clifton 1993; Hurley 1996; Hurley & Healey 1996). Thus, we expected that feeding percentages at rotated sites would take longer to approximate the normal feeder preference than those at new sites because birds at new sites would not be relying on spatial patterns to determine feeder content, while those at rotated sites would be using misleading spatial patterns.

Study Subjects

The Coppery-headed Emerald (*Elvira cupreiceps*) is a small bird (7.5cm, 3.2g) with a short, decurved bill. This species is not known for aggressive behavior. We observed only female *Elvira* at our feeders. The Green-crowned Brilliant (*Heliodoxa jacula*) is a large bird (13cm, 9.5g) with a straight bill. It is not commonly an aggressive species. The Green Hermit (*Phaethornis guy*) is a larger bird (15cm, 6g) with an exceptionally long, decurved bill. Green Hermits are not known to be aggressive. The Purple-throated Mountain-gem (*Lampornis castaneiventris calolaema*) is a medium sized bird (10.5cm, 6g) with a nearly straight bill. Males of this species are often very aggressive and have been known to defend resources territorially. The Striped-tailed Hummingbird (*Eupherusa eximia*) is medium-small (9.5cm, 4.3g) bird with a straight bill. Male Striped-tailed Hummingbirds are known to be extremely aggressive considering their small size. The Violet Sabrewing (*Campylopterus hemileucurus*) is a large bird (15cm, 11.5 g) with a decurved bill. Males of this species are not considered to be as aggressive as their superior size would indicate. The Magenta-throated Woodstar (*Calliphlox bryantae*) is a small bird (9cm, 3.5g) with a straight bill. Despite their diminutive stature, both sexes of this species can be aggressive, especially in intra-specific interactions, though larger species often ignore them (Stiles & Skutch 1989).

METHODS

Our three study sites were located in the lower montane wet forest above the Estación Biológica, Monteverde, Puntarenas, Costa Rica. Two sites were on the Sendero Principal at 1605 meters above sea level. The third site was on Sendero Cariblanco at 1600 meters above sea level. Each site consisted of three commercial, red hummingbird feeders hung between two and three meters above the ground with blue rope. Feeders all had identical red plates hanging approximately 0.25 meters below them. The feeders were arranged, in roughly triangular patterns, (as viewed from above) and spaced five to eight meters apart. One feeder at each site contained a 20% sugar solution and had fruit (to attract fruit flies) on the red plate hanging beneath the feeder (A), another had a 20% sugar solution (feeder B). The third feeder (C) at each site contained a 25% sugar solution (all concentrations are expressed as percent by volume). The feeders at each site were rotated twice, in a counter-clockwise direction, such that feeder A moved to where C had been, feeder C moved to where feeder B was, and feeder B moved to where A had been. The rotations were done well after the establishment of a site, so

that every feeder was at each location for at least four days. Rotations were done to eliminate any possible effects of a habitat preference.

Data were collected over a period of 28 days and observations were made daily between 6:30 AM and 12:00 PM. Solitary visits were defined as visits where the feeding bird's decision to leave the feeder was not visibly influenced by other birds. Data recorded for each solitary hummingbird visit consisted of gender, species, feeder and number of dips (the number of times the bird's beak disappeared inside the feeder). Visits ended when the bird left the collector's field of vision or perched somewhere other than on the feeder. A chi-squared test was used to determine if the number of visits per species*gender category (defined by the species and gender of birds: i.e. female Violet Sabrewings are a species*gender category) deviated from random for the solitary data. We used a 2-way ANOVA to test the effects of feeder type and hummingbird species on the average number of dips per visit.

Competition data were taken whenever a second bird chased the feeding bird or when the feeding bird left the feeder to chase a newcomer. All competitive interaction analyses were based on males of four species of hummingbirds that were abundant enough to permit statistical testing: specifically the Violet Sabrewing, Green-crowned Brilliant, Purple-throated Mountain-gem and the Striped-tailed Hummingbird (these can be seen in Fig. 1). We chose to look exclusively at male birds for this part of our experiment because they are thought to show far more aggressive behavior than the females (Stiles & Skutch 1989). For each interaction we recorded the feeder, gender and species of both birds and the outcome of the interaction. The type of interactions recorded were either newcomer chases resident (initial bird feeding), or resident chases newcomer. A chi-squared test was used to determine if a resident or a newcomer tends to be a chaser more often. In addition, winners (birds that returned to feed after an interaction) were tallied. We used another chi-squared test to determine if the residents or the newcomers win a significant proportion of interactions. Pair-wise comparisons of competitive interactions were made using contingency tables for each species at their preferred feeder and also over all feeders.

A third type of data was collected for the days following the establishment of a new site or the rotation of feeders at an established site. A timeline showing the timing of feeder rotation and data collection is inserted here. This represents an example of the events occurring over the duration of our study period for only one of our three sites; however, the other two were managed in a similar fashion. There was an acclimation period of six days after a new site was set up during which the birds were allowed to test the feeders to become adjusted to the contents of each feeder. Data were taken during these six days to construct a primary learning curve, but were kept apart from the data taken afterwards. After this six-day period competition and solitary data were taken. The percentage of solitary visits for each species of hummingbird at each feeder was tabulated. These percentages were considered to be the normal feeding preferences for the hummingbirds since they represented choices made by birds accustomed to the spatial

pattern of the feeder. These normal feeding preference data were used to compare all learning data taken during the study with. If the learning data for any given day after a site rotation or establishment were found to be within ten percent of the normal feeding preference data at each of the three feeders, then they were considered to be normal feeding and were added to solitary feeding and competition data. Once a day's data at a given site were considered to be normal feeding, every subsequent day's data at that site were counted as normal until the next feeder rotation. The data from the first day after rotation of the feeders from each of the three sites were compiled as day one data; data taken on the second day after feeder rotation was compiled as day two data and so forth for the first five days. Lastly, the data that were collected during the acclimation periods were separated by day and compiled from all three sites. We graphed the feeding percentages at each feeder for the first five days following site establishment and feeder rotation and compared both to the "normal feeding preference".

Day 1; Set
Up Site 1

Day 6; Started
Taking Data

Day 10; Rotated
Feeders

Day
14

Day 18; Rotated
Feeders

Day
22

Day 26;
Removed Site

Acclimation Period

Took Normal
Feeding Data

Took
Learning
Data

Took Solitary
Feeding Data

Took
Learning
Data

Took Solitary
Feeding Data

RESULTS

Do any of the 13 species*gender categories show a preference for one of the three diets available?

Chi-squared results showed significant feeder preferences for seven of the 13 species*gender categories and significant feeder avoidance for three species*gender categories. Six categories preferred feeders A or C, one preferred feeder B and three species*gender categories avoided feeder B. Three categories showed no significant preference (Table 1).

Is the average number of dips per feeding affected by the resource type or species?

There was no significant difference between the average number of dips at the three feeders ($F = 0.875$, $P = 0.4170$, $df = 2$), nor was there a significant effect of both species and resource type ($F = 1.584$, $P = 0.1482$, $df = 61$). The average number of dips across species was found to be significantly different ($f = 11.535$, $P < 0.00001$, $df = 3$). In a Scheffe post-hoc comparison of species. Striped-tailed Hummingbirds took a significantly greater number of dips per visit than each of the other three species tested (Table 2 and Fig. 2). None of the other species pairs showed a significant difference in the number of dips per visit. Green-crowned Brilliants (std. dev. = 5.646) and Striped-tailed Hummingbirds (std. dev. = 5.641) both had higher standard deviations in average number of dips per visit. Violet Sabrewings (std. dev. = 3.388) and Purple-throated Mountain-gems (std. dev. = 2.961) both had lower standard deviations.

Are competitive interactions random across feeders?

There were significantly more competitive interactions at feeder C than at the other two feeders ($\chi^2 = 32.57$, $P < 0.05$). The contingency table for interactions between male Striped-tailed Hummingbirds and males of the three other competition species showed no significant deviation from random (χ^2 P-value = 0.9234). The contingency table comparing male Violet Sabrewings to other males showed significant deviation from random, with feeder C being heavily preferred (χ^2 P-value = 0.0002) (Tables 3 and 4).

Does the resident or the newcomer tend to be a chaser?

Newcomer birds were chasers significantly more often than resident birds ($\chi^2 = 310.42$, $df=1$, $cv = 3.84$, $P < 0.05$).

Who wins more often, resident or newcomer?

Our results showed that newcomers were winners significantly more often than residents ($\chi^2 = 49$, $df= 1$, $cv = 3.84$, $P < 0.05$). Thus, newcomers tend to be both chasers and winners. **Which species dominate other species?**

Our results showed that male Violet Sabrewings are the chaser significantly often in competitive interactions with males of the other three species. Male Purple-throated Mountain-gems chased male Striped-tailed Hummingbirds significantly often. However there is no significant difference in the number of times that male Green-crowned Brilliants chase or are chased by male Purple-throated Mountain-gems and male Striped-tailed Hummingbirds (Table 5).

Do hummingbirds learn more quickly when the resources are known but rotated, or when they are previously unknown?

From our learning curve graphs we can speculate that the hummingbirds at our study sites learned the rewards of a new, unlimited resource in three days. It seems that the graphs for learning at new sites and rotated sites are similar (Figs. 3 and 4). This suggests that hummingbirds learn the quality of resources equally quickly, whether they are new or simply different from the expected resource.

DISCUSSION

Solitary Feedings

The general trend in our solitary feeding data is a strong preference for the 25% sugar solution of feeder C. This finding is consistent with our prediction that overall feeder C would be preferred. It is also consistent with previous studies, which show that hummingbirds prefer the highest concentration of sugar available to them in feeders (Roberts 1996).

Although only one of the hummingbirds we looked at, the female Green-crowned Brilliant, significantly preferred the feeder (A) associated with fruit flies, no species or gender significantly avoided it. We think that the female Green-crowned Brilliant was able to choose feeder A more often than C because it does not waste as much energy in competition as male hummingbirds. However, it would be able to take advantage of the fruit flies associated with feeder A because of its straight bill.

Some of the other straight billed species tended to have a preference for A, but did not significantly prefer it. The Violet Sabrewings and the Green Hermits were the only two species studied to have long, decurved beaks. Both species tended to have less preference for feeder A than other species. This is probably a result of their curved bills impeding fly catching (Stiles 1995).

Male Magenta-throated Woodstars were the only species or gender to show a significant preference for feeder B. One possible reason that they preferred feeder B is that it was least often defended by larger, more aggressive species. Another possible explanation is that small sample size ($n = 26$) was responsible for the unusual result. The reason for the low number of solitary visits is that their diminutive size requires that they flee any interactions. The Magenta-throated Woodstars did not intimidate even the small Striped-tailed Hummingbirds, and they were occasionally observed being chased by females of various other species. The female Coppery-headed Emerald showed almost equal preference for feeders A and C. The Coppery-headed Emerald probably uses this strategy because it utilizes the protein source, but sometimes needs extra energy to flee from the larger birds. The male Purple-throated Mountain-gem and the male Striped-tailed Hummingbird both significantly avoided Feeder B. Birds in these two species* gender categories showed a trend for preferring feeder C. The two smaller male species were involved in many competitive interactions and probably chose not to risk being

involved in an interaction at a feeder of inferior value. All three of these species have small bills that allow them to easily catch fruit flies making feeder A a good resource for them.

Five of the species * gender categories significantly preferred feeder C. Both male and female Violet Sabrewings are large hummingbirds and need the more easily accessible energy that higher concentrations of sugar provide. Also, their size possibly gives them an advantage in feeding undisturbed at their preferred feeder by deterring would-be aggressors. We observed male Violet Sabrewings interacting more than the other species and genders. Because competitive interactions require much energy, the aggressive Violet Sabrewings probably needed a resource higher in sugar content (Tiebout 1993). Male Green-crowned Brilliants also preferred feeder C and like the Violet Sabrewing were observed in many competitive interactions. The female Purple-throated Mountain-gems and the female Stripped-tailed Hummingbirds both preferred feeder C and fed at A and B relatively equally. This result for the female Purple-throated Mountain-gem may be the result of small sample size ($n = 44$). But more likely this is an indication that female Purple-throated Mountain-gems and the female Stripped-tailed Hummingbirds need a more high-energy diet than the males of the same species. This is possibly a result of the females feeding less often due to competition. We observed some aggressive behavior in both the female Purple-throated Mountain-gems and the female Stripped-tailed and this could be responsible for their preference for a high-sugar diet.

Three of the species * gender categories that we looked at had no feeder preference. These three all had relatively small sample sizes. Both the male and female Green Hermits showed no feeder preference. This may be partially explained by their long decurved bills since they would have a particularly hard time catching the fruit flies. However, their bill morphology should not preclude their preference of feeder C. A likely reason that feeder C was not preferred is that it is subject to higher levels of competitive interactions, and the less aggressive Green Hermits could not feed there often without being involved in these. The Female Magenta-throated Woodstar on the other hand has a small bill and could easily catch fruit flies. However, it is an extremely small species and like the Green Hermit, it probably chooses to feed wherever it perceives the least chance of competition, rather than where it prefers to (Table 1).

Another consequence of the Magenta-throated Woodstars' position at the bottom of the dominance hierarchy was that when a feeder was free of other birds, Magenta-throated Woodstars took full advantage. They did this mainly by feeding longer at each visit. While there were insufficient data on solitary feedings by Magenta-throated Woodstars to run an ANOVA on, we observed that their average number of dips per visit seemed to be much higher than that of other species.

Although most of the species significantly preferred feeder C, they did not tend to take a significantly higher number of dips at this feeder. This is most likely a result of adaptive hummingbird behavior, which might have evolved by selection for birds that fed the longest "safe" amount of time. This would be a compromise between a long

feeding, providing high nutrition but a great risk of attack by predators or competing birds and a short feeding, providing low nutrition but relative safety from attack. If this behavior were occurring, hummingbirds would take a similar number of dips per feeding no matter what the quality of resource was.

Competitive Interactions

That competitive interactions were more common at the feeder preferred by the majority of hummingbird species studied suggests that birds are more willing to engage in costly, aggressive behavior over a favored resource.

Circumstance is important in competitive interactions. Newcomers held an advantage over residents in every situation. This is most likely a result of several factors working in concert. A newcomer is taking an aggressive action and so is labeling himself as the aggressor. This may intimidate the resident bird, or it may simply surprise him and cause him to take evasive action. Another possible explanation is that the physical difficulties of defending a feeder from a charging bird are greater than simply bolting towards an unsuspecting bird. This, combined with the handicap imposed on the resident by having to back away from the feeder before taking aggressive action, provides ample reason for a resident bird to flee the newcomer the majority of the time. Also, the observed trend may simply be a function of aggressive birds tending to initiate interactions, and non-aggressive birds avoiding interactions. Along with dominating competitive interactions, the newcomer won significantly more interactions than the resident did. This is probably due to the same advantages of being a newcomer outlined above.

In competitive interactions between males of the four species observed for competition, the Violet Sabrewings were clearly dominant. Contrary to what was suggested by Stiles & Skutch (1989), they were aggressive towards each of the other three species significantly more often than they were the victims of aggression. The Violet Sabrewings are the largest of the four hummingbird species, suggesting that size is an important factor in dominance. The Striped-tailed Hummingbird was the smallest of the four species and was chased most often by the other three species. This too, was surprising in light of the comments of Stiles & Skutch (1989), which suggested that the Striped-tailed Hummingbird was a more dominant species. This result also supports the notion that size is crucial in dominance hierarchies. The interactions observed between the Purple-throated Mountain-gem and the Striped-tailed Hummingbird were significantly in favor of the larger Purple-throated Mountain-gem. The most interesting interactions occurred between the two middle sized birds, the Purple-throated Mountain-gem and the Green-crowned Brilliant. No significant difference was found between the number of times males of these species chase each other. There were not many observations of interactions between these two species ($n = 23$), however, a significant number of those interactions took place at feeder A. This is possibly a result of the larger, more dominant Violet Sabrewings monopolizing feeder C. While neither species

preferred feeder A in solitary feeding situations, both have ideal beaks for fly catching. It is possible that they use feeder C to provide short bursts of energy, but are willing to fight over the protein source because it is an essential portion of their diets (Long 1997). Because this pair appears with only cursory data, to be competitively equal it would prove rewarding to devote a future study to the details of their relationship.

The Effects of Competitive Success on Feeding Strategies

The dominance hierarchy that we determined using our observed competition data shows that males of the three other species chosen for interactions dominate the Stripped-tailed Hummingbird (Table 5, Fig. 1). A pair-wise comparison of average number of dips per visit for the four common species shows that all species pairs that took significantly different numbers of dips per visit involved Striped-tailed Hummingbirds (Table 2 and Fig. 2). Since the Striped-tailed Hummingbird is at the bottom of the dominance hierarchy it tends to be chased off more by larger species. The competitive inferiority of the Striped-tailed Hummingbird might result in a strategy that attempts to take as much food as possible at every feeding. This “anxious” strategy would attempt to make up for frequent aggressions from other birds by gathering an excess of food at each visit. Support for the utilization of this strategy comes from the two-way ANOVA test, which shows that the Striped-tailed Hummingbird takes almost two dips more per feeding than the other three species. We expect that the diminutive Magenta-throated Woodstar uses a similar feeding strategy. This supposition was supported by our observations; however, due to a small sample size we were unable to include them in the test.

Green-crowned Brilliant did not differ significantly in ANOVA results from the other species however; they did exhibit a wide range of average dips per visit. One explanation for this is that Green-crowned Brilliants use a strategy that results in two different behaviors. This "opportunistic" strategy would promote few visits of many dips in situations with a relatively low abundance of competitors and many visits of few dips at times when there was high abundance of competitors. This reflects their tendency to perch noted by Stiles and Skutch (1989). This strategy would allow the perching bird to reduce the amount of time spent at the feeder and to gain the advantage in competitive interactions by having the option to become the newcomer.

Both male Violet Sabrewings and male Purple-throated Mountain-gems were observed using a third strategy, which might be called "unconcerned." This strategy consists of making feeder visits of approximately similar and relatively normal length. This strategy most likely results from the ability of these two species to dominate competitive interactions. Since they are not worried as much about being chased away by a competitor, they do not have a special mechanism for avoiding chases. Rather their average number of dips is only limited by the behavior noted above whereby hummingbirds are selected to feed for a certain amount of time to optimize both nutrition and safety.

Learning Rates in an Unstable Environment

Our two graphs showing feeder preference directly following site establishment and feeder rotation seem to show similar patterns. Both graphs indicate that by the third day following the establishment of new conditions, the hummingbirds seemed to be choosing feeders at similar frequencies to the normal feeding preference. This result is surprising when compared with other studies that examine hummingbird memory. We expected to find that hummingbirds would be slower to return normal feeding frequencies after feeder rotation than they would be after a new site was established. This would be in following with the idea of spatial location is the most important memory cue for hummingbirds (Gayle & Clifton 1993; Hurley 1996; Hurley & Healey 1996). However, upon close examination, there is evidence in our study that spatial patterns are playing a significant role in feeder choice. The data for day one in Fig. 4 look almost like normal feeder preference for the feeders in the previous day's pattern. This means that the percentage of visitation to feeder A is similar to the percentage of visitation to feeder C in normal feeding preference. This suggests that the spatial pattern of the feeders was the most important factor in determining the hummingbirds' feeder choice. Also, the sites that were rotated were already established and thus, received higher visitation than those sites that were new. This would act to speed learning at the rotated sites, possibly canceling out the negative impact of the unexpected feeder locations on learning rates. The higher competition at the well-established sites would also force many birds to feed at a feeder located in a position other than where they expected their preferred feeder to be. This would allow them to realize that the feeder pattern had been switched. We observed this behavior on the day after we switched one of our sites. Many birds were competing over the feeder (A) located where feeder C had been the day before, while feeder C did not receive nearly the level of visitation. This portion of the study deserves to be re-examined at greater length focusing on learning on a finer time scale. It would also be useful to look at the learning rates of each species and gender group separately.

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Table 1 The number of solitary feeding visit to feeders A, B and C, chi-squared value and significant feeder preference or avoidance for each species and gender. Asterisks indicate significant chi-squared values.

Gender, Species	Visits to A	Visits to B	Visits to C	X ²	Feeder Preferred/Avoided
Female Coppery-headed Emerald	27	5	22	14.77*	Avoided Feeder B
Female Green-crowned Brilliant	29	7	17	13.76*	Preferred Feeder A
Male Green-crowned Brilliant	63	28	131	74.14*	Preferred Feeder C
Female Green Hermit	11	9	20	5.15	None
Male Green Hermit	9	4	9	2.27	None
Female Purple-throated Mountain Gem	9	9	26	13.14*	Preferred Feeder C
Male Purple-throated Mountain Gem	48	22	52	13.05*	Preferred Feeder B
Female Striped-tailed Hummingbird	24	13	36	10.87*	Preferred Feeder C
Male Striped-tailed Hummingbird	83	49	93	14.18*	Avoided Feeder B
Female Violet Sabrewing	24	16	61	34.24*	Preferred Feeder C
Male Violet Sabrewing	90	73	193	71.06*	Preferred Feeder C
Female Magenta-throated Woodstar	11	4	7	3.36	None
Male Magenta-throated Woodstar	5	16	5	9.31*	Preferred Feeder B

Table 2 Results of Scheffe Post-hoc test on ANOVA data. Tested for effect of species on number of dips per visit.

Species Compared	Mean Diff.	Crit. Diff.	P-Value	Spp. Responsible For Difference
Green-Crowned and Mountain-gem	-0.071	1.254	0.9989	None
Green-crowned and Stripe-tailed	-1.964	1.067	<.0001	Stripe-tailed
Green-crowned and Violet Sabrewing	-0.23	0.974	0.9325	None
Mountain-gem and Stripe-tailed	-1.893	1.236	0.0004	Stripe-tailed
Mountain-gem and Violet Sabrewing	-0.159	1.156	0.9856	None
Violet Sabrewing and Stripe-tailed	1.734	0.95	<.0001	Stripe-tailed

Table 3 A. Observed frequency of interactions at the three feeder types between male Violet Sabrewings and males of the other three species included in the competition data. $X^2 = 1.960$ B. Observed frequency of interactions at the three feeder types between male Stripe-tailed Hummingbirds and the other three species included in the competition data. $X^2=26.172$.

A. Interaction Between Violet Sabrewing and:	Feeder A	Feeder B	Feeder C	Totals
Violet Sabrewing	24	47	95	166
Striped-tailed Hummingbird	33	21	44	98
Purple-throated Mountain-gem	15	11	17	43
Green-crowned Brilliant	15	27	20	62
Totals	87	106	176	369
B. Interactions Between Striped-tailed Hummingbirds and:	Feeder A	Feeder B	Feeder C	Totals
Striped-tailed Hummingbird	12	9	13	34
Violet Sabrewing	33	21	44	98
Purple-throated Mountain-gem	24	12	22	58
Green-crowned Brilliant	12	10	16	38
Totals	81	52	95	228

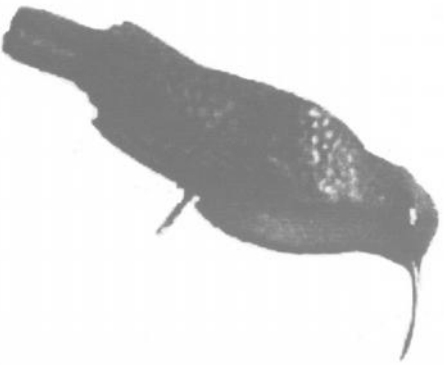
Table 4 Observed frequency of interactions at the three feeder types between male Green-crowned Brilliants and male Purple-throated Mountain-gems and the chi-squared value for that interaction.

Interaction Between	Feeder A	Feeder B	Feeder C	x^2
Purple-throated Mountain-gem and Green-crowned Brilliant	14	2	7	9.48

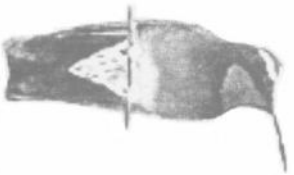
Table 5 A. Frequency of aggressions and corresponding chi-squared values for inter-specific interactions between males of four hummingbird species at all feeders.

B. Frequency of aggressions and corresponding chi-squared values for inter-specific interactions between males of four hummingbird species at feeder C (the preferred feeder for all four species).

A. Interaction Between:	Aggressive Interaction Initiated	χ^2
Violet Sabrewing	52	
Green-crowned Brilliant	12	25
Violet Sabrewing	93	
Stripe-tailed Hummingbird	21	45.4
Violet Sabrewing	51	
Purple-throated Mountain gem	10	27.56
Green-crowned Brilliant	21	
Stripe-tailed Hummingbird	18	0.24
Green-crowned Brilliant	14	
Purple-throated Mountain-gem	13	0.04
Purple-throated Mountain-gem	58	
Stripe-tailed Hummingbird	14	26.88
B. Species	Aggressive Interactions Initiated	χ^2
Violet Sabrewing	17	
Green-crowned Brilliant	4	8.04
Violet Sabrewing	41	
Stripe-tailed Hummingbird	10	18.84
Violet Sabrewing	22	
Purple-throated Mountain-gem	6	9.14
Green-crowned Brilliant	9	
Stripe-tailed Hummingbird	8	0.06
Green-crowned Brilliant	4	
Purple-throated Mountain-gem	7	0.82
Purple-throated Mountain-gem	28	
Stripe-tailed Hummingbird	5	16.04



Violet Sabrewing
15 cm, 11.5 g



Purple-throated Mountain-gem
10.5 cm, 6 g



Green-crowned Brilliant
13 cm, 9.5 g



Striped-tailed Hummingbird
9.5 cm, 4.3 g

Fig. 1 Males of the four species included in competitive interaction data. Arranged left to right in order of the observed dominance hierarchy.

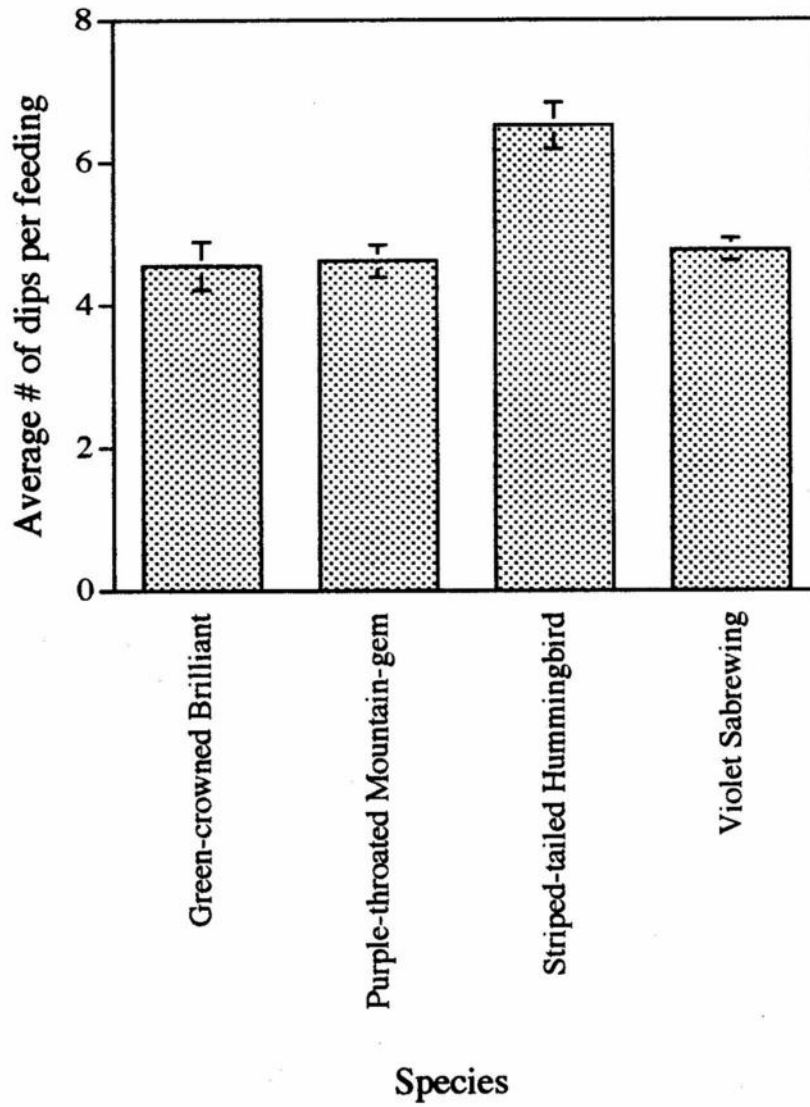


Fig. 2 The average number of dips per feeding by four species of hummingbirds, with standard error bars.

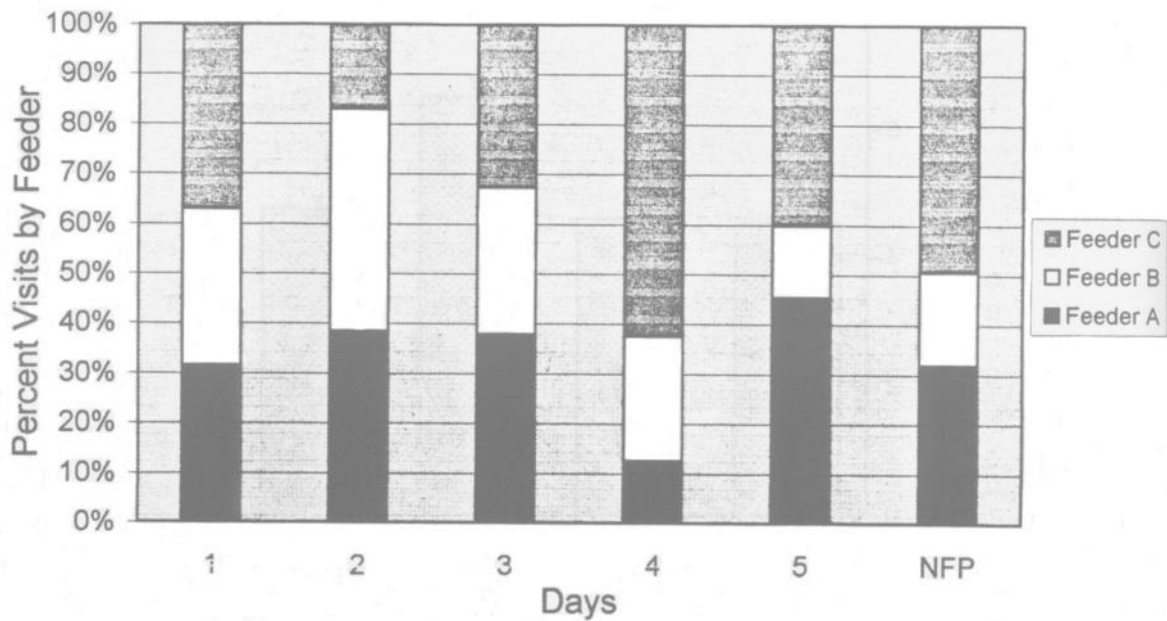


Fig. 3 Change in feeder preference during the first five days after a new site was established. Data were compiled at two different sites. Feeders with 20% solution and protein source (A). 20% sugar solution (B) and 25% sugar solution (C) were observed. The number of days indicates time since sites were established. Normal Feeding Preference (NFP) is the data compiled at well-established feeders at three different sites.

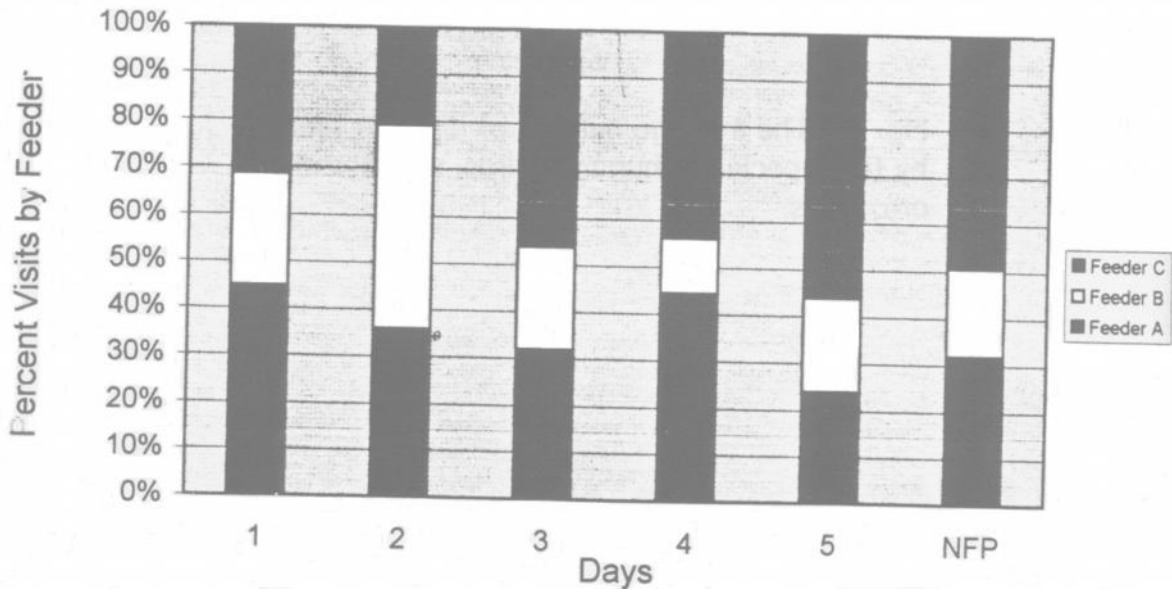


Fig. 4 Feeder preference over the first five days after a well-established site was rotated. Data were compiled at three different sites. Feeders with 20% solution and protein source (A), 20% sugar solution (B) and 25% sugar solution (C) were rotated such that B followed A. A followed C and C followed B. The number of days indicates time since feeders were rotated. Normal Feeding Preference (NFP) are the data compiled at well-established feeders at all three sites.