Nectar Accumulation Rates of *Etlingera elatior* and the Possible Effects on Foraging Patterns of Some Costa Rican Hummingbird Species

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Abstract - There are many plant-pollinator relationships that can manipulate behavior of one another. This can be seen in nectar production rates (NPR) and hummingbirds. I observed and collected nectar from *Etlingera elatior*. I collected nectar at varying time intervals, mimicking a hummingbird's feeding patterns. Hourly extraction of nectar showed the highest accumulated nectar and highest average nectar production rate. Hummingbirds were also observed feeding later on *E. elatior* than on other species of plants which were feed on earlier in the day. There was also a uniform peak for NPR for all flowers on the inflorescence that correlated with the time that hummingbirds started feeding. Implications for these results were that removing nectar hourly not only increase the volume of nectar produced but also the NPR. There is both territoriality and traplining present for hummingbird strategies. Nectar producing strategies for *E. elatior* are suggested to be one of constant NPR and varied nectar quantities to cause hummingbirds to forage longer. Further suggestions could be made if nectar sugar concentration were studied.

INTRODUCTION

In many plant pollinator interactions there is a dichotomy that causes specific plant characteristics and sequentially the pollinator forms certain strategies to thrive off those characteristics, and vice versa. Nectar production is one of these important plant characteristics that contributes to a plants success, along with spatial distribution of their flowers, floral density and floral architecture (Real and Rathcke, 1991). Based on nectar production, a pollinator, in this case hummingbirds, can devised several feeding and/or foraging strategies. The plant too can have different strategies for how it produces its nectar. Two of the main hummingbird strategies that have been studied by researchers such as Temeles et al. (2006), Stiles (1975) and others would be described as "traplining" and "territoriality". Stiles (1975) describes traplining as a birds suggested route from flower patch to patch visiting in a particular sequence. This route may involve mainly plants that are not territorialized and those that have inflorescences with many flowers containing high-quality nectar rewards (Temeles et aI., 2006 and Stiles, 1975). Territoriality on the other hand, explained by Stiles (1975) is only beneficial if the nectar rewards are great enough to be able to expend the energy to defend the territory. These adapted behavioral strategies are only based on how, where, and when the plant produces its nectar. Castellanos et al. (2002) cite that plant species including hummingbirds as pollinators typical produce more nectar that is more dilute. Castellanos et al. (2002) also describes how nectaries should be able to regulate nectar volume once it either has been removed or if the concentration changes due to an environmental effect, such as evaporation because of humidity. Castellanos et al. (2002) also cites from others research that hummingbird adapted species may produce nectar during periods of the day just befpre birds are active. There are many implications to why plants would adapt to some of these strategies just based off of nectar production. Most of the reason plants have formed these approaches would be to benefit the success of their offspring. A more satisfying nectar reward will attract more birds, which may disperse pollen at a greater rate. Varying amounts of nectar throughout the day guides hummingbirds to look for "bonanzas" of nectar by testing each flower, further dispersing their pollen (Feinsinger, 1978).

Most research on nectar sampling that has been done by Stiles (1975), Real and Rathcke (1991), Pleasants (1983), and Aizen and Basilio (1998) does not mimic the actually rate at which hummingbirds may feed. Although there are some hummingbird specific studies by Navarro (1999), Castellanos et al. (2002), Temeles et al. (2006) and Feinsinger (1978) that have proven to be helpful. Most of the later studies mentioned conduct nectar extraction hourly to every two hours with ranges from 0600 to 1800+ hours.

In this study nectar removal patterns will be set up to try and mimic the frequency of hummingbird visits and feeding. This will most likely effect the total accumulation of nectar and the nectar production rates of the plant species. This data collected will optimistically translate into certain strategies for both hummingbird and plant.

Study site and plant information- This study was conducted at Selva Verde Lodge and Rainforest Reserve's Botanical Garden in Sarapiqui, Heredia, Costa Rica (loo34'N;84°2'W). Studies were conducted between May 23 and 28, 2008. This area is located on about 500 acres of primary lowland forest. The plant studied, *Etlingera eiatior,* more commonly known as the torch ginger was very common in the Botanical Garden. *Etlingera elatior* is a part of the Zingiberaceae family and order Zingiberales. There are approximately 50 genra and over 1000 species indigenous to the tropics (Dahlgren et aI., 1985). This species of *Etlingera* have long stalks 4-6m tall that have bright pink rounded or conical head-like inflorescences. The flowers are 4-5cm long hidden by red bracts with a yellow rim. The plants prefer an altitude ranging from sea level to 1300m. They also happen to be the only species of *Etlingera* in Costa Rica (Gargiullo, 2008).

MATERIAL AND METHODS

Nectar sampling- I surveyed La Selva Lodge's Botanical Garden May 23, 2008 for a group of *Etlingera elatior* that would be suitable for both observations and data collection. A single inflorescence was chosen and bagged with wedding veil to prevent hummingbirds from feeding on the nectar.

The next morning (0600) nectar was collected from three different flowers on the inflorescence. Each flower had nectar removed at different time intervals (Flower I-every 30 minutes; Flower 2-ever 60 minutes; Flower 3-every 120 minutes), until 1200 CST. After taking each sample, the inflorescence was rebagged. The number of flowers present on the inflorescence varied each day. There were twenty-one flowers present Day 1 (May 24, 2008). Therefore every seventh flower was chosen for nectar collection. Fifteen flowers were present on Day 2 (May 27, 2008), with collection on every fifth flower.

Ne~tar was extracted from the flowers using a 20μ1 capillary micropipette. The nectar was mouth pipetted to make sure all nectar was removed. Due to bubbles that formed in the capillary tube, the nectar was pipetted out onto a piece of parafilm. It was carefully sucked back up into the capillary tube avoiding bubbles and measured. The nectar was measured in millimeters by a ruler. A conversion was used to calculate the actual volume (μl) of nectar present in the tube. This process was repeated for Day 2.

The natural accumulation of nectar was calculated using the same inflorescence on May 28, 2008. There were four of the twenty-three flowers on

Table1. Nectar volumes (μl) taken from *E. elatior* flowers 1-3 on Day 1 and Day 2 at La Selva Lodge Botanical garden

	Time (CST)	Day 1	Day 2
a. *Flower 1*			
	0600	7.25	11.30
	0630	3.26	1.74
	0700	3.26	2.90
	0730	0.87	3.19
	0800	2.32	5.80
	0830	2.90	3.48
	0900	0.58	2.68
	0930	0.00	2.32
	1000	0.00	2.32
	1030	0.00	0.00
	1100	0.00	0.98
	1130	0.00	2.46
	1200	0.00	
Total (μl)		20.44	39.17
b. *Flower2*			
	0610	7.54	15.36
	0710	6.81	7.97
	0810	13.19	8.41
	0910	3.33	7.54
	1010	1.59	7.83
	1110	2.03	8.41
	1210	1.74	8.7
Total (μl)		36.23	64.22
c .*Flower* 3			
	0620	6.16	15.65
	0820	9.13	18.55
	1020	5.51	14.49
	1220	3.19	14.78
Total (J:l.I)		23.99	63.47

the inflorescence used for sampling. During these trials instead of taking the nectar out completely, after measurements were written down, it was replaced. This was repeated every 3D minutes for each flower, from 0600-1200.

Data analysis- The total volume of nectar produced for Day 1 and 2 were averaged and compared to Day 3 total average volume of nectar using a Chi-square test. The nectar volumes taken from Day 1 and Day 2 were converted into Nectar Production Rates (hereafter NPR) with units in μl *Iminute.* The average NPR were calculated and compared for each flower.

RESULTS

Comparison of total nectar accumulations- Total nectar produced for Day 1 and Day 2 varied. There was more nectar produced on Day 2 than Day 1 by an average of 51.33% ± 9.45. However the same pattern for nectar production was exhibited on each day. The least amount of nectar produced on both days was in Flower 1 (Day 1 = 20.44 μl; Day 2 =

Table 2. Comparison of natural nectar *total* volumes and nectar total volumes of flowers subjected to different removal schedules by Chi-Square test

	Day 1 and Day 2 (μl; mean ± SD)	Day 3 (μl; mean ± SD)	Degrees of freedom		
Flower 1	29.81 ± 13.24	26.45 ± 17.97	1	0.86	
Flower 2	50.22 ± 19.79	26.45 ± 17.97	1	6.34	*
Flower 3	43.73 ± 27.92	26.45 ± 17.97	1	2.03	

* statisically significant p > 0.05

39.17μ1) by an average percentage of 41.50% ± 3.54 compared to the most nectar produced in Flower 2 (Day 1 = 36.23μ1; Day 2 = 64.22μ1). Nectar produce in Flower 3 (Day 1 = 23.99μ1; Day 2 = 63.47μl) was much closer to the volume of nectar produced in Flower 2 by and average of 17.48% ± 23.06 (Table 1).

When comparing the treated total nectar volumes (Average of Day 1 and Day 2 into 3 groups) and natural total nectar volumes (average of all four flowers) by the Chi-square test, Flower 2 was shown to be significantly different (X^2 = 6.34, df = 1, p>0.05). Therefore there was a significant difference due to the treatment (removal every hour) compared to normal or natural nectar production (Table 2).

Nectar Production Rates (NPR}- The NPR varied for each flower. The average highest NPR of Flower 1, whose nectar was harvested every 30 minutes, was 0.135 μl Iminute. The average NPR increased from 0630-0700, 0730-0800, and 1030-1130. The average NPR decreased from 0700-0730, 0800-1030, and 1130-1200. There was generally an average peak ofNPR between 0800 and 0830. There was only one peak, representing the highest average NPR, for Flower 2 (0.180 μ1 Iminute). There was an increase in NPR from 0710-0810, followed by a decrease from 0810 to 1010. This last decrease was followed by a small increase (from 0.079 to 0.087) were the data leveled off. The trend observed in the average NPR of Flower 3 was a steady, almost linear decrease from 0820 to 1220 (y = -0.0202x + 0.1519; R2 = 0.8986).

DISCUSSION

Variation of nectar accumulation- Humidity was low, the sun was bright and the rain did not start until after 1200 on Day 1. In contrast, there was high humidity resulting in early rain (1100) on Day 2. This difference in temperature and humidity could account for the variation seen in the total nectar volumes (Table 1). Brown (1959) cited that humidity strongly influences nectar secretion. Real and Rathcke (1991) made a point in citing that variation in temperature, humidity and soil moisture can influence high rates of nectar production. These factors have a direct influence on the plant metabolism, which can cause them to be important

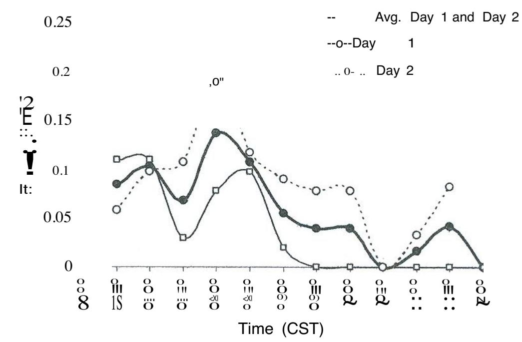

Fig. 1. The NPR for Flower 1 on Day 1 and Day 2 and the average NPR for Flower 1 of *Etlingera elatior*.

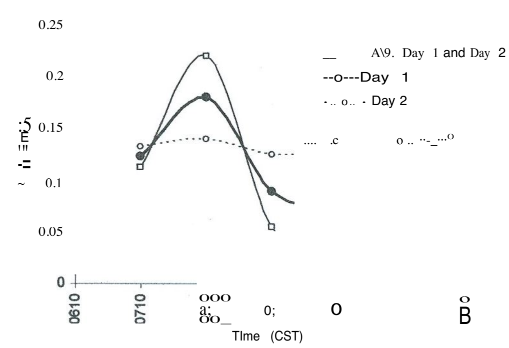

Fig. 2. The NPR for Flower 2 on Day 1 and Day 2 and the average NPR for Flower 2 of *Etlingera elatior*.

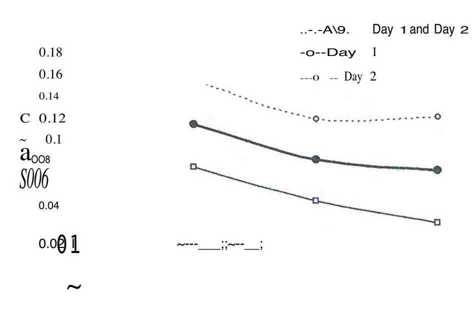

Fig. 3. The NPR for Flower 3 on Day 1 and Day 2 and the average NPR for Flower 3 of *Etlingera elatior*.

determinants of nectar secretion rates (Aizen and Basilio, 1998). These studies maintain that an increase in these environmental factors can increase nectar productivity, however it is Shuel (1951) that cited an inverse correlation between nectar sugar content and relative humidity. He showed that even thought the actual volume of nectar produced may increase; sugar concentration does not necessarily increase. If sugar concentration of nectar sampled in this study were collected simultaneously, there might have been a more defmitive correlation seen here.

By varying the times at which nectar was collected, volumes were showed to fluctuate among flowers on the same inflorescence. The least amount of nectar was collected from samples every 30 minutes. This may be due to the constant disruption of the floral nectaries. Constant collection of nectar with a glass pipette may cause damage to the floral nectary (Castellanos et aI., 2002). There is also evidence that the floral nectary of Flower 1 on Day 1 may have been damaged due a stop in nectar secretion at 0930. Since the most nectar was extracted from Flower 2 on both days and was considered to be statistically different than the normal nectar accumulation, one would assume that this hourly mimicked feeding would be optimal for foraging hummingbirds. Among others Navarro (1999) also found that removing nectar caused an increase in the total volume of nectar produced. For hummingbirds to fit this nectar production pattern, they would most likely be considered trapliners. Temeles (2006) cites by trapliners delaying revisits (in this case every hour), it would be able to increase its food accumulation and hence the profit obtained. The only problem with this idea is that territoriality was observed on both days. Stronger territoriality was observed Day 1 by a male *Florisuga mellivora,* common name White-necked Jacobin. This leads one to believe that there is more of an interrelationship between traplining and territoriality. Can these hummingbirds exhibit both characteristic strategies? On Day 2 only some territoriality was exhibited and more traplining was seen to be favored by the hummingbirds. One would assume this would be due to the excess volume of nectar compared to Day 1. Ivlev (1961) found that selectivity does increase with over all food density. Maybe the increase in the available food caused hummingbirds to become more selective on where they choose to feed. This theory could be supported better if the nectar sugar concentration was known. If this excess volume of nectar on Day 2 contained more than enough to sustain the 6-12 kcal of daily energy a 4-6 gram hummingbird needs then this idea of change in behavior could be plausible (Stiles, 1975).

Implications for NPR- The average highest nectar production rate was exhibited in Flower 2. This corroborate that extracting nectar from the flower hourly not only increase the overall volume of nectar but also the rate of production. The hourly mimicked feeding also allowed the plant to produce nectar at a more constant rate. This may cause hummingbirds the freedom of being able to rely on this flower as a dependable food source. This consistent rate would also reinforce the hourly feeding. Since energy costs of foraging are so expensive for hummingbirds, they are more than likely going to try to look for patterns that will guarantee satiation. The red color of *E. elatior* bracts would be another strategy that would enable birds to rapidly recognize and exploit it as a reliable food source, especially for trapliners which may have migrated to a new food source (Grant and Grant, 1968). Combining these two attributes strongly suggests that *E. elatior* is looking for a trapliner strategy from a hummingbird.

In all flowers the average highest NPR was seen to peak between 0800 and 0830. Bfu'quez and Corbet's (1991) research also showed that there was at least one maximum in NPR each day. The fact that each day every flower peaked in nectar production rates could correlate with the observation that most hummingbirds did not start foraging on *E. elatior* until around 0900. Hummingbirds were observed feeding on *Heliconia* species as early as 0530, and not having many visiting past 0930. To interpret this data one could explain this phenomenon as a change in behavior due to an increase in food density. If sugar concentrations were known for both *E. elatior* and *Heliconia* and the nectar reward for *E. elatior* happened to be greater, the conclusion could be made that the hummingbirds choose to forage on the *Heliconia* to sustain calories until NPR have peaked in *E. elatior.* This proposal can only be accepted by further testing. It has been said by Baker (1975) that with later feeding nectar may become more concentrated. Another idea may be that the rewards for both *E. elatior* and *Heliconia* species may be the same, but since feeding on *Heliconia* starts earlier there may be more nectar available in the rate peaking *E. elatior.*

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