NECTAR AVAILABILITY AND FLOWER PREFERENCES OF HIGH-ALTITUDE TROPICAL HUMMINGBIRDS

D. DÜNYA ÖNEN, NATHAN H. RAINES, ABIGAIL L. ADAMS, ANDREW R. CARRERAS, AND BRIAN D. BATES

Research advisors: David R. Peart, Elizabeth M. Wolkovich. Faculty editor: David R. Peart

Abstract: Hummingbirds are important pollinators for tropical flowers, especially at high elevations. We hypothesized that flower nectar production influences hummingbird flower preferences, and that these preferences vary between hummingbird species. We observed 5 species of hummingbirds at two flower patches near the Cuericí Biological Station, Cerro de la Muerte, Costa Rica, recording which flowers they visited as well as the flower composition of the sites. Hummingbirds preferred certain flower species over others, and flower preference differed between hummingbird species. Some hummingbird species preferred flowers with high but inconsistent nectar rewards while others sampled randomly from the environment.

Key Words: hummingbird foraging, nectar reward, flower density

INTRODUCTION

Many plant species exhibit a "bonanza" pattern of highly variable nectar production among their flowers (Feinsinger, 1978), with some flowers producing hardly any nectar while neighboring flowers produce copious amounts. As a result, hummingbird pollinators visit more flowers as they search for the nectar lodes (Feinsinger, 1978). Flowers in Costa Rica's high altitude environments depend heavily on hummingbird pollination and display a variety of strategies to attract pollinators. We hypothesized that some hummingbird species selectively visit plant species with these highly variable but potentially higher nectar rewards, while other hummingbird species prefer plant species that provide consistent but small nectar rewards.

We tested the following propositions: 1) hummingbirds preferentially forage on certain plant species, 2) hummingbird species differ in their preferences, and 3) some plant species produce highly variable, high-nectar reward flowers, while other species produce consistent but low-reward flowers.

METHODS

We conducted our study at two 20 x 20 m flower patches near the Cuericí Biological Station at Cerro de la Muerte, Costa Rica. We estimated the density composition of each flower species by having four people visually assess the percent coverage of each species in each patch and then averaging the estimates. The first patch contained primarily *Fuchsia paniculata* and *Sechium edule.* The second patch contained primarily *Wigandia urens*, *Hemichaeana fruticosa*, and *Razisea spicata.* To quantify nectar volume per flower, we bagged five random flower clusters of each species for 12 hours and then measured nectar volumes with capillary tubes. We

also assessed nectar robbing in *Razisea spicata* by counting the number of piercings at the base of 20 individual flower corollas.

We monitored both patches simultaneously between 11:00 and 12:00 and 14:00 and 18:00 on 27 January and 5:30 and 7:30 on 28 January, observing 105 individual hummingbird visits. We recorded for each hummingbird visit the time spent actively foraging, the species visited and the number of flowers visited per plant.

We performed a chi-squared test to determine if hummingbirds preferentially foraged on different flower species and if flower preference differed between hummingbird species. We evaluated species differences in nectar production by comparing the coefficients of variation (standard deviation /mean of nectar content).

RESULTS

At patch 1, we observed Magnificent Hummingbirds, Purple-Throated Mountain Gems, Gray-Tailed Mountain Gems, Fiery Throated Hummingbirds, and Volcano Hummingbirds. At patch 2, we observed Magnificent and Volcano Hummingbirds.

Hummingbird species differed in their relative visitation of different flower species within a patch (patch 1: $\chi^2 = 43.47$, $P < 0.0001$; patch 2: $\chi^2 = 5.04$, $P = 0.02$; Table 1). In patch 1, Gray-Tailed Mountain Gem Hummingbirds preferentially foraged on *Sechium edule* while Magnificent and Volcano Hummingbird foraging did not differ from the null model based on flower density. In patch 2, both Volcano and Magnificent Hummingbirds preferentially foraged on *Wigandia urens* (Table 1).

Flower species differed in both total volume of nectar available and in variance in nectar volume from flower to flower (Table 2). The Gray-Tailed Mountain Gem's preferential foraging behavior appears to be driven by nectar rewards in *Sechium edule*. In patch 2, flower preference in Volcano and Magnificent Hummingbirdwas not related to flower density, nectar availability, or nectar consistency. We noted that 9 *Razisea spicata* flowers out of 20 were nectar robbed.

DISCUSSION

We showed that (1) hummingbirds discriminate between flower species and (2) that different hummingbird species preferentially forage on different flower species. Results also supported our third proposition that some flower species produce highly variable, high-nectar reward flowers, while other species produce consistent, but low-reward flowers.

In patch 1, the Gray-Tailed Mountain Gem may employ the high-risk, high-reward foraging strategy. However, the Volcano and Magnificent Hummingbirds did not display flower preferences.

In patch 2, hummingbirds preferentially foraged on *Wigandia urens,* which was not the most abundant flower species, the highest in nectar volume, nor the most consistent nectar reward.

TABLE 1. Number of visits hummingbird species by patch at Cuericí Biological Station, Costa Rica, made to different flower species compared to expectations from two null models: hummingbird species have no flower preference and all hummingbirds have the same flower preference. These are represented in the table as: expected visits with no flower preference, expected visits with same flower preference, respectively.

Patch 1	*F. paniculata*		*S. edule*		flower preference	
	obs.	exp.	Obs.	exp.	χ^2	p
Gray-tailed	1	11.5, 9.9	12	1.2, 3.1	103.43	<0.0001
Magnificent	36	33.6, 28.9	2	3.6, 9.2	0.89	0.35
Volcano	21	20.4, 17.5	2	2.2, 5.5	0.04	0.85
Fiery	2	1.8, 1.5	0	0.2, 0.5	-	-
Purple throat	0	18.6, 2.3	3	0.3, 0.7	-	-

Patch 2	*H. fruticosa*		*R. spicata*		*W. urens*		flower preference	
	obs.	exp.	obs.	exp.	obs.	exp.	χ^2	p
Magnificent	1	3.9, 1.0	6	5.2, 3.5	6	2.6, 8.5	6.73	0.03
Volcano	1	3.9, 1.0	1	5.2, 3.5	11	2.6, 8.5	32.69	<0.0001

TABLE 2. Flower density (visual estimate of the percentage of all flower habitat covered by that species), nectar content (mean ± SE), and coefficient of variation (standard deviation / mean) for 5 flower species in two sites at Cuericí Biological Station, Costa Rica.

Flower species	Estimated flower density (% of habitat)	Mean nectar (μl) ±SE	Stdev/mean. nectar
Fuchsia paniculata	88.5	2.5 ± 0.18	0.314
Hemichaeana fruticosa	30	2.9 ± 1.4	1.079
Razisea spicata	40	6.0 ± 2.8	1.047
Sechium edule	11.5	138.4 ± 76.3	1.233
Wigandia urens	20	1.1 ± 0.35	1.110

Physical mismatches between hummingbird and flower morphology did not appear to drive flower preference as nectar appeared equally accessible to all bird species. Our findings suggest some other factors beside nectar availability and flower density may influence hummingbird foraging. In patch 2, relative floral prominence may increase the likelihood of visitation, explaining the high hummingbird visitation to the highly visible clumps of *Wigandia urens* which tended to protrude from the surrounding vegetation (although this speculation is not substantiated by experimental investigation into the direct role or flower prominence). Furthermore, the most dense and nectar rich flower species in patch 2, *Razisea spicata*, may have had low hummingbird visitation due to the high rate of nectar robbing.

LITERATURE CITED

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