NECTAR VOLUME DISTRIBUTION AND CHARACTERISTICS OF THE HUMMINGBIRD-POLLINATED FLOWER *CENTROPOGON TALAMANCENSIS*

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Abstract: Centropogon talamancensis is a flower pollinated by the hummingbird *Eugenes fulgens*, and is susceptible to nectar robbing by *Diglossa plumbea*. Feinsinger (1978) found that nectar volume in hummingbird-pollinated flowers at Monteverde was unevenly distributed within plants, with most flowers containing no nectar. The benefits to plants of this bonanza reward system may be a feature of pre-montane cloud forests, or may be ubiquitous among hummingbird pollinated flowers. To test these alternatives, we measured nectar distributions in *C. talamancensis* at Cerro de la Muerte. We found that *C. talamancensis* in montane forests also provide highly variable nectar rewards. Additionally, we hypothesized that pollinators would be unable to predict nectar reward from external characteristics; as predicted, neither corolla length nor the number of scars from nectar robbers were correlated with nectar volume. Apparently, the bonanza reward system is not restricted to pre-montane cloud forests, and may be a common component of hummingbird - flower interactions.

Key words: Bonanza!, Cerro de la Muerte, corolla length, Diglossa plumbea, Eugenes fulgens, *flowerpiercer, pollination*

INTRODUCTION

Centropogon talamancensis, a pink flower with a long, curved corolla, supplies a nectar reward to the magnificent hummingbird, *Eugenes fulgens*, a specialist pollinator. The nectar of *C. talamancensis* may also be stolen by *Diglossa plumbea*, the slaty flowerpiercer, a specialist nectar robber. In a study of ten species of hummingbird-pollinated plants in Monteverde, Costa Rica, Feinsinger (1978) found that nectar volume was unevenly distributed within plants, with most flowers containing no nectar and a few containing copious nectar. Feinsinger (1978) proposed that this pattern of distributing nectar among flowers was adaptive because it maximized the duration of hummingbird visits while minimizing energy expenditure on nectar production. The "bonanza" reward system might be ubiquitous among hummingbird pollinated flowers on flowers, or might be restricted to pre-montane cloud forests. For example, hummingbirds in higher, cooler montane forests might select for more predictable rewards because their energetic demands for thermoregulation are greater. We tested these alternatives by evaluating the nectar reward system in *C. talamancensis* at Cerro de la Muerte.

We also evaluated some more specific details of the reward system. We examined the relations among nectar volume, corolla length, number of flowers per plant, and frequency of nectar robbing for *C. talamancensis*. Under Feinsinger's adaptive model, pollinators should be unable to predict nectar reward from external characteristics. So we predicted that corolla length would be unrelated to nectar volume, as any correlation would result in selective pollination. Similarly, we predicted that nectar-robber scars would not vary with nectar volume, as nectar-robber birds should not be able to determine nectar volume before puncturing flowers.

METHODS

We placed individual cloth bags (to preclude nectar consumption) over 42 open *C. talamancensis* flowers on 17 plants along the west end of the loop trail north of the Cuerici Biological Station, Cerro de la Muerte, Costa Rica, be-

tween 0745 and 0900 on 29 January 2004. "Plants" were defined based on aboveground connections of stems and/or vines. We removed the bags 24 h later and measured nectar volume of each flower with a 20 µl capillary tube. We also measured the corolla length of each flower from the base of the bud to the tip of the longest petal and counted the number of open flowers per plant and number of nectar-robber scars. We used a one-way ANOVA model to test for variation among plants in nectar volume and corolla length. Prior to analyses, we log-transformed nectar volume + 1 to improve normality.

RESULTS

The distribution of nectar volume in *C. talamancensis* was highly variable, with 55% of flowers offering no nectar reward to pollinators (Fig. 1). Of open flowers, 29% had one or more nectar-robber scars (range = 0 - 57% among plots with ≥ 5 flowers). There were between 1 and 16 open flowers per plant. The mean corolla length ± 1 SE was 4.55 ± 0.05 cm. Corolla length differed significantly between plants ($F_{16,25}$ = 3.83, P = 0.001).

A correlation matrix revealed no significant relationships among corolla length, number of flowerpiercer scars, number of flowers per plant, and nectar volume (Table 1). Also, evaluation of all possible multiple linear regression models showed that no combination of variables (paired or all three combined) could explain a significant fraction of the variation in nectar volume.

DISCUSSION

C. talamancensis at Cerro de la Muerte displays the uneven nectar distribution reported by Feinsinger (1978) from a different ecosystem. This could be an adaptation of plants to manipulate the visitation behavior of hummingbirds. Results supported some predictions de-

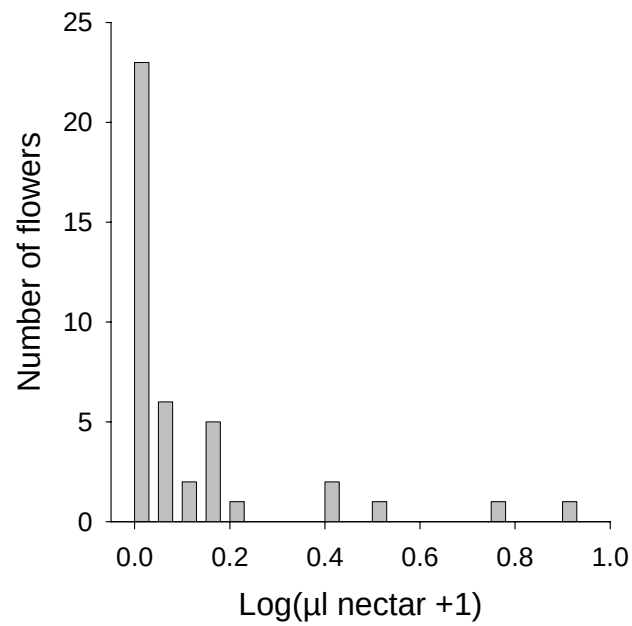

Figure 1. Frequency distribution of nectar secretion per flower in *C. talamancensis* at Cerro de La Muerte, Costa Rica. Values represent log-transformed nectar volumes per flower (n = 42).

Table 1. Correlation matrix of *C. talamancensis* flower characteristics measured at Cerro de la Muerte (n = 42 flowers). No correlations were statistically significant.

	Corolla length (cm)	Nectar-robber scars	Flowers per plant	Nectar volume (µl)
Corolla length (cm)	-	0.05	-0.24	-0.18
Nectar-robber scars	-	-	-0.18	-0.04
Flowers per plant	-	-	-	-0.16
Nectar volume (µl)	-	-	-	-

rived from this adaptive explanation. Specifically, there was no correlation between corolla length and nectar volume, which might be expected if nectar volume was just an artifact of variation among plants short in carbohydrate supplies for flower expansion and nectar production. If hummingbirds could determine nectar volume through external characteristics, such as corolla length, then hummingbirds would likely only visit flowers that offered high rewards. Similarly, nectar-robber scars were also unable to predict which flowers contain the most nectar, as the number of previous nectar-robber scars and nectar volume of a flower were uncorrelated. In addition, individual plants varied significantly in the corolla length of their flowers but not in their nectar distributions. Flowers of *C. talamancensis* apparently provide variable nectar volume without providing obvious external characteristics, which presumably compels hummingbirds to visit more flowers.

Bonanza reward systems may be a rather general feature of hummingbird pollinated plants even across climatic zones that must create quite different energetic challenges for the hummingbirds. To our knowledge, it remains unknown whether insect pollinated plants in these same systems also tend to create bonanza reward systems. It might work for the same reasons as it does with hummingbirds, or it might not because insects learn differently or have different innate responses to variable reward systems.

LITERATURE CITED

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. Ecological Monographs 48: 269 - 87.