APPENDIX A: Taxonomic groups of invertebrates found in Quebrada Los Leones at 10 and 40 m upstream and downstream from trout farm effluent, Cerro de la Muerte, C.R. *Hirudinea is a class level designation.

Order	Family	Upstream		Downstream	
		40 m	10m	10 m	40 m
Amphipoda	Unknown	25	20	16	89
Coleoptera	Amphizoidae	1	2	1	0
	Dryopidae	0	2	0	1
	Carabidae	0	0	2	0
	Haliplidae	0	0	6	0
	Unknown	31	19	8	16
Diptera	Unknown	16	47	35	38
Ephemeroptera	Ephemeridae	1	0	0	0
	Heptageniidae	0	1	1	1
	Leptophlebiidae	1	0	0	0
	Tricorythidae	0	1	0	0
	Baetiidae	11	9	2	19
	Unknown	1	0	0	2
Isopoda	Asellota	3	0	0	1
Hirudinea*	Unknown	2	1	0	1
Mollusca	Unknown	10	10	1	14
Odonata	Unknown	0	0	1	0
Plecoptera	Perlidae	2	4	4	9
Trichoptera	Brachycentridae(A)	156	174	62	314
	Brachycentridae(B)	62	57	10	96
	Hydrodpsychidae	2	8	4	20
	Leptoceridae	1	1	0	0
	Rhyacophilidae	0	1	0	5
Total		**325**	**362**	**153**	**626**

Effects of volume and sugar concentration of nectar on hummingbird foraging preference

E. A. FRENCH, M. S. KIM, J. D. MANISCALCO, C. E. T. PAINE, AND J. P. PLATT

Abstract. Since net energy gain is important for optimal foragers, we predicted that hummingbirds (Trochilidae) would preferentially feed on flower species that have higher volumes and sugar concentrations of nectar. We found that there was a trend for preferential feeding on flowers of higher sugar concentrations, while nectar volume had no effect. This implies that hummingbirds do not forage solely on the basis of a flower's relative abundance, but rather preferentially feed on flower types that offer higher rewards.

Key words: *Trochilidae*, Panterpe insignis, Selasphorus flammula, Colibri thalassinus, *optimal foraging*

INTRODUCTION

Plants use different strategies to disperse pollen for sexual reproduction. The majority of tropical plants depend upon biotic pollination (Hartshorn 1983). In order to attract pollinators, many flowers produce a sugar-rich nectar as a reward.

If all flowers provide their pollinators with equal rewards, then the proportion of visits to each flower species would reflect that species' relative abundance within the patch. However, if different flowers offer different rewards, then optimal foragers would benefit by seeking the flower that provides the maximum net energy gain per unit time. We hypothesized that flowers differ in both the sugar concentrations and volumes of nectar that they produce, and that foraging hummingbirds will preferentially visit flowers with higher rewards.

METHODS

On the morning of 30 January 1999, we surveyed the disturbed habitat above the farm 0.3 km east of Estación Biologica Cuerici to locate foraging hummingbirds (Trochilidae). The species of each bird (*Panterpe insignis*, *Selasphorus flammula*, or *Colibri thalassinus*) and the flower type it was foraging on were recorded. Once a bird was seen foraging at a flower, we moved on until a new bird was found. Thus, one foraging observation was obtained per sighting, which allowed us to treat these as independent observations. Data collection involved 20 observer-hours.

To assess relative flower abundance, ten 10 m transects were randomly located in the study area and the number of individual flowers of each type visited by hummingbirds was counted in a 1 m band along each transect (100 m^2 total). *Bomarea* was included in our abundance sampling) though no hummingbirds were seen foraging on it, as it is believed to be hummingbird pollinated (Skutch and Stiles 1989). We measured sugar concentrations in nectar for each flower species with an American Optical T/C hand refractometer. After flowers were bagged to exclude pollinators for 22 hours, we extracted nectar using 10 µl capillary tubes to determine approximate volume for one flower per species.

RESULTS

We sampled 7 flower types (Table 1); a red, tubular, hummingbird pollinated flower (red morphotype) was unidentified, and tentatively grouped in the Acanthaceae. Sugar concentration of nectar ranged from 45 degrees brix for *Wigandra* to 13 for *Monochaetum* (Table 1) and differed significantly among the flowers sampled (ANOVA, $F=134.48$, $df=6, 14$, $P<0.0001$). Nectar volume ranged from 7.5 µl in *Bomarea* to <0.1 µl for *Monochaetum*. The relative abundance of flower types differed by three orders of magnitude. *Monochaetum* was the most common species while *Bomarea*, *Fuschia*, and *Gaultheria* were all rare (Table 1). There was no association between relative abundance of the flower types and sugar concentration ($r=0.49$, $P=0.26$) nor nectar volume ($r=0.49$, $P=0.32$).

Table 1. Characteristics of flowers visited by foraging hummingbirds within the study area 0.3 km east of Estación Biologica Cuerici, Costa Rica (Means ±1 SE). Sugar concentration was the only characteristic with significant differences (see text).

Flower Type	Relative Abundance (%, n=10)	Sugar Concentration of Nectar (°brix, n=3)	Volume of Nectar (µl, n=1)	Number of Hummingbird Visits (n=98)
Monochaetum sp. (Melastomaceae)	78.3 ± 5.9	13.0 ± 1.0	<0.1	18
Red morphotype (Acanthaceae)	15.7 ± 5.5	18.7 ± 1.2	1.0	21
Hemichaema fruticosa (Scrophularecaceae)	3.1 ± 1.7	18.7 ± 0.7	0.8	7
Wigandra sp. (Hydrophyllaceae)	2.3 ± 2.1	45.0± 0.0	2.1	46
Bomarea sp. (Amaryllidaceae)	0.4 ± 0.4	25.0± 1.2	7.5	0
Fuschia sp. (Onagraceae)	0.2 ± 0.2	30.0 ± 0.7	2.4	5
Gaultheria erecta (Ericaceae)	0.0 ± 0.0	17.3 ± 1.2	—	1

There was a significant difference in the number of hummingbird visits to each flower type (Table 1; G=295.5, df=5, P<0.0001). Hummingbird preference was not determined by the relative abundance of flower types; they showed the highest preference for *Wigandra*, a relatively rare flower, and the least preference for *Monochaetum*, the most abundant flower. The other four flower types were visited in proportion to their abundance (Fig. 1).

An ANOVA was run to test the effects of nectar concentration, flower abundance, and their interaction on hummingbird flower visitation frequencies. There was a trend for preference on flowers with higher sugar concentrations (F=11.86, df=1, P=0.075). There was no effect, however, of the interaction between flower abundance and sugar concentrations (F=8.05, df=1, P=0.11) nor flower abundance (F=6.37, df=1, P=0.13) on hummingbird foraging preference. *Wigandra* had the highest sugar concentration and the second highest nectar volume of flower types visited by hummingbirds (Table 1). *Monochaetum* had the lowest sugar concentration and lowest nectar volume (Table 1). The differences in nectar volume between flower types was not correlated with hummingbird preference (r=0.2, P=0.75).

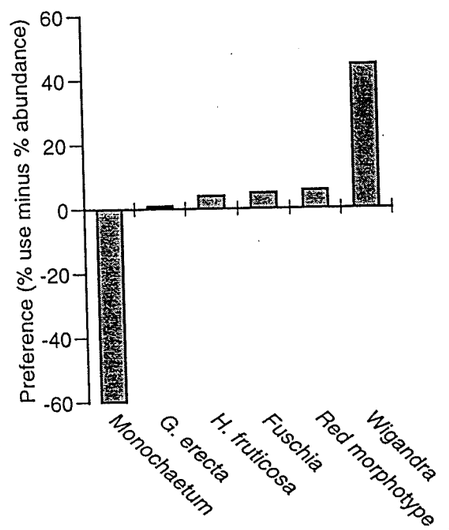

Fig. 1. Hummingbird preference (percent use minus percent abundance) of flower types at Estación Biológica Cuerici, Costa Rica There are significant differences in the preferences of hummingbirds for different flower types.

Discussion

Differential sugar production by flowers may indicate different pollination strategies. The correspondence between sugar

they feed preferentially on flower types highest in sugar concentration in an attempt to maximize their net energy gain per unit time. We suspect that pollinators deplete nectar volume early in the day, perhaps explaining why hummingbirds seemed to forage without regard to nectar volume.

The absence of foragers on *Bomarea* partially contradicts the idea of optimal nectar foraging. It had the second highest sugar concentration and the highest nectar volume of the flower types surveyed, yet was not seen to be visited by hummingbirds in our study. This suggests that other factors, such as corolla depth, may also be important for establishing foraging patterns, since most birds observed (93 of 98) had bills too short to forage effectively on *Bomarea*.

Since sugar concentration of the nectar only partially explains hummingbird foraging, further study of nectar quality at the molecular level is warranted. The types of sugars present and amino acid content may differ between flowers and these may be important factors in the attraction of pollinators. Sugar concentration, along with corolla depth, sugar composition and other factors, determine hummingbird foraging preferences.

Literature Cited

Hartshorn, G. S. 1983. Chapter 7: Introduction to Plants. Pp. 118-157 *in* D. H. Janzen, ed. *Costa Rican Natural History*. University of Chicago Press: Chicago.

Skutch, A. F. and Stiles, G. F. *A Guide to the Birds of Costa Rica*. Cornell University Press, New York. 1989.