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Patterns in Floral Nectar Characteristics of Some Bird-Visited Plant Species from Costa Rica¹

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ABSTRACT

Nectar samples from a wide range of flowers (120 samples, 112 species, 22 families) visited by hummingbirds (subfamilies Phaethorninae and Trochilinae) were collected over a wide range of elevations and environments in Costa Rica. Some species visited are believed to be pollinated principally by perching birds, lepidopterans, and bees, however. We measured sugar composition (% fructose, glucose, and sucrose), daily secretion rates, and sugar concentration. In general, sugar compositions of all hummingbird nectars were found to be highly clustered toward the high-sucrose end of the composition spectrum and not significantly different from sugar compositions of other hummingbird nectar assemblages from northwestern Mexico and the southwestern United States. Significant correlations were detected between elevation and the percentage of fructose and of sucrose in the nectar, with the fructose percent positive and the sucrose negative. These correlations were found to be due to both elevation and hummingbird-group effects. Daily secretion rate and sugar concentration were both negatively correlated with elevation. Discriminant analysis indicated that nectar sugar concentration and daily secretion rates together could usually predict whether a species was pollinated by hermit (Phaethorninae) or nonhermit (Trochilinae) hummingbirds and could often predict which eco-morphological group of nonhermits.

Key words: Costa Rica; hummingbirds; nectar; Phaethorninae; pollinators; Trochilinae.

FLORAL NECTAR IS THE MOST IMPORTANT REWARD offered to potential pollinators in the angiosperms as a whole, although other rewards may be offered by particular species or groups (Simpson & Neff 1983). Although nectar contains a wide variety of chemicals (Baker & Baker 1975, 1982, 1983a), three common sugars—fructose, glucose, and sucrose—dominate the total solutes (Baker & Baker 1979, 1983b). Within species, sugar compositions have been found to be generally constant and vary relatively little with environmental conditions (Baker & Baker 1982, Freeman & Head 1990, Villarreal & Freeman 1990).

The relative concentrations of these three common sugars, as well as other solutes, have been found to vary according to the type of pollinator (Percival 1961, Baker & Baker 1975, 1979, 1983a). Flowers pollinated by hummingbirds typically produce nectars that are rich in sucrose relative to fructose and glucose (Stiles 1976, Baker & Baker 1979, Freeman *et al.* 1984, 1985). Total concentration

of these three sugars also varies with pollinator type (Percival 1965, Baker & Baker 1975) and elevation (Hainsworth & Wolf 1976, Stiles 1978), with hummingbird flowers producing relatively dilute nectars (Baker & Baker 1975, Bolten & Feinsinger 1978).

Because they produce relatively large volumes of easily collected nectar, hummingbird flowers are particularly appropriate for detailed, quantitative analyses of variation in nectar composition with respect to particular pollinator types, taxonomic group, and environmental conditions. To date, however, most studies have been limited in this respect because the paper chromatography method used was not sensitive enough to detect small differences in sugar composition within a given nectar type. Sugar analyses with high-performance liquid chromatography (HPLC) allow the determination of nectar composition with greater precision and accuracy (Freeman & Wilken 1987). A sample of 40 hummingbird-pollinated species from the southwestern United States yielded means of 15 percent fructose, 11 percent glucose, and 74 percent sucrose, with a rather tight clustering of nectars when com-

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position was plotted on a ternary diagram (Freeman *et al.* 1984). A subsequent sample of 16 putative hummingbird-pollinated species from the northern edge of the tropics in southern Sinaloa and southern Durango, Mexico, yielded means of 19 percent fructose, 11 percent glucose, and 70 percent sucrose (Freeman *et al.* 1985). These data suggest adaptive convergence in the sugar compositions of nectars of hummingbird-pollinated flowers that presumably reflects taste preferences and/or digestive physiology of these birds (*cf.* Stiles 1976, Martinez del Rio & Karasov 1990).

Hummingbirds, however, are an overwhelmingly tropical group (Greenwalt 1960), and the aforementioned nectar samples are from areas in which hummingbird diversity is limited, and many major groups of tropical hummingbird flowers do not occur. In Costa Rica, much closer to the equator, the two subfamilies of hummingbirds (Phaethorninae = hermits; Trochilinae = nonhermits) and most major tropical taxa of their food plants are well represented in an area of great ecological and topographical diversity (*cf.* Janzen 1983, Stiles & Skutch 1989). In this paper we analyze a large sample (over 100 species) of nectars of hummingbird-visited flowers of Costa Rica. We wanted to determine whether the nectar sugar compositions of these Central American species were similar to, and as tightly clustered as, those of the southwestern United States and northwestern Mexico. Further, since the sample was so large and collected over a wide range of habitats and elevations, we hoped to detect additional nectar-hummingbird patterns which had not been described previously.

METHODS AND MATERIALS

Between 1984 and 1988, nectar samples were collected from 112 species of flowers observed to be commonly visited (and in most cases pollinated) by hummingbirds in various regions of Costa Rica over an elevation range from sea level to 3100 m. Voucher specimens of plant species discussed here have been deposited in the herbaria of the Universidad de Costa Rica and the Instituto Nacional de Biodiversidad de Costa Rica (formerly the Museo Nacional de Costa Rica).

Nectar samples were collected from individual flowers in the field with micropipets. These liquid samples were rapidly dried on 6-mm disks of Whatman #1 filter paper, stored in glassine envelopes, then transmitted through the mails to the laboratory for analysis.

For each species sampled, the elevation of the

collection site and the putative pollinator (based mostly upon direct observation although in a few cases inferred from floral morphology) were recorded. For most flower species, daily nectar secretion (in $\mu\text{l}/\text{day}$) was estimated for a sample of 3–10 flowers that were bagged from dawn through mid-to late afternoon. For most species total sugar concentration (as equivalent sucrose molarity) was measured using a National, temperature-compensated, refractometer.

In the laboratory, sugars were identified and quantified using high performance liquid chromatography (HPLC). The analytical methodology has been outlined previously (Elisens & Freeman 1988) except that Alltech 150 mm Econosphere NH_2 5- μ cartridges were used exclusively. For a few species, two independent samples (different date and locality) were available. These were *Bomarea costaricensis* (Amaryllidaceae), *Cavendishia callista*, *C. crassifolia*, and *Psammisia ramiflora* (Ericaceae), and *Heliconia irrasa*, *H. latispatha*, and *H. tortuosa* (Musaceae). Other species were represented by single samples. Nearly all samples, however, consisted of several subsamples (individual flowers). To assure that the values obtained were, in fact, representative of a particular species, only samples that contained at least two subsamples consistent with regard to sugar analysis were included in this study. In nearly all cases, three or more internally consistent sugar analyses were available for each species.

For purposes of analysis, putative principal pollinator was scored according to the following system: 1 = hermit hummingbirds (Phaethorninae); 2 = nonhermit hummingbirds with long and/or curved bills; believed to forage in a hermit-like manner, *i.e.*, long-distance trapliners (*cf.* Stiles & Wolf 1979); 3 = "typical" nonhermit (Trochilinae) hummingbirds of medium size, medium-length straight bills, usually territorial or short-distance trapline foragers; 4 = very small, short-billed nonhermit hummingbirds that often visit very low-nectar, insect-pollinated flowers; 5 = passerine (perching) birds; 6 = bees; and 7 = lepidopterans. The rationale for dividing the hummingbirds in this manner is based upon considerations of flower choice and community structure in these birds (*cf.* Feinsinger & Colwell 1978, Stiles 1985). However, for some comparisons we simply contrast flowers visited (or pollinated) by hermits vs nonhermits.

For parametric comparisons (*t*-test and ANOVA) of mean sugar proportions, the raw data were arcsine transformed (Sokal & Rohlf 1981). When the assumptions of the ANOVA could not be met (due to heterogeneity of variances or non-normality)

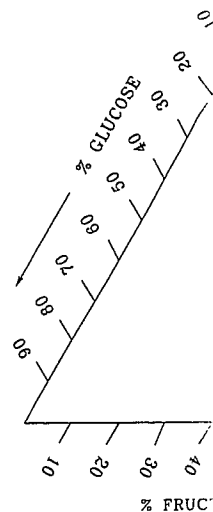


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RESULTS

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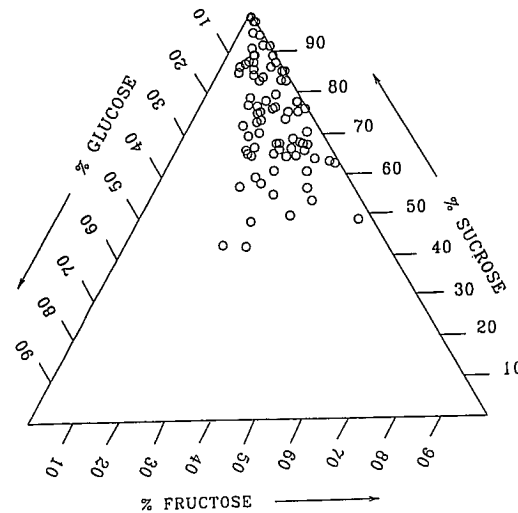


FIGURE 1. Ternary diagram of sugar compositions of non-*Heliconia* hummingbird-pollinated species.

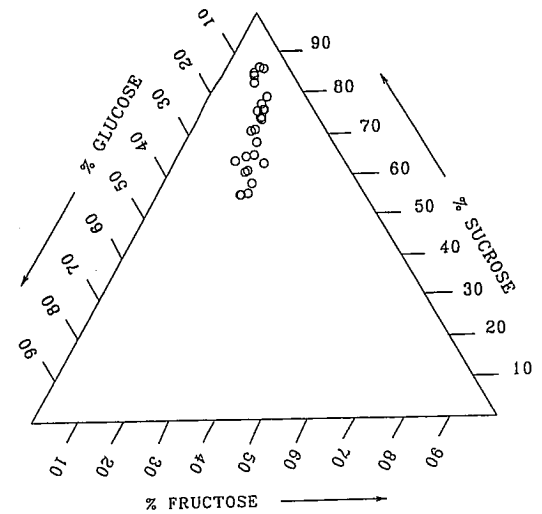


FIGURE 2. Ternary diagram of sugar compositions of *Heliconia* flowers.

the nonparametric Mann-Whitney *U*-test or Kruskal-Wallis test was used. Sugar compositions of different groups of Costa Rican nectars (based upon elevation and/or putative pollinator) were also compared by one-way ANOVA.

Sites of collections of nectar were assigned to six elevation categories as follows: lowland = 100 m or less; foothills = 101-800 m; lower mid-elevation = 801-1400 m; upper mid-elevation = 1401-2200 m; montane = 2201-3000 m; and paramo-subparamo = >3000 m. These categories correspond fairly closely to the Holdridge altitudinal life-zone belts (*cf.* Hartshorn 1983), save that we separate lowland and foothill zones based upon topography and bird distributions (*cf.* Stiles & Skutch 1989). For some comparisons we also separated samples from the dry Guanacaste lowlands from those of other lowland areas with more humid climates.

RESULTS

Data are presented in Table 1, summarized in Table 2, and plotted on ternary diagrams in Figures 1-3. Nectars of nearly all species believed to be pollinated by hummingbirds cluster towards the high-sucrose end of these diagrams (Figs. 1, 2). However, there are some interesting differences between plant families in nectar composition. The following considers only those families for which data for several (*N* ≥ 5) species are available. Acanthaceae have nectars with moderate to high sucrose percentages

(mostly 50-80%). The ratio of fructose to glucose (%fructose/%glucose) varies from somewhat less than 1 to 3 or more, with a weak tendency for species having nectar higher in sucrose to have lower F/G ratios (Spearman *r_s* = -0.406, *P* = 0.25, *N* = 10). Ericaceae have nectars with moderate to high sucrose percentages (mostly 75-95%) with fairly balanced ratios of fructose to glucose (F/G from 0.86-2.5). Here, a weak tendency exists for the

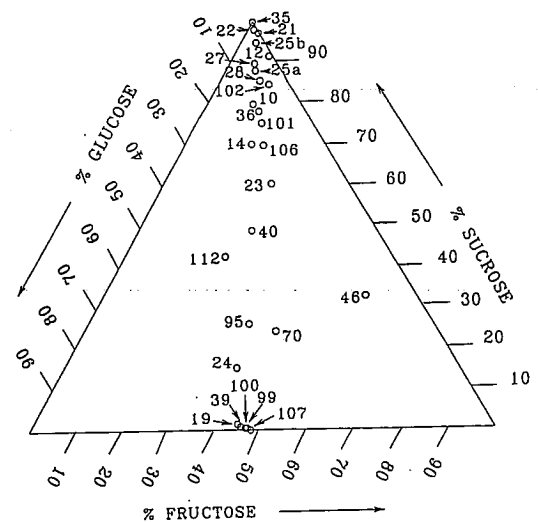


FIGURE 3. Ternary diagram of sugar compositions of flowers visited by hummingbirds but not believed pollinated by them.

TABLE 1. Data on 120 samples (representing 112 species) of floral nectars of hummingbird-visited taxa from Costa Rica. Sugar composition percentages are \pm one SD.

Taxon	Local-ity ^a	Elevation (veg. type) ^b	Pollinators ^c	Major hummingbird visitor(s)	N	% Fructose	% Glucose	% Sucrose	Daily nectar secretion (μ)	Sugar concentration (equiv. sucrose M)
ACANTHACEAE										
1 <i>Apelandra deppeana</i>	2	10 m (L,D)	1	1, 3	5	23.5 \pm 1.4	7.3 \pm 2.2	69.2 \pm 1.8	35	0.62
2 <i>A. storckii</i>	1	60 m (L)	1	1	5	26.1 \pm 1.8	19.1 \pm 1.4	54.8 \pm 3.2	50	0.69
3 <i>Dactyloctenium aegyptium</i>	3	1600 m (UM)	3	3	3	20.3 \pm 1.4	19.8 \pm 6.3	59.9 \pm 7.5	nd ^d	nd
4 <i>Hansteinia blepharorachis</i>	3	1500 m (UM)	3	3	3	21.0 \pm 0.2	12.6 \pm 2.9	66.4 \pm 2.7	nd	nd
5 <i>Justicia aurea</i>	1	50 m (L)	1	1, 3	5	30.3 \pm 3.6	9.2 \pm 2.7	60.5 \pm 6.1	75	0.67
6 <i>J. macrantha</i>	3	1450 m (UM)	1	1, 2, 3	5	11.6 \pm 3.2	16.4 \pm 2.3	72.0 \pm 5.4	18	0.65
7 <i>Odontonema callistachyum</i>	1	50 m (L)	3	3	4	32.2 \pm 0.7	17.8 \pm 3.9	50.0 \pm 4.5	16	0.63
8 <i>Razisea spicata</i>	3	1550 m (UM)	1	1	3	32.5 \pm 2.6	10.2 \pm 1.6	57.3 \pm 2.6	20	0.64
9 <i>R. wilburii</i>	1	50 m (L)	3	3	5	18.0 \pm 0.7	11.8 \pm 5.0	70.1 \pm 5.7	11	0.68
10 <i>Ruellia inundata</i>	2	10 m (L,D)	7	3, 4	6	10.1 \pm 1.9	10.6 \pm 2.5	79.2 \pm 4.4	4.5	1.15
AMARYLLIDACEAE										
11 <i>Bomarea angustifolia</i>	4	3100 m (P)	3	3, 4	3	31.1 \pm 7.4	5.1 \pm 1.2	63.8 \pm 6.5	15	0.42
12 <i>B. chontalensis</i>	1	50 m (L)	7 ^e , 3 ^f	3	3	8.2 \pm 4.9	0.5 \pm 0.4	91.4 \pm 4.8	10	0.62
13a <i>B. costaricensis</i>	4	3100 m (P)	2	2	5	28.6 \pm 3.0	3.6 \pm 2.4	67.8 \pm 5.4	45	0.41
13b <i>B. costaricensis</i>	3	1550 m (UM)	2	2, 3	4	28.4 \pm 2.5	1.5 \pm 0.5	70.1 \pm 2.9	nd	0.53
APOCYNACEAE										
14 <i>Mandevilla birsuta</i>	5	570 m (FH)	7 ^e , 1 ^f	1	6	13.9 \pm 1.7	16.1 \pm 2.1	70.0 \pm 3.7	35	1.00
BROMELIACEAE										
15 <i>Aechmea maria-reginae</i>	1	50 m (L)	3	3	5	11.7 \pm 0.5	11.6 \pm 0.6	76.8 \pm 0.8	20	0.75
16 <i>Pitcairnia brittoniana</i>	3	1500 m (UM)	2, 3	3	2	12.6 \pm 0.0	11.9 \pm 0.4	75.6 \pm 0.4	nd	nd
CANNACEAE										
17 <i>Canna</i> sp.	1	50 m (L)	1	1	8	18.3 \pm 1.6	17.1 \pm 2.2	64.7 \pm 3.9	55	0.81
GLIUSIACEAE (GUTTIFERAE)										
18 <i>Symphonia globulifera</i>	1	150 m (FH)	1, 3	1, 3	6	19.3 \pm 1.3	23.3 \pm 1.4	57.4 \pm 2.4	50	0.48
COMBRETACEAE										
19 <i>Combretum farinosum</i>	2	10 m (L,D)	5	3	7	47.8 \pm 0.5	52.2 \pm 0.5	0.0	20	1.00
20 <i>Cotus malortianus</i>	1	50 m (L)	1, 6	1	7	0.3 \pm 0.4	0.2 \pm 0.3	99.5 \pm 0.8	75	0.97
21 <i>C. puberulentus</i>	6	1000 m (LM)	1	1	4	1.6 \pm 0.9	0.1	98.3 \pm 0.9	85	0.98
22 <i>C. scaber</i>	5	570 m (FH)	1	1	6	0.8 \pm 0.4	0.5 \pm 0.5	98.7 \pm 0.8	50	0.94

17	<i>Canna</i> sp.	1	50 m (L)	1	1	8	18.3 ± 1.6	17.1 ± 2.2	64.7 ± 3.9	55	0.81
CLUSIACEAE (GUTTIIFERAE)											
18	<i>Symphonia globulifera</i>	1	150 m (FH)	1, 3	1, 3	6	19.3 ± 1.3	23.3 ± 1.4	57.4 ± 2.4	50	0.48
COMBRETACEAE											
19	<i>Combretum farinosum</i>	2	10 m (L,D)	5	3	7	47.8 ± 0.5	52.2 ± 0.5	0.0	20	1.00
20	<i>Costus malortieanus</i>	1	50 m (L)	1, 6	1	7	0.3 ± 0.4	0.2 ± 0.3	99.5 ± 0.8	75	0.97
21	<i>C. pulverulentus</i>	6	1000 m (LM)	1	1	4	1.6 ± 0.9	0.1	98.3 ± 0.9	85	0.98
22	<i>C. scaber</i>	5	570 m (FH)	1	1	6	0.8 ± 0.4	0.5 ± 0.5	98.7 ± 0.8	50	0.94

TABLE 1. Continued.

Taxon	Local-ity ^a	Elevation (veg. type) ^b	Pollinators ^c	Major humming-bird visitor(s)	N	% Fructose	% Glucose	% Sucrose	Daily nectar secretion (μ)	Sugar concentration (equiv. sucrose M)
CUCURBITACEAE										
23	<i>Gurania costaricensis</i>	1	50 m (L)	7, 3?	3	23.3 ± 0.2	16.5 ± 0.3	60.2 ± 0.4	10	0.65
24	<i>G. leytana</i>	1	50 m (L)	7, 3?	3	38.4 ± 3.5	46.1 ± 0.7	15.3 ± 3.6	18	0.65
ERICACEAE										
25a	<i>Cavendishia callista</i>	5	570 m (FH)	3	3, 2	7.0 ± 1.5	5.6 ± 2.0	87.4 ± 3.6	22	0.60
25b	<i>C. callista</i>	6	1000 m (LM)	2	2	2.6 ± 0.5	1.3 ± 0.2	96.2 ± 0.6	40	0.69
26	<i>C. capitulata</i>	3	1450 m (UM)	3, 4	3	7.9 ± 1.6	6.1 ± 0.7	86.0 ± 2.3	6	0.71
27	<i>C. costaricensis</i>	7	1400 m (LM)	3	8	5.7 ± 0.9	4.7 ± 0.6	89.6 ± 1.5	25	0.66
28a	<i>C. crassifolia</i>	8	2550 m (UM)	3	5	8.6 ± 0.4	7.4 ± 0.5	83.9 ± 0.9	15	0.60
28b	<i>C. crassifolia</i>	3	1550 m (M)	3	5	6.0 ± 2.1	7.0 ± 0.5	87.0 ± 5.3	30	0.65
29	<i>C. endresii</i>	6	1000 m (LM)	3	4	16.1 ± 2.9	17.6 ± 2.7	66.4 ± 5.5	11	0.59
30	<i>C. quereze</i>	6	1000 m (LM)	3	4	7.5 ± 1.5	7.7 ± 2.2	84.8 ± 3.7	6	0.77
31	<i>C. smithii</i>	8	2650 m (M)	2, 3	3	6.2 ± 1.0	6.7 ± 0.4	87.2 ± 1.3	25	0.56
32	<i>Macleania glabra</i>	4	3100 m (P)	3	3	17.1 ± 2.7	6.9 ± 0.6	76.0 ± 2.8	20	0.48
33a	<i>Psammissia ramiflora</i>	3	1600 m (UM)	1, 2	6	5.3 ± 1.2	4.4 ± 0.8	90.3 ± 2.0	35	0.68
33b	<i>P. ramiflora</i>	6	1000 m (LM)	2	6	7.2 ± 1.2	4.1 ± 0.9	88.8 ± 1.8	38	0.75
34	<i>Satyria warcewiczii</i>	3	1530 m (UM)	2	5	8.8 ± 3.8	5.6 ± 3.3	88.3 ± 7.1	nd	nd
35	<i>Vaccinium consanguineum</i>	4	3100 m (P)	6	4	u	u	100.0	1.5	0.70
FABACEAE										
36	<i>Calliandra</i> sp. nov.	6	1000 m (LM)	7, 3?	3	10.4 ± 0.2	12.6 ± 0.6	77.1 ± 0.8	nd	nd
37	<i>Erythrina cochleata</i>	1	50 m (L)	2	2	26.2 ± 4.9	18.4 ± 4.8	55.4 ± 9.8	28	0.76
38	<i>E. costaricensis</i>	9	1200 m (LM)	2	5	21.9 ± 2.5	13.4 ± 1.1	63.8 ± 3.1	21	0.97
39	<i>E. poeppigiana</i>	9	1200 m (LM)	5	4	45.2 ± 2.7	53.8 ± 2.6	1.0 ± 0.2	80	0.48
40	<i>Inga vera</i>	9	1200 m (LM)	7	6	24.7 ± 2.0	26.8 ± 3.0	48.5 ± 5.0	nd	nd
GENTIANACEAE										
41	<i>Symbalanthus pulcherrimus</i>	8	2650 m (M)	2	2	25.1 ± 5.3	10.3 ± 5.1	64.7 ± 10.4	40	0.62
GESNERIACEAE										
42	<i>Allipectus ichthyoderma</i>	8	2650 m (M)	3	3	28.4 ± 3.2	5.7 ± 1.1	65.9 ± 3.0	12	0.59
43	<i>A. tetragonus</i>	3	1500 m (UM)	1	1	20.2 ± 4.5	4.9 ± 2.0	74.9 ± 6.4	35	0.71
44	<i>Besteria columneoides</i>	1	100 m (L)	3	6	11.5 ± 6.6	0.9 ± 1.3	87.7 ± 7.6	14	0.79
45	<i>B. formosa</i>	3	1600 m (UM)	3	5	17.0 ± 6.2	1.1 ± 0.9	82.0 ± 6.2	15	0.57

TABLE 1. Continued.

Taxon	Local-ity ^a	Elevation (veg. type) ^b	Pollinators ^c	Major humming-bird visitor(s)	N	% Fructose	% Glucose	% Sucrose	Daily nectar secretion (μ)	Sugar concentration (equiv. sucrose M)
46 <i>Columnnea gloriosa</i>	8	2600 m (M)	3	3	2	57.8 \pm 10.5	10.2 \pm 0.6	32.1 \pm 11.1	10	1.09
47 <i>C. linearis</i>	1	50 m (L)	3	3	6	15.8 \pm 1.7	0.2 \pm 0.2	84.1 \pm 1.7	17	1.03
48 <i>C. lepidocaula</i>	3	1500 m (UM)	3, 1?	3, 1?	4	15.6 \pm 0.4	0.0	84.4 \pm 0.4	25	0.88
49 <i>C. magnifica</i>	8	2650 m (M)	2, 3	2, 3	2	15.4 \pm 1.8	2.0 \pm 1.1	82.7 \pm 0.7	20	0.84
50 <i>C. microcalyx</i>	3	1500 m (UM)	3, 2?	3, 2?	3	8.9 \pm 1.0	0.0	91.1 \pm 1.0	15	0.94
51 <i>C. nicaraguensis</i>	5	570 m (FH)	1	1, 3	5	10.2 \pm 2.1	0.7 \pm 0.6	89.1 \pm 2.7	29	0.98
52 <i>C. oxyphylla</i>	5	570 m (FH)	1	1	3	23.3 \pm 2.1	0.7 \pm 0.6	76.1 \pm 2.7	23	0.86
53 <i>C. purpurata</i>	1	50 m (L)	1, 3	1, 3	2	16.2 \pm 3.7	4.4 \pm 0.6	79.4 \pm 4.3	27	1.07
54 <i>C. querceti</i>	6	1000 m (LM)	3	3	5	20.8 \pm 6.5	1.3 \pm 0.6	77.9 \pm 5.9	12	0.98
55 <i>Drymonia conchocalyx</i>	3	1500 m (UM)	2, 1	2, 1	8	18.6 \pm 4.0	14.3 \pm 1.7	67.2 \pm 5.4	55	0.76
56 <i>D. multiflora</i>	3	1550 m (UM)	3	3	4	22.6 \pm 0.2	19.7 \pm 0.9	57.9 \pm 0.7	11	0.89
57 <i>D. warszewicziana</i>	6	1000 m (LM)	3, 4	3, 4	5	35.5 \pm 4.1	11.3 \pm 1.2	53.2 \pm 5.0	8	0.95
58 <i>Kobleria spicata</i>	6	1000 m (LM)	3	3	5	22.2 \pm 1.4	2.5 \pm 1.1	75.4 \pm 1.3	13	0.58
59 <i>K. strigosa</i>	7	1000 m (LM)	3	3	4	20.6 \pm 1.8	6.3 \pm 1.5	73.1 \pm 0.5	15	0.60
60 <i>Solenophora calycosa</i>	7	1300 m (LM)	1, 2?	1, 2?	6	21.0 \pm 3.3	2.0 \pm 1.4	75.3 \pm 0.4	nd	nd
LAMIACEAE										
61 <i>Sida</i>	4	3100 m (P)	3, 4	3, 4	4	10.1 \pm 1.5	7.6 \pm 1.0	82.4 \pm 2.6	6	0.87
62 <i>Scutellaria costaricana</i>	6	1000 m (LM)	1	1	6	16.8 \pm 4.5	6.3 \pm 3.1	76.9 \pm 6.9	25	0.59
LOASACEAE										
63 <i>Loasa spectabilis</i>	4	3100 m (P)	2	2	8	27.3 \pm 1.5	4.8 \pm 1.7	67.9 \pm 3.1	36	0.55
LOBELIACEAE										
64 <i>Centropogon granulatus</i>	5	570 m (FH)	1	1	4	12.2 \pm 0.8	0.0	87.8 \pm 0.9	55	1.01
65 <i>C. ochraceum</i>	8	2600 m (M)	3	3	3	38.5 \pm 7.8	2.9 \pm 1.2	58.6 \pm 8.2	15	0.54
66 <i>C. solanifolius</i>	3	1500 m (UM)	1	1, 2?	2	11.6 \pm 0.4	1.5 \pm 0.4	87.0	35	0.69
67 <i>C. talamancensis</i>	4	3100 m (P)	2	2	6	37.5 \pm 2.6	0.9 \pm 1.1	59.2 \pm 2.5	30	0.45
68 <i>C. valerii</i>	4	3100 m (P)	3	3	6	48.1 \pm 6.9	2.8 \pm 1.0	49.1 \pm 7.7	19	0.47
69 <i>Lobelia laxiflora</i>	3	1300 m (LM)	3	3	5	27.2 \pm 6.7	4.3 \pm 1.8	68.6 \pm 8.4	20	0.60
LORANTHACEAE										
70 <i>Gaiadendron punctatum</i>	4	3100 m (P)	6, 3?	3	6	41.3 \pm 5.0	35.8 \pm 2.1	22.9 \pm 6.8	5	0.60
MALVACEAE										
71 <i>Malvastrum palmanum</i>	3	1500 m (UM)	1	1, 2, 3	4	22.0 \pm 2.0	9.4 \pm 1.7	68.6 \pm 3.4	70	0.68

	3	1	3	2	3	38.5 ± 7.8	2.9 ± 1.2	58.6 ± 8.2	15
66	3	1	3	2	3	11.6 ± 0.4	1.5 ± 0.4	87.0	1.01
67	4	2	1, 2?	2	2	37.5 ± 2.6	0.9 ± 1.1	59.2 ± 2.5	0.54
68	4	3	3	6	3	48.1 ± 6.9	2.8 ± 1.0	49.1 ± 7.7	0.69
69	3	3	3	5	3	27.2 ± 6.7	4.3 ± 1.8	68.6 ± 8.4	0.45
LORANTHACEAE									
70	4	6, 3?	3	6	6	41.3 ± 5.0	35.8 ± 2.1	22.9 ± 6.8	0.47
MALVACEAE									
71	3	1	1, 2, 3	4	4	22.0 ± 2.0	9.4 ± 1.7	68.6 ± 3.4	0.60

TABLE 1. Continued.

Taxon	Local-ity ^a	Elevation (veg. type) ^b	Pollinators ^c	Major humming-bird visitor(s)	N	% Fructose	% Glucose	% Sucrose	Daily nectar secretion (μ)	Sugar concentration (equiv. sucrose M)
MUSACEAE										
72	10	650 m (FH)	1	1	3	16.2 ± 0.4	18.8 ± 0.4	65.0 ± 0.6	nd	nd
73	7	1600 m (UM)	1	1	5	20.1 ± 0.9	17.8 ± 1.8	62.1 ± 2.4	100	0.76
74	10	500 m (FH)	1	1	5	14.0 ± 0.8	15.2 ± 0.3	70.7 ± 1.0	95	1.00
75a	1	50 m (L)	1	1	5	9.1 ± 0.5	9.1 ± 0.6	81.9 ± 1.0	65	1.02
75b	12	40 m (L)	1	1	5	12.5 ± 1.4	10.0 ± 1.6	77.6 ± 3.0	62	1.00
76	6	1035 m (LM)	1	1	5	20.2 ± 0.1	23.9 ± 0.4	55.9 ± 0.6	50	0.71
77a	1	30 m (L)	3	3	5	18.1 ± 0.4	21.1 ± 0.4	58.9 ± 0.7	80	0.66
77b	1	60 m (L)	3	3	5	18.8 ± 0.6	19.9 ± 1.0	61.3 ± 1.6	85	0.65
78	4	2100 m (UM)	2, 1?	2, 1?	11	19.9 ± 1.3	23.6 ± 1.7	56.5 ± 2.9	65	0.75
79a	1	50 m (L)	3	3	5	14.1 ± 1.7	11.8 ± 1.7	74.1 ± 3.4	75	0.90
79b	11	40 m (L)	3	3	5	13.4 ± 0.8	10.1 ± 0.8	76.5 ± 2.0	80	0.92
80	1	50 m (L)	3	3	6	13.0 ± 0.8	11.1 ± 0.8	75.9 ± 1.5	45	0.79
81	12	20 m (L)	1	1	5	12.8 ± 2.3	11.6 ± 1.4	75.7 ± 3.6	55	1.11
82	1	50 m (L)	1	1	5	9.6 ± 1.0	4.7 ± 1.3	85.7 ± 2.3	70	0.75
83	3	1600 m (UM)	3	3	2	19.7 ± 0.1	24.9 ± 1.1	55.5 ± 1.1	25	0.68
84	11	40 m (L)	1	1	2	12.4 ± 0.4	8.5 ± 0.2	79.1 ± 0.6	nd	nd
85	12	30 m (L)	1	1	5	14.8 ± 1.8	11.5 ± 0.6	73.7 ± 1.6	nd	nd
86	1	50 m (L)	1	1, 3	5	7.4 ± 0.3	6.7 ± 0.3	86.0 ± 0.3	110	0.92
87	6	1000 m (LM)	1	1	4	13.4 ± 4.0	17.3 ± 5.4	69.3 ± 9.4	70	0.71
88	13	1350 m (LM)	3	3	6	16.7 ± 1.7	18.8 ± 1.7	64.5 ± 3.4	55	0.75
89	12	50 m (L)	1	1	5	16.3 ± 0.7	15.1 ± 1.6	68.6 ± 2.2	65	1.03
90	14	50 m (L)	1	1	5	7.9 ± 0.3	8.1 ± 0.5	84.0 ± 0.8	100	0.73
91a	3	1550 m (LM)	1, 2	1, 2	6	18.5 ± 2.7	20.9 ± 2.1	73.9 ± 0.5	70	0.86
91b	1	100 m (L)	1	1	5	8.3 ± 0.5	7.7 ± 0.5	82.4 ± 0.5	90	nd
92	1	75 m (L)	1	1	6	13.3 ± 0.8	16.1 ± 0.5	70.6 ± 1.2	70	0.95
93	12	50 m (L)	1	1	5	10.5 ± 0.4	7.1 ± 0.3	82.4 ± 0.5	90	0.80
ONAGRACEAE										
95	8	2600 m (M)	6, 7	3, 4	5	35.2 ± 1.9	38.4 ± 2.7	26.4 ± 2.5	2.5	0.51
96	4	3100 m (P)	4	4, 3	6	16.4 ± 1.2	18.3 ± 1.2	65.3 ± 2.5	4	0.56
97	4	3100 m (P)	2	2, 3	3	27.2 ± 0.5	30.5 ± 1.2	42.3 ± 1.7	33	0.42

TABLE 1. Continued.

Taxon	Local-ity ^a	Elevation (veg. type) ^b	Pollinators	Major humming-bird visitor(s)	N	% Fructose	% Glucose	% Sucrose	Daily nectar secretion (μ)	Sugar concentration (equiv. sucrose M)
PASSIFLORACEAE										
98 <i>Passiflora vitifolia</i>	1	50 m (L)	1	1	3	10.7 \pm 0.1	5.7 \pm 0.3	83.6 \pm 0.4	120	0.79
PHYTOLACCACEAE										
99 <i>Phytolacca rugosa</i>	4	3100 m (P)	6	4	7	47.7 \pm 1.0	52.3 \pm 1.0	0.0	1.5	0.72
POLYGALACEAE										
100 <i>Monnina crepini</i>	4	3100 m (P)	6	4	6	45.9 \pm 0.8	53.5 \pm 0.5	0.6 \pm 1.2	2	0.73
RUBIACEAE										
101 <i>Cephaelis elata</i>	5	550 m (FH)	3	3, 4	4	14.0 \pm 1.7	11.2 \pm 2.4	74.8 \pm 3.7	15	0.68
102 <i>C. tomentosa</i>	5	550 m (FH)	3, 4	3, 4	5	11.2 \pm 0.7	5.8 \pm 0.8	83.0 \pm 1.5	13	0.65
103 <i>Gonzalegunia rosea</i>	3	1450 m (UM)	4, 7	4	5	23.5 \pm 1.4	16.8 \pm 0.9	59.7 \pm 2.2	3.5	0.72
104 <i>Hamelia patens</i>	1	50 m (L)	3	3, 4	6	15.2 \pm 3.7	11.2 \pm 3.2	73.6 \pm 6.9	18	0.78
105 <i>Pentagonia donnell-smithii</i>	1	50 m (L)	1, 6?	1	6	4.1 \pm 0.6	1.2 \pm 0.6	94.7 \pm 0.8	30	1.21
106 <i>Sabicea panamensis</i>	5	700 m (FH)	7	4	3	18.0 \pm 8.1	12.3 \pm 0.8	69.7 \pm 8.6	3.5	0.81
107 <i>Warzewiczia coccinea</i>	5	200 m (FH)	7, 4?	4	5	46.7 \pm 0.5	53.0 \pm 0.6	0.2 \pm 0.2	4	0.64
SCROPHULARIACEAE										
108 <i>Castilleja iratzensis</i>	4	3100 m (P)	4	4	7	27.9 \pm 0.7	8.0 \pm 3.4	64.2 \pm 3.4	4	0.56
109 <i>Gibsoniothamnus</i> sp. nov.	5	450 m (FH)	1	1	3	21.4 \pm 0.9	10.6 \pm 1.1	68.0 \pm 1.3	50	0.82
SIMAROUBACEAE										
110 <i>Quassia amara</i>	15	40 m (L,D)	3	3	9	14.3 \pm 2.3	12.8 \pm 4.3	72.9 \pm 4.6	nd	nd
TROPAEOLACEAE										
111 <i>Tropaeolum moritzianum</i>	4	3000 m (M)	3, 4	3, 4	3	13.2 \pm 3.8	8.2 \pm 4.5	78.5 \pm 8.1	8	0.90
ZINGIBERACEAE										
112 <i>Renealmia</i> sp. nov.	6	1000 m (LM)	1	1	5	21.9 \pm 0.7	36.1 \pm 2.7	41.9 \pm 3.0	85	0.71

^a Localities: 1 = Estación Biológica La Selva; 2 = Estación Biológica Palo Verde; 3 = Monte Verde; 4 = Villa Mills-Cerro de la Muerte; 5 = El Plástico-Las Horquetas; 6 = La Montura; 7 = Río La Hondura-La Ventana; 8 = Madreselva; 9 = San Pedro-Universidad de Costa Rica; 10 = Palmar Sur; 11 = vic. Golfo; 12 = vic. Golfo; 13 = Cariblanco-Cinchona; 14 = Tres Ríos; 15 = La Pacifica.

^b Vegetation types: L = moist to wet lowlands; L,D = dry lowlands; FH = foothills; LM = lower middle elevation forests; UM = upper middle elevation forests; M = montane forests; P = paramo + subparamo.

^c Pollinators: 1 = hermit hummingbirds; 2 = hermit-like nonhermits; 3 = typical nonhermits; 4 = very small, short-billed nonhermits; 5 = passerine (perching) birds; 6 = bees; 7 = lepidoptera.

^d No data.

111	<i>Tropaeolum moritzianum</i>	4	3000 m (M)	3, 4	3, 4	3	13.2 ± 3.8	8.2 ± 4.5	78.5 ± 8.1	8	0.90
ZINGIBERACEAE											
112	<i>Renealmia</i> sp. nov.	6	1000 m (LM)	1	1	5	21.9 ± 0.7	36.1 ± 2.7	41.9 ± 3.0	85	0.71

^a Localities: 1 = Estación Biológica La Selva; 2 = Estación Biológica Palo Verde; 3 = Monte Verde; 4 = Villa Mills-Cerro de la Muerte; 5 = El Plástico-Las Horquetas; 6 = La Montura; 7 = Río La Honda-La Ventana; 8 = Madreselva; 9 = San Pedro-Universidad de Costa Rica; 10 = Turrialba; 11 = Palmar Sur; 12 = vic. Golfito; 13 = Cariblanco-Cinchona; 14 = Tres Ríos; 15 = La Pacifica.
^b Vegetation types: L = moist to wet lowlands; L₁D = dry lowlands; FH = foothills; LM = lower middle elevation forests; UM = upper middle elevation forests; M = montane forests; P = paramo + subparamo.
^c Pollinators: 1 = hermit hummingbirds; 2 = hermit-like nonhermits; 3 = typical nonhermits; 4 = very small, short-billed nonhermits; 5 = passerine (perching) birds; 6 = bees; 7 = lepidopterans.
^d No data.

TABLE 2. Statistical description of nectar sugar composition data of 104 samples of hummingbird-pollinated species from Costa Rica.

Group	N	Mean percentage (±SE)			Mean elev. (m)	Mean daily prod. (µl)	Mean conc. (equiv. sucrose M)
		Fructose	Glucose	Sucrose			
Total	104	17.4 ± 0.9	9.8 ± 0.7	72.8 ± 1.3	1120	39.8 ± 3.0 (N = 93)	0.75 ± 0.02 (N = 94)
Hermits	43	14.7 ± 1.1	10.1 ± 1.2	75.1 ± 2.0	611	60.4 ± 4.3 (N = 38)	0.83 ± 0.03 (N = 38)
Hermit-like nonhermits	15	20.1 ± 2.6	9.4 ± 2.3	70.5 ± 3.9	2019	36.6 ± 3.6 (N = 15)	0.65 ± 0.04 (N = 15)
Typical nonhermits	43	18.8 ± 1.7	9.2 ± 1.0	72.0 ± 2.0	1217	23.7 ± 3.5 (N = 39)	0.72 ± 0.03 (N = 39)
Very small, short-billed nonhermits	3	22.6 ± 3.4	14.4 ± 3.2	63.1 ± 1.7	2550	3.8 ± 0.2 (N = 3)	0.61 ± 0.05 (N = 3)

F/G ratio to increase with increasing sucrose percentage ($r_s = 0.352$, $P = 0.25$, $N = 13$). Gesneriaceae have nectars with moderate to high (50–90%) sucrose percentages. Fructose is usually greatly in excess of glucose, and F/G ratios show a strong tendency to increase with increasing sucrose percentages ($r_s = 0.717$, $P < 0.001$, $N = 19$). Lobeliaceae nectars are moderately to fairly high in sucrose (50–88%), and fructose is far in excess of glucose in all. F/G ratios show no relation to sucrose percentages ($r_s = 0.077$, $P > 0.5$, $N = 6$). Musaceae (*Heliconia*) nectars show moderate to fairly high sucrose percentages (55–85%), with fructose and glucose fairly evenly balanced. However, there is a strong tendency for F/G ratios to increase with increasing sucrose percentage ($r_s = 0.681$, $P < 0.001$, $N = 27$). Rubiaceae nectars show moderate to high sucrose percentages (60–95%), with fructose and glucose fairly evenly balanced. However, there is a moderate tendency for F/G ratios to increase with increasing sucrose percentages ($r_s = 0.486$, $P = 0.25$, $N = 6$) is observed.

The small number of samples available for the other families precludes further statistical analysis, although a few families appear notable for high sucrose percentages (e.g., Costaceae); or, high (Scrophulariaceae, Loasaceae) or low (Onagraceae) F/G ratios. In general, however, nectars of hummingbird-pollinated Costa Rican flowers can be well characterized by high sucrose percentages (50–95%) and with fructose and glucose either closely balanced or with slight to very pronounced excess of the former. The ratios of these two sugars vary with respect to sucrose percentage in a family-specific manner as described above.

Nectars of flowers visited but not believed to be primarily pollinated by hummingbirds are plotted in Figure 3. At the bottom of this figure is a cluster of species whose nectars contain little or no sucrose. Several of these species are probably pollinated mostly by passerine birds, including *Combretum farinosum* (sample number 19 of Table 1) and *Erythrina poeppigiana* (#39); bees (*Monnina crepini*, #100; *Phytolacca rugosa*, #99); or lepidopterans (*Warszewiczia coccinea*, #107); and probably *Gurania costaricensis* (#23) and *G. leyvana* (#24). Two species producing nectars somewhat higher in sucrose, but still decidedly hexose-dominant, are *Gaiadendron punctatum* (#70) and *Fuchsia arborescens* (#95). Bees are probably the primary pollinators of both, but hummingbird visitation to both of these highland species is frequent (Wolf *et al.* 1976). Another somewhat problematical nectar is that of *Columnea gloriosa* (#46)

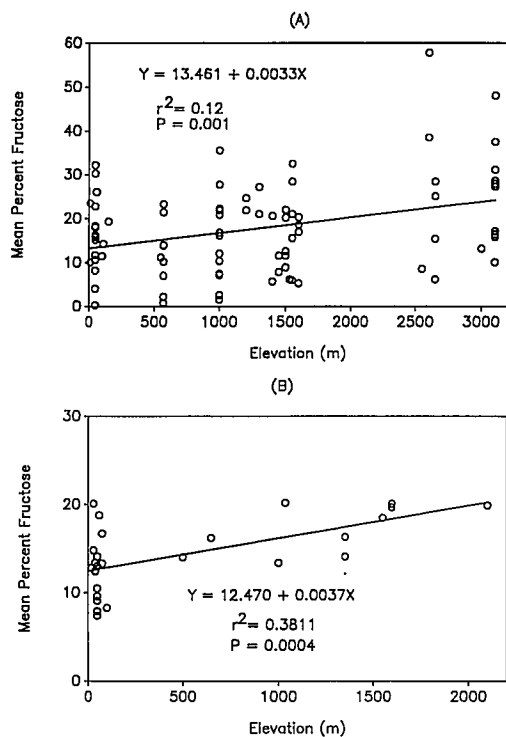


FIGURE 4. Relationship between fructose composition and elevation in (A) non-*Heliconia* and (B) *Heliconia* samples of hummingbird-pollinated flowers.

which, from morphology and observation of visitation, appears to be a typical hummingbird flower, but with an unusually low sucrose percentage and a very high fructose percentage. However, it is a member of a family (Gesneriaceae) with mostly high F/G ratios and, together, sucrose and fructose total about 90 percent. Thus, the nectar of *C. gloriosa* is more hummingbird-like than is immediately obvious. Other nectars on this figure include those of *Vaccinium consanguineum* (35), whose small, bee-pollinated flowers are visited by small hummingbirds mainly when other flowers are scarce. Several largely or mostly lepidopteran-pollinated flowers, such as *Ruellia inundata* (10), *Mandevilla hirsuta* (14), *Inga vera* (40), *Calliandra* sp. nov. (36), *Gonzalegunia rosea* (103), and *Sabicea panamensis* (106), have nectars similar in composition to those of typical hummingbird-pollinated flowers. *Vaccinium* is notable for its essentially pure-sucrose nectar, but the hummingbird-like nectars of the other species indicate that lepidopterans may respond to nectar sugars in a manner similar to hummingbirds or, alternatively, that hummingbirds may be important pollinators in at least some of these species.

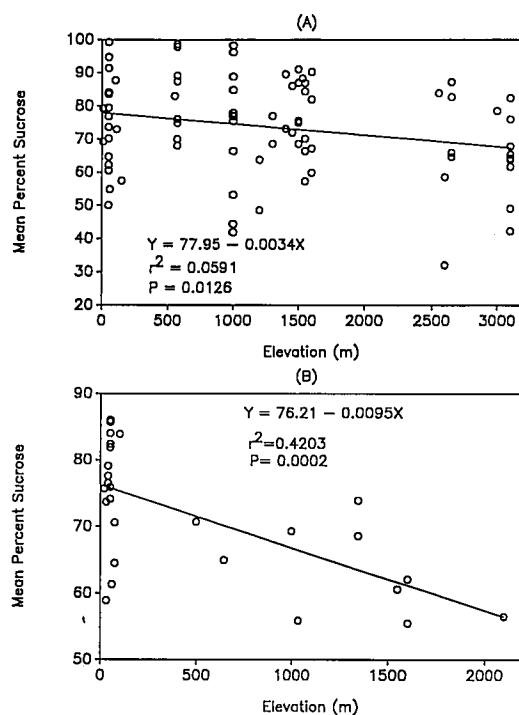


FIGURE 5. Relationship between sucrose composition and elevation in (A) non-*Heliconia* and (B) *Heliconia* samples of hummingbird-pollinated flowers.

A summary of the sugar compositions of the hummingbird nectars is shown in Table 2. The centroid of the entire 104 determinations is 17.4 percent fructose, 9.8 percent glucose, and 72.8 percent sucrose. A comparison of the percentages of fructose and glucose in the hummingbird cluster of the Costa Rican sample as a whole indicated that the mean percent of fructose was significantly greater than that of glucose ($Z = 6.230$; $P < 0.0001$). This confirms a similar observation seen in the previous sample of hummingbird nectars (Freeman *et al.* 1984) and suggests that hummingbirds may prefer nectars with more fructose than glucose. The significant difference, however, is due to the 77 non-*Heliconia* samples ($Z = 6.479$, $P < 0.0001$) and does not occur within the 27 *Heliconia* samples ($Z = 0.389$, $P = 0.697$).

The elevational distributions of the flowers pollinated by different groups of hummingbirds in Costa Rica are shown in Table 2. The mean elevations of samples pollinated by these groups vary greatly and significantly ($t = 23.616$; $df = 3$; $P < 0.001$). The mean daily rates of nectar secretion also vary greatly and significantly ($t = 45.537$; $df = 3$; $P < 0.001$) as does mean sugar concentration ($t =$

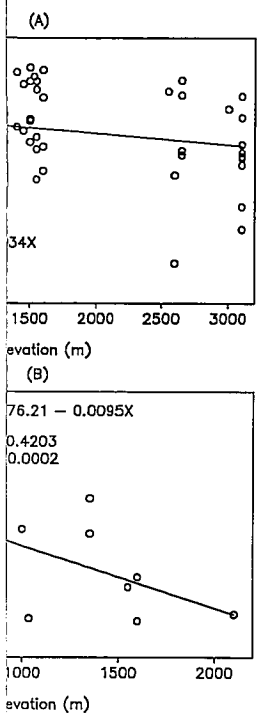


Figure 5. Relationship between sucrose composition in (A) *Heliconia* and (B) *non-Heliconia* pollinated flowers.

...sugar compositions of the... shown in Table 2. The... determinations is 17.4... percent glucose, and 72.8 per... of the percentages of... hummingbird cluster of... as a whole indicated that... was significantly greater... = 6.230; $P < 0.0001$).

...ervation seen in the pre-... bird nectars (Freeman *et*... that hummingbirds may... fructose than glucose. The... ver, is due to the 77 non-... 4.79, $P < 0.0001$) and... 27 *Heliconia* samples (Z

14.952; $df = 3$; $P = 0.002$). It is, therefore, possible that hummingbirds affect these nectar parameters. On the other hand, the hummingbird groups were not significantly different in regard to mean sugar compositions (fructose $t = 6.481$, $df = 3$, $P = 0.09$; glucose $t = 1.922$, $df = 3$, $P = 0.589$; sucrose $t = 4.156$, $df = 3$, $P = 0.245$).

Correlations were sought between sugar composition and elevation within a sample of 104 nectars within the hummingbird-pollinated samples. Since we had a relatively large number of *Heliconia* samples (27) representing 24 species, this group was separated from the 77 non-*Heliconia* samples. Fructose means were 17.6 percent and 14.3 percent for the non-*Heliconia* (Fig. 1) and *Heliconia* (Fig. 2) subsamples, respectively. These means were not significantly different ($U = 1282$, $P = 0.147$). The same comparison of sucrose compositions yielded means of 73.5 percent and 71.5 percent, also not significantly different ($U = 1231$, $P = 0.279$). Glucose means were 8.7 percent and 14.2 percent and these means are significantly different ($U = 543.5$, $P = 0.0001$). Except for glucose, the *Heliconia* and non-*Heliconia* subsamples were similar, and the data for the subgroups were pooled for analysis.

In regard to glucose composition, analysis of covariance indicated that no significant regression was present ($F[1, 104] = 1.619$; $P = 0.206$). Thus, glucose composition does not vary significantly with elevation. Significant regressions were, however, found between composition and elevation in fructose and sucrose (Figs. 4, 5). A test of fructose composition slopes in both the *Heliconia* and non-*Heliconia* groups (Fig. 4) indicated a significant positive relationship ($F[1, 104] = 15.756$; $P < 0.0001$). Further, a test for homogeneity of slopes indicated that they were not significantly different ($F[1, 103] = 0.034$; $P = 0.854$). Thus, the fructose composition of both samples appears to have responded to elevation in the same way.

A concomitant negative relationship was found between sucrose composition and elevation (Fig. 5). The test for zero slopes indicated a significant regression ($F[1, 104] = 10.567$; $P = 0.002$) and the test of equality of slopes indicated no significant difference ($F[1, 103] = 2.060$; $P = 0.154$). Both coefficients of determination of the regressions in the non-*Heliconia* samples were quite low. This result is not intuitively surprising when it is remembered that 21 families are represented within the sample.

Multiple regression was then used to simultaneously test for the effects of hummingbird groups and elevation in the fructose regression. Hum-

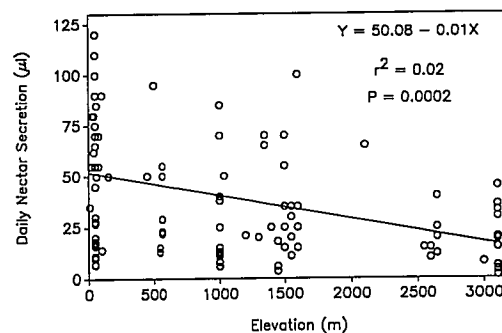


FIGURE 6. Relationship between daily nectar secretion rates and elevation in hummingbird-pollinated flower samples.

mingbird groups were not found to contribute significantly to the regression ($t = 0.980$, $P = 0.331$) while the elevation effect was significant ($t = 3.650$, $P = 0.0004$). In the same way, the sucrose-elevation relationship was due to the effects of elevation ($t = 2.090$, $P = 0.0395$) and not hummingbird groups ($t = 0.75$, $P = 0.458$).

Significant negative relationships were detected by multiple regression between elevation and both nectar secretion rates (Fig. 6) and nectar sugar concentrations in Fig. 7 (secretion $t = 3.17$, $P = 0.002$; concentration $t = 4.60$, $P < 0.0001$) when all hummingbird group data were pooled. However, within the hermit group secretion rates were not significantly related to elevation ($t = -0.51$, $P = 0.616$) while sugar concentration was ($t = -2.82$, $P = 0.008$). Within the nonhermit sample both were negatively related (secretion $t = -2.20$, $P = 0.026$; concentration $t = -3.42$, $P = 0.001$).

While numerous significant relationships can be demonstrated within these nectar data, can they be used to predict hummingbird pollinator groups with accuracy? The five nectar characteristics measured in this study were related to hummingbird pollinators by stepwise discriminant analysis (BMDP program 7M). The 93 samples of hummingbird-pollinated flowers which did not contain any missing data were used.

All four hummingbird classifications were used. The sequence of importance of the variables as discriminators was nectar secretion rate ($F[3, 89] = 16.75$), sugar concentration ($F[3, 89] = 5.34$), percentage fructose ($F[3, 89] = 2.12$), percentage sucrose ($F[3, 89] = 1.53$), and percentage glucose ($F[3, 89] = 0.62$). Sugar composition parameters were not significant contributors to the MANOVA. In this classification, group 1 (hermit hummingbirds) was correctly identified in 68.4 percent of the

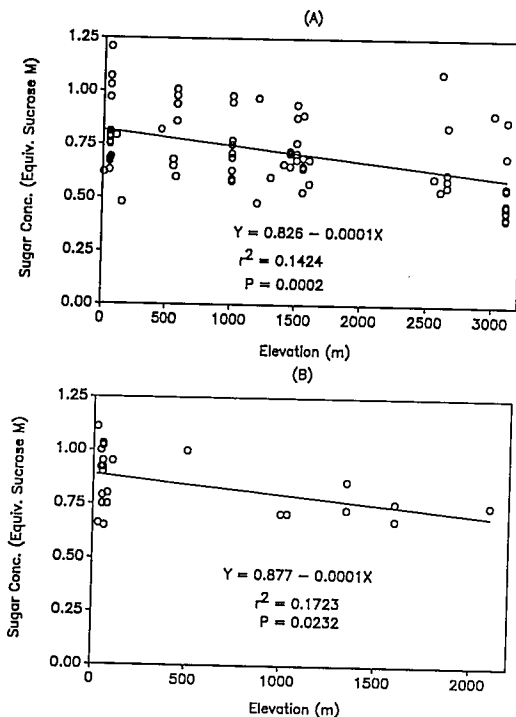


FIGURE 7. Relationship between nectar sugar concentration and elevation in (A) non-*Heliconia* and (B) *Heliconia* flower samples.

cases, group 2 (hermit-like nonhermits) 46.2 percent, group 3 (typical nonhermits) 51.3 percent, and group 4 (small, short-billed nonhermits) 100.0 percent.

The same nectar variables were used but hummingbirds were divided into two groups: hermits of the subfamily Phaethorninae and nonhermits of the subfamily Trochilinae, which included groups 2, 3, and 4. The relative importance of the variables remained the same: secretion rate $F[1, 90] = 42.75$, sugar concentration $F[1, 90] = 13.26$, percentage fructose $F[1, 90] = 6.01$, percentage sucrose $F[1, 90] = 3.22$, and percentage glucose $F[1, 90] = 0.06$. In this MANOVA only percentage glucose and sucrose were not significant contributors. This classification was correct in 73.7 percent of the hermit group cases and correct in 85.5 percent of the nonhermit group cases.

DISCUSSION

Sucrose was the predominant sugar in the nectars of all hummingbird-pollinated species that we examined. This corroborates previous studies (Stiles

1976; Baker & Baker 1983a; Freeman *et al.* 1984, 1985) that suggested that sucrose-rich nectar was characteristic of such nectars, to the extent that it might be considered part of a "syndrome" for hummingbird pollination (Stiles 1981). More striking still is the similarity in the proportions of sucrose, fructose, and glucose between the large and taxonomically diverse Costa Rican sample and smaller samples of hummingbird flowers from the southwestern United States and northwestern Mexico (*cf.* Freeman *et al.* 1984, 1985). No significant differences were detected by Kruskal-Wallis tests in median concentrations of sucrose ($T = 2.25$, $P = 0.325$), glucose ($T = 0.776$, $P = 0.776$), or fructose ($T = 4.107$, $P = 0.128$) among these three samples. Moreover, fructose concentration was significantly higher than that of glucose in the U.S. and Mexican samples as well as that from Costa Rica ($F[1, 56] = 7.72$, $P = 0.007$ and $F[1, 46] = 10.30$, $P = 0.002$, respectively). Thus, nectars of all three geographic groups of hummingbird flowers share a common sugar composition: adaptive convergence has evidently occurred, presumably reflecting the taste preferences and/or digestive physiology of the hummingbirds.

Hummingbird taste preferences have been investigated in three recent studies. Hainsworth and Wolf (1976) concluded that sugar composition had little effect on feeding preferences, but their experimental design failed to control for effects of feeder position (*cf.* Martinez del Rio 1990a). On the other hand, Stiles (1976) and Martinez del Rio (1990a) both documented strong preferences for sucrose only solutions over glucose only solutions over fructose only solutions, all being preferred to mixtures without sucrose, or over either hexose by itself. These preferences accord very well with the sugar compositions of hummingbird flower nectars studied to date and support the hypothesis that the taste preferences of these birds has been an important selective factor promoting convergence of these nectars.

The difficulty with this hypothesis is that the significance of these taste preferences to the hummingbirds has remained uncertain. Apparently digestive physiology is not involved, as hummingbird assimilation efficiencies for all three sugars are similar and very high ($\geq 97\%$) and the processing times for sucrose, sucrose-fructose, and glucose-fructose mixtures are similar (Martinez del Rio 1990a). Therefore, Martinez del Rio (1990a) has proposed "taste imprinting," the establishment of a long-lasting preference for sucrose by the hummingbird due to having been fed as nestlings on sucrose-rich nectars by their mother. In effect, the taste prefer-

1983a; Freeman *et al.* 1984, that sucrose-rich nectar was preferred to the extent that it is part of a "syndrome" for hummingbirds (Stiles 1981). More striking are the proportions of sucrose, fructose, and glucose between the large and taxonomic samples and smaller samples of flowers from the south and northwestern Mexico (*cf.* Stiles 1985). No significant differences were found by Kruskal-Wallis tests in sucrose ($T = 2.25$, $P = 0.76$, $P = 0.776$), or fructose among these three samples. Sucrose concentration was significantly higher in the U.S. and Mexican samples from Costa Rica ($F[1, 56] = 10.30$, $P = 0.002$) and $F[1, 46] = 10.30$, $P = 0.002$). Thus, nectars of all three geographical areas share a common feature: adaptive convergence, presumably reflecting the digestive physiology of the

hummingbirds. In these studies, Hainsworth and Stiles (1990) found that sugar composition had no effect on preferences, but their experimental control for effects of feeder type (Stiles 1990a). On the other hand, Martinez del Rio (1990a) found preferences for sucrose only in solutions over fructose, but not when hexose was preferred to mixtures with fructose by itself. These results are in line with the sugar composition of flower nectars studied to date. The hypothesis that the taste preference of these nectars is

that the preference is for sucrose is uncertain. Apparently disinvolved, as hummingbird preferences for all three sugars are similar (Stiles 1985) and the processing times for sucrose, and glucose-fructose (Stiles 1985; Martinez del Rio 1990a). Stiles (1990a) has proposed the establishment of a long-term preference by the hummingbird as nestlings on sucrose-rich nectar. In effect, the taste prefer-

ences would then be a consequence, rather than a cause, of the high sucrose compositions of hummingbird flower nectars. The difficulty with this interpretation, in our view, is that such a mechanism is inadequate to explain the very great similarity in sugar compositions of nectars from very different geographical areas. Were such learning the only factor involved, one would expect that different local constellations of nectariferous plants (not necessarily pollinated by hummingbirds) available to nesting females would produce local variations in early experience, which in turn should produce considerable cultural "drift" in space and time, much as occurs with song dialects in birds (Baker & Cunningham 1985). However, the geographical variation in nectar compositions one might expect to result from such variation in preferences evidently does not occur (at least among the three geographical samples analyzed here).

Sucrose-rich nectars may reduce consumption by some other flower visitors, notably passerine (perching) birds. Several partly nectarivorous or frugivorous passerines strongly prefer hexose over sucrose solutions and, if given only the latter, may develop diarrhea, lose weight, and even die (Schuler 1977, Martinez del Rio & Karasov 1990). Evidently these birds lack sucrase, the enzyme that hydrolyzes sucrose into glucose and fructose, in which form sugar is absorbed from the intestine (Martinez del Rio 1990b). Nectars of flowers pollinated by perching birds consist mainly or entirely of hexoses (Baker and Baker 1983a; see also Table 1). Since many of these passerines may rob nectar, a sucrose-rich nectar may protect hummingbird flowers from their attentions. However, other passerines that frequently rob nectar from hummingbird flowers, like *Diglossa* spp. and *Coereba* (*cf.* Stiles 1981) have presumably evolved a sucrose-hydrolyzing enzyme. Were protection from passerine nectar robbers a major factor in the evolution of sucrose-rich nectar by hummingbird flowers, one might predict that in areas where such passerines have developed the ability to digest sucrose, selection for high-sucrose nectars might be relaxed, and/or selection might favor adaptations that incorporate such passerines into the pollinator spectrum. *Diglossa* occurs only at high elevations (Stiles & Skutch 1989) and there is indeed a decline in sucrose percentage with elevation. But this decline appears gradual rather than "stepped" at the elevations above which *Diglossa* is common. Interestingly, floral adaptations which may favor pollination by *Diglossa* do occur in the high Andean genus *Brachotum* (Melastomataceae), previously considered to be pollinated only by hum-

mingbirds (Stiles *et al.* 1992). Although far from rare in Costa Rica, *Coereba* is extraordinarily abundant on many West Indian islands (*cf.* Bond 1961), and it is here that the above predictions might best be tested with respect to this species.

Among hummingbird-pollinated flowers as a group, taxonomic affinities, and hence evolutionary history, play a secondary role in determining nectar composition. Species of certain plant families have nectars with relatively consistent sucrose compositions. The ratio of glucose to fructose is consistent within some families, but varies markedly between families. Moreover, in different families the latter ratio may vary directly, inversely, or not at all with sucrose percentage. Such differences might reflect, in part, phylogenetic inertia in groups that evolved hummingbird pollination independently, perhaps from different ancestral pollination systems (*cf.* Grant & Grant 1968). Bee and lepidopteran-pollinated plants visited by hummingbirds each show a wide range of nectar sugar compositions, possibly reflecting that both insect groups are taxonomically and ecologically very diverse. It may be unrealistic to expect only a single nectar type among the many flowers pollinated by insects of each group (*cf.* Baker & Baker 1983a).

Different components of nectar apparently respond in different ways to environmental factors such as elevation (or temperature) among the species studied. Relative sucrose concentration declines with elevation, but fructose percentage increases, while glucose percentage is little affected. The net result is that the hexose component of nectars of hummingbird flowers increases with elevation. The gradual nature of this increase suggests that a physiological response, possibly to decreasing temperatures, is involved rather than a reduced selection for sucrose-rich nectars where *Diglossa* is present (see above). Nevertheless, the higher hexose content of highland nectars might originally have facilitated the switch to nectarivory by the presumably finchlike ancestors of *Diglossa*, which lacked the ability to digest sucrose (Martinez del Rio & Karasov 1990, Martinez del Rio 1990b). The lower caloric values of the nectars of highland hummingbird flowers (reflecting lower sugar concentrations, lower nectar volumes, or both) might be due to slower rates of photosynthesis (and hence sugar production) or slower rates of nutrient uptake by the roots (*cf.* Raven *et al.* 1986) in the cold tropical highlands. A more complex and sugar-specific mechanism will be required to explain the changes in the relative proportions of the three major sugars with elevation. Because most sugar is translocated within the plant

as sucrose, which is the major sugar in the phloem sap (the source of sugar in nectar: *cf.* Durkee 1983), one might expect that secretion of sucrose-rich nectar would be more economical than hexose-rich nectar. Given the possible energy limitations of high-elevation plants operating at low ambient temperatures, the hexose content of nectar should decrease with elevation. But the opposite appears to be the case. However, we still do not know just how nectar is actually concentrated and secreted, with two mechanisms, eccrine and granulocrine, having been proposed (review in Durkee 1983). The different responses of the three major sugars in nectar to increasing elevation would seem to favor the eccrine mechanism, which supposes different carrier molecules and enzyme systems for the transport of each sugar across the secretory cell membrane, analogous to the system in vertebrate intestines (*cf.* Martinez del Rio 1990a). Clearly, we need to know much more about the comparative physiology of nectar secretion. Because of their large nectaries and high nectar volumes, hummingbird flowers might be ideal subjects for such studies.

Nectars of flowers pollinated by different groups of hummingbirds treated here did not differ appreciably in sugar composition, suggesting that taste preferences are quite homogeneous within the Trochilidae. Other parameters of nectar, notably nectar volume and (to a lesser extent) total sugar concentration, do vary according to the taxonomic or ecological attributes of the respective hummingbird pollinators, to the extent that these features can be used with considerable success to predict which type of hummingbird pollinates a given flower. Flowers pollinated by hermit hummingbirds (subfamily Phaethorninae) have the highest average nectar volumes and concentrations, hence the highest caloric values. These features make these flowers attractive to these relatively large, wide-ranging hummingbirds called "high-reward trapliners" by Feinsinger & Colwell (1978). The species with lowest energy demands are the small, short-billed nonhermits. Most of these weigh no more than 3.0–3.5 g and most visit many flowers with low nectar volumes pollinated largely by insects. Flowers pollinated by the

"bee-hummingbirds" had much lower nectar volumes, but only slightly lower sugar concentrations, than those pollinated by other hummingbirds. They are most common at high elevations where low temperatures reduce insect activity (Cruden 1972, Stiles 1981). Interestingly, in the plant communities assayed for nectar production by Cruden *et al.* (1983) and Opler (1983), small hummingbirds predominate, which may partly explain the conclusion of these authors that hummingbird flowers contain far less nectar than do those pollinated by large insects like sphingids. By contrast, hermit flowers, with their high caloric values, are centered at low elevations in keeping with the lowland distribution of the hermits as a group (Stiles 1981).

Flowers pollinated by hermit-like nonhermits (also "high-reward traplining") and "typical" nonhermits, both of the subfamily Trochilinae, are less clearly discriminated by our analysis. This may reflect the fact that the former occur most frequently at elevations above those at which hermits are common, where nectar volumes and concentrations tend to be lower. The "typical" nonhermits include species with a wide range of sizes, bill types, and foraging strategies. Within a given species, foraging behavior may vary with sex, season, or dominance status (*cf.* Stiles 1985). This may explain in part the modest overlap seen between nectar features of flowers pollinated by these two nonhermit groups. In general, the results of these analyses support the conclusion of Stiles (1976) and Martinez del Rio (1990a) that energetic factors are more important than taste preferences *per se* in determining which flowers are visited by hummingbirds.

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