

EFFECTS OF SUGAR COMPOSITION AND CONCENTRATION ON FOOD SELECTION BY SAUSSURE'S LONG-NOSED BAT (*LEPTONYCTERIS CURASOAE*) AND THE LONG-TONGUED BAT (*GLOSSOPHAGA SORICINA*)

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In the Neotropics, bat-pollinated plants secrete relatively dilute nectars dominated by hexoses (glucose and fructose) with only small amounts of sucrose. We investigated the concentration and sugar composition preferences of Saussure's long-nosed bat (*Leptonycteris curasoae*) and the long-tongued bat (*Glossophaga soricina*) to test the hypothesis that bats prefer the predominant characteristics (sugar composition and concentration) found in their natural diets. We offered bats pairs of test diets in large outdoor enclosures that allowed free flying. We used artificial nectars that simulated compositions and concentrations found in flowers visited by these 2 species at the study site. Contrary to our predictions, bats showed no preference between sugar types when test solutions had the same concentration. However, *L. curasoae* preferred concentrated over dilute solutions independent of sugar type. Only 1 preference for concentrated over dilute solutions was recorded for *G. soricina*. Both species of bat appeared to perceive sugar types as energetically equivalent in most trials. Our study rejects the hypothesis that nectar-feeding neotropical bats act as a selective pressure on nectar composition in chiropterophilous plants. Other possible explanations for the predominance of hexose in chiropterophilous flowers need to be evaluated.

Key words: bats, Chiroptera, chiropterophilous flowers, concentration preferences, dry forest, energetic equivalence, Mexico, pollination ecology, sugar preferences

Floral nectars are sugar solutions that also contain small amounts of other substances such as amino acids, proteins, lipids, ascorbic acid, and alkaloids (Baker and Baker 1983). Floral nectars vary in both sugar concentration and composition (Baker et al. 1998; Galleto and Bernardello 2004; Nicolson 2002). The composition of nectar depends on several factors such as the flowering season (Torres and Galleto 1998), the floral stage (Pleasant 1983), and the structure of the floral nectary (Davis et al. 1998). Nectar composition and concentration also depend upon environmental factors such as temperature and humidity (Vezza et al. 2006). Additionally, large

intraplant variations in nectar production have been reported for several species (Bernardello et al. 2004; Freeman and Wilken 1987; Reid et al. 1985; Severson and Erickson 1984).

Nectar characteristics are seen as adaptations to increase the frequency of visits by potential pollinators as part of a co-evolving system (Simpson and Neff 1983). Several studies conclude that preferences exhibited by nectarivorous foragers should select for the evolution of nectar characteristics (Heinrich and Raven 1972) and that nectarivores should prefer nectars with sugar composition similar to those found in their natural diet (Baker and Baker 1983; Baker et al. 1998; Erhardt 1991; Martínez del Río et al. 1988, 1992; Wykes 1952). Indeed, the variable distribution of sugars in the nectars of plants pollinated by different groups of animals is a good example of the diversity of rewards assumed to be molded by the preferences of pollinators (Baker and Baker 1983). Under experimental conditions, there is evidence that birds prefer

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TABLE 1.—Experimental design, sugar composition of test diets (%), and pairwise comparisons of concentrations.

Equivalent species	Diet	Fructose : glucose : sucrose
<i>Acanthocereus occidentalis</i>	Sucrose dominated (SD)	28.97%:17.06%:53.98%
<i>Ceiba grandiflora</i>	Hexose dominated 1 (HD1)	46.82%:39.43%:13.75%
<i>Pseudobombax ellipticum</i>	Hexose dominated 2 (HD2)	41.58%:23.05%:35.37%
Trials	Experiment 1 (SD:HD1)	Experiment 2 (HD1:HD2)
1	20%:20%	20%:20%
2	27%:18%	18%:15%
3	18%:27%	15%:18%

sugar concentrations and compositions similar to those found in their natural diet (Blem et al. 2000; Fleming et al. 2004; Lotz and Schondube 2006; Martínez del Río et al. 1992). In birds, preferences for sugar concentration and composition seem to be linked to their capacities for assimilation of sugar, and their abilities to differentiate among sugar concentrations (Lotz and Schondube 2006). Nevertheless, a laboratory study of bats found no relationship between sugar composition of chiropterophilous flowers in the wild and sugar preferences in the laboratory (Herrera 1999). However, it is noteworthy that this study was conducted under laboratory conditions with artificial nectar concentrations.

To further test the conjecture that sugar preferences of bats coincide with the composition of flower nectars in natural diets we examined the preferences of the New World nectar-feeding bats Saussure's long-nosed bat (*Leptonycteris curasoae*) and the long-tongued bat (*Glossophaga soricina*; Phyllostomidae: Glossophaginae). We used nectars with ecologically realistic composition and concentrations, simulating nectar of flowers consumed by these nectarivorous bats in the region. We predicted that bats would prefer hexose-dominated relative to sucrose-dominated nectars and concentrations similar to the average concentration of flowers found in natural diets (18%). Finally, we assessed whether bats perceived different sugar compositions as energetically equivalent. We expected that bats would perceive different nectar diets as energetically equivalent, independently of whether they discriminate between nectar compositions.

MATERIALS AND METHODS

Study site.—Our study was conducted at the Chamela-Cuixmala Biosphere Reserve on the central Pacific coast of Mexico (approximately 19°22'–19°35'N, 104°56'–105°03'W). The predominant vegetation type is tropical lowland deciduous forest (Lott 1993). There are 1,100 plant species recorded at this site, and the flowers of at least 22 species are visited by bats (Stoner et al. 2003). *L. curasoae* is a flower specialist (Stoner et al. 2003), whereas *G. soricina* is a nectarivore that also feeds on fruit and insects when flowers are unavailable (Alvarez et al. 1999; Herrera 1999).

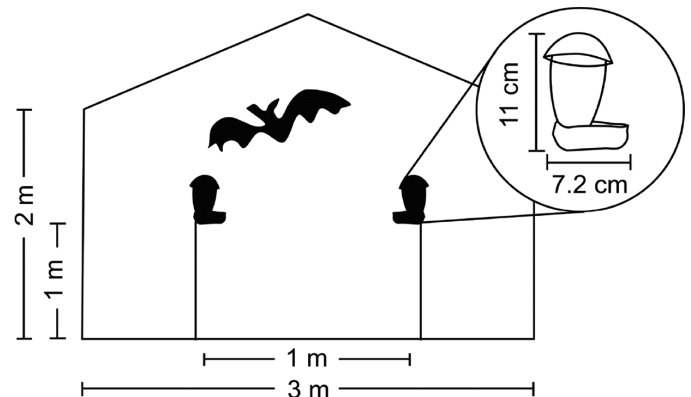


FIG. 1.—Preference experiments were conducted within enclosures (2 × 3 × 3 m) allowing individual bats to fly freely. These enclosures were placed within the natural environment of tropical dry forest where the bats were captured. Feeders faced each other.

Nectar.—To evaluate the sugar and concentration preferences of bats, we prepared 3 artificial nectars equivalent in sugar composition and concentration to nectar of bat-pollinated flowers consumed by nectarivorous bats in the Chamela region (Table 1). Nectar concentration and sugar composition were measured for 3 of the most common species in the diet of bats (Stoner et al. 2003): *Ceiba grandiflora* (Bombacaceae; $n = 35$ flowers from 21 individuals), *Pseudobombax ellipticum* (Bombacaceae; $n = 20$ flowers from 5 individuals), and *Acanthocereus occidentalis* (Cactaceae; $n = 9$ flowers from 5 individuals). The number of flowers sampled per plant varied because of differences in flowering strategies among species and the differences in the number of open flowers among individuals. Mature flower buds were covered with mesh bags 1 h before sunset. One hour after anthesis, nectar was extracted with capillary glass tubes and placed on Whatman No. 1 filter paper (Sigma Chemical Company, St. Louis, Missouri) for analysis of sugar composition. One drop of nectar was placed on a hand refractometer and concentration was measured in sucrose equivalents (% sugar = (sugar mass/total mass) × 100). Sugar composition was analyzed using the medium infrared Reflectance method (Flores et al. 2003).

Care and housing of bats.—Bats were captured and humanely handled under the guidelines from the Oficina de Fauna Silvestre, Mexico, to JES (permit FAUT-0193), and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). We used mist nets to capture adult nonreproductive males of the 2 species. After capture, bats were transferred to the laboratory and maintained in colonies of 8 individuals in aluminum cages (60 × 60 × 60 cm). Bats were fed the diet described by Mirón (2005) supplemented with a vitamin and mineral mix (NEKTON-Plus, Pforzheim, Germany) and fructose and sucrose (50%:50%). Body mass, wing membrane elasticity, and hair condition of all bats was monitored daily. All bats maintained constant body mass and appeared healthy while in captivity. At the conclusion of our experiments, bats were released at the capture site.

Preference tests.—We offered pairs of test diets to individual bats in large flight cages (2 × 3 × 3 m) immersed within their

natural habitat in the forest (Fig. 1). Feeders were placed 1 m apart at a height of 1 m. Trials lasted 10 h and were conducted from 1900 to 0500 h. Feeders were filled and placed at 1900 h. The amount consumed was measured (g) and feeder position was switched at the middle of the experiment at 0000 h to evaluate potential positional biases (Jackson et al. 1998). The amount consumed was remeasured at 0500 h. A control feeder of each test diet was placed outside the flight cages to assess evaporation. These feeders were covered with mesh bags to prevent visits from insects or bats. No differences were observed in any of the control feeders indicating that evaporation did not account for any liquid lost during the experiment.

Experiment 1.—To test for sugar and concentration preference we offered bats 2 experimental diets that differed in sugar composition and concentration. One of the test diets was sucrose dominated (SD: composition: fructose [F]: 28.97%, glucose [G]: 17.06%, sucrose [S]: 53.98%) and the other was hexose dominated (HD1: composition: F: 46.82%, G: 39.43%, S: 13.75%). Three trials were conducted with these 2 test diets. In the 1st trial, both diets had the same total sugar concentration (20% weight: volume [w/v]). Thus, in this trial we examined the preferences of bats for sugars with different compositions. Although the concentration of these test solutions was the same, the solutions differed slightly in energetic content. The HD diet contained approximately 2% less energy per unit volume than the SD diet (see Fleming et al. 2004). In trial 2, we tested diets that simulated the natural concentrations found in flowers in the field. The sucrose diet (SD) simulated *A. occidentalis* and contained 27% (w/v) sugar, whereas the hexose diet (HD1) simulated *C. grandiflora* and contained 18% (w/v) sugar. In trial 3 we inverted the concentrations of trial 2. Thus, the sucrose diet (SD) contained 18% sugar whereas the hexose diet (HD1) contained 27% (w/v) sugar. Trials 2 and 3 examined the effect of sugar concentration on the preferences of the bats. The 3 trials with each of the 2 test diets were conducted with 6 different individuals of both species on 3 consecutive nights.

Experiment 2.—A 2nd experimental series was performed using diets that consisted primarily of hexoses but with differing content of sucrose. We offered bats 2 hexose-dominated diets (HD1: F: 46.82%, G: 39.43%, S: 13.75%; and HD2: F: 41.58%, G: 23.05%, S: 35.37%). As in experiment 1, this experiment consisted of 3 trials. In the 1st trial, test diets had the same concentration (20%). Again, although the concentration of these test solutions was the same, the solutions differed slightly in energetic content. In trial 2 the test diets had the concentrations found in the field (HD1: 18%; HD2: 15%) and in trial 3 we inverted the concentrations of trial 2 (HD1: 15%, HD2: 18%; Table 1). Each trial was conducted using 6 bats of both species on 3 consecutive nights.

Data analysis.—To estimate preference we used the ratio of the nightly ingestion of 1 of the test diets divided by total nightly ingestion: preference = (ingestion of diet A)/(total ingestion). A preference value of 0.5 indicates bats consume both solutions in equal amounts (Martínez del Río 1990). We arcsine square-root transformed the data to normalize preference values (Zar 1996) and used 1-sample *t*-tests to test the

null hypothesis that preference was not significantly different from 0.5.

Positional biases.—Positional biases in nectar-feeding animals have been documented (Jackson et al. 1998). A positional bias is present when an animal tends to visit 1 of the feeders independently of the identity of the solution in it. We used a sign test in each trial to assess whether bats changed sides more frequently than expected by chance assuming a 0.5 probability of side change. We expected that when bats had a significant preference for a given solution, this preference would result in a side change upon moving the position of the feeder. Conversely, when bats showed no preference, we expected that visits would be random and each feeder would receive a similar amount of visits (i.e., with a similar amount of nectar withdrawn). The side the bats 1st prefer is defined as the side from which they drink the greatest amount of nectar during the 1st part of the night. A side change is documented when they drink more nectar from the other feeder during the 2nd half of the night.

Energetic equivalence.—To determine whether bats perceived the sugars in the offered solutions as energetically equivalent, we determined whether an increase in consumption of 1 solution resulted in a significant decrease in consumption of the other, and whether the magnitude of this decrease was consistent with the ratio in energy content of the 2 solutions. For example, if the concentrations of the 2 test solutions were equal, then the expected slope of the line relating the intake of 1 solution against that of another should be -1 . This implies that ingesting 1 g of 1 solution would decrease the intake of the alternative solution by 1 g. When the 2 solutions had different concentrations, the slope of this regression line should equal the ratio of the 2 concentrations of the 2 test solutions. For example, if the solutions had sugar concentrations of 18% and 27%, respectively, then the expected slope of the line relating intake of the 18% solution on the *y* axis with that of the 27% solution on the *x* axis should be equal to $-27/18 = -1.5$. In this situation, an increase in the ingestion of 1 g of the 27% solution implies a decrease of 1.5 g of the 18% solution. The observed slope for each bat for each trial was estimated (SAS Institute Inc. 2003) by relating intake of the 2 test solutions using the following linear model:

$$y = \beta_0 + \beta_1 x_1 + \sum_{i=1}^6 \beta_i x_i + \epsilon.$$

In this model *y* is the consumption of solution 1, *x*₁ is the consumption of solution 2, β_1 is the estimate of the common slope relating *y* and *x*₁, and β_i is the “effect” of bat *i* on the intercept (*x*_{*i*} equals 0 if the bat is other than *i* and 1 if it is bat *i*). We did not include interaction terms because we would have ended up with 8 possible interactions, which are very difficult to interpret. Our approach recognizes that some bats may have different slopes, but estimates the average slope and tests whether it differs from that expected. Because we found that animals sometimes ate preferentially of alternate solutions in the 2 periods of the night (see “Results”), we included data for both the 1st and 2nd half of the night. Including these data

TABLE 2.—Preferences for diets of different sugar composition and concentration in 2 species of nectarivorous bats. Preference values were calculated as the ratio of consumption of 1 of the test diets divided by the total nightly ingestion. A preference was deemed significant when this preference was significantly different from 0.5 after a 1-sample *t*-test (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Experiment 1 (SD:HD1)		Experiment 2 (HD1:HD2)	
Concentration	Preference \pm SE	Concentration	Preference \pm SE
<i>Leptonycteris curasoae</i>			
20%:20%	0.44 \pm 0.04	20%:20%	0.42 \pm 0.05
27%:18%	0.17 \pm 0.03***	18%:15%	0.83 \pm 0.02***
18%:27%	0.77 \pm 0.03***	15%:18%	0.26 \pm 0.03***
<i>Glossophaga soricina</i>			
20%:20%	0.48 \pm 0.05	20%:20%	0.43 \pm 0.03
27%:18%	0.37 \pm 0.05	18%:15%	0.55 \pm 0.05
18%:27%	0.65 \pm 0.05*	15%:18%	0.41 \pm 0.03

points increased the range of x_1 in our analyses and thus increased the accuracy for estimating the slopes. Using the 36 data points for each trial (6 bats \times 3 nights \times 2 foraging bouts per night), a *t*-test was used to compare the expected slope with the observed slope (Zar 1996). Significant differences indicate that bats do not perceive the 2 solutions as energetically equivalent.

RESULTS

Sugar composition and concentration preferences.—The specialist nectarivore *L. curasoae* showed no preferences for 1 test solution over the other when concentrations of the test solutions were equal (Table 2, trial 1); however, in all cases, *L. curasoae* preferred concentrated over dilute solutions when offered test diets with different concentrations (Table 2, trials 2 and 3). This species always preferred the more concentrated solution. The more generalist omnivore, *G. soricina*, exhibited no significant preferences for any of the test solutions (Table 2, trials 1 and 2) except for the 27% hexose-dominated solution (HD1) over the 18% sucrose-dominated solution (Table 2, trial 3).

Positional biases.—No positional biases were observed for *L. curasoae* (Table 3). In 3 out of the 4 trials in which *L. curasoae* significantly preferred a test solution, individuals changed the side at which they fed more frequently than expected by chance (sign test $P < 0.05$), changing sides when test solutions were moved in the middle of the night. This behavior shows that they continue feeding on the preferred solution regardless of the position. In spite of the fact that the difference was not significant for 1 trial in which *L. curasoae* showed preferences, the pattern was in the same direction (13/18), and indeed, would have been significant with only 1 more side change. In addition, in 2 out of 2 experiments in which individual *L. curasoae* did not prefer a test solution (i.e., because they were the same concentration), they changed sides at frequencies that did not differ significantly from those expected by chance, showing that the position of test solutions did not affect the side from which they fed.

TABLE 3.—Number of side changes observed during each trial for each bat species. A sign test assuming a 0.5 probability of side change as a null hypothesis was used to test for significant differences. The critical 0.05 value for the sign test is 14 or more changes in 18 trials (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Experiment 1 (SD:HD1)		Experiment 2 (HD1:HD2)	
Trial	Side change/total	Trial	Side change/total
<i>Leptonycteris curasoae</i>			
20%:20%	5/18	20%:20%	11/18
27%:18%	16/18*	18%:15%	18/18*
18%:27%	13/18	15%:18%	16/18*
<i>Glossophaga soricina</i>			
20%:20%	11/18	20%:20%	7/18
27%:18%	9/18	18%:15%	8/18
18%:27%	12/18	15%:18%	7/18

Similarly, no positional biases were observed for *G. soricina* (Table 3). In all 5 trials that *G. soricina* showed no preference for test solutions, the frequency with which *G. soricina* changed sides did not differ significantly from the value expected by chance (sign test $P > 0.05$). This shows that they randomly drank from both feeders regardless of the position. In the 1 trial that they showed preferences for 1 test solution over the other, the side change was greater than in all of the other trials (12/18); however this difference was not significant (sign test $P > 0.05$).

Energetic equivalence.—In *L. curasoae*, the consumption of 1 test solution significantly affected the consumption of the other solution in all trials (r^2 ranged from 0.45 to 0.71, $P < 0.001$ for 5 trials; $r^2 = 0.31$, $P < 0.06$ for 1 trial; $n = 36$ data points per trial; Fig. 2). Furthermore, in 3 of 6 trials the observed slopes were not significantly different from the expected slopes, indicating that sugars are perceived as energetically equivalent (Table 4). In the 3 other trials these slopes were negative, but significantly lower than those expected (Table 4).

Similarly, in *G. soricina*, the consumption of 1 test solution significantly affected the consumption of the other solution in all trials (r^2 ranged from 0.74 to 0.86 in the 6 trials, $P < 0.005$ for all trials, $n = 36$ data points per trial; Fig. 3). The estimated slopes were not significantly different from those predicted in 5 of 6 trials (Table 4), indicating that sugars are perceived as energetically equivalent. In only 1 trial these slopes were significantly lower than those expected (Table 4).

DISCUSSION

Our results did not support all of our expectations and predictions. First, when solutions had equal concentrations, bats showed no significant preference for solutions with different sugar compositions; therefore, they did not prefer hexose-dominated over sucrose-dominated solutions as we had predicted. Second, *L. curasoae* significantly preferred concentrated over dilute solutions. We had originally predicted that these bats would prefer what is most common in their natural diet (18% concentration). Preference for concentrated solutions was not common in *G. soricina*. We observed such a preference

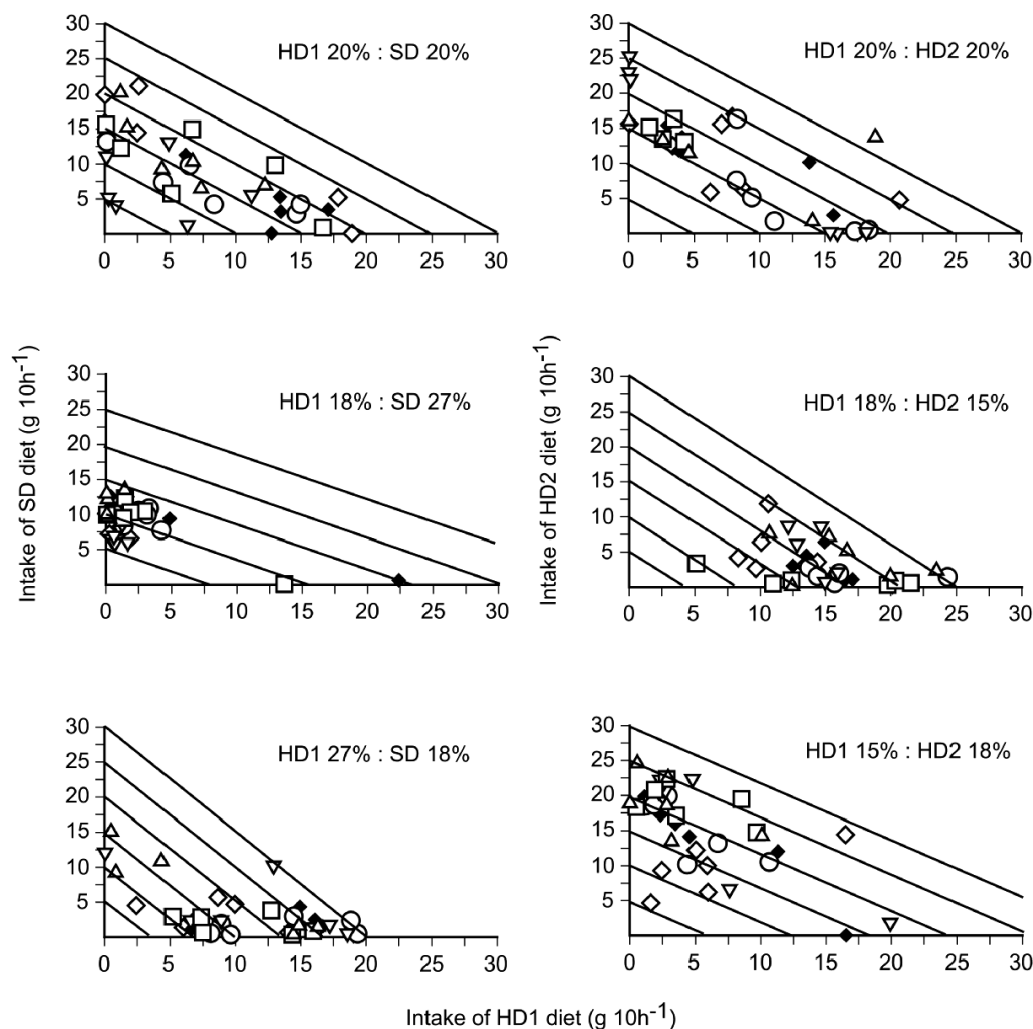


FIG. 2.—Energetic equivalence of test diets for *Leptonycteris curasoae*. The panels on the left represent experiment 1, whereas those on the right represent experiment 2. See Table 4 for observed and expected slopes.

only in 1 of 4 trials in which solutions differed in sugar concentration by 9%. As predicted, in some of the trials bats perceived hexose-rich and sucrose-rich diets as energetically equivalent.

Sugar preferences in bats and their implications.—Several authors have suggested that the preferences of pollinators act as selective pressures that maintain sugar compositions in nectar (Baker and Baker 1983; Baker et al. 1998; Martínez del Río et al. 1992). Furthermore, some studies have hypothesized that the preferences of pollinators differ as a result of variation in digestive traits (Hernández and Martínez del Río 1992). For example, the notion that nectar-feeding animals discriminate among different sugar types is based on the observation that several bird species are either incapable of or poor at digesting sucrose (Martínez del Río and Stevens 1989). Our results suggest that nectar-feeding bats are equally capable of assimilating sucrose, glucose, and fructose. Indeed, Herrera (1999) reported no differences in the efficiency with which bats assimilated sucrose, glucose, and fructose (see also Winter 1998).

Our results do not support the hypothesis that pollinator preferences act as selective pressures on nectar composition, at least in bat-pollinated plants. In particular, we found no evidence that bats preferred one sugar combination over another when they had a choice between solutions of equal concentration. These results are similar to those reported by Law (1993), who found no significant preferences for Old World blossom bats (*Syconycteris australis*) when offered pure sucrose, pure glucose, or an equal volume mixture of sucrose, glucose, and fructose. Nevertheless, Herrera (1999) reported that 2 frugivorous phyllostomid bats (*Artibeus jamaicensis* and *Sturnira lilium*) and a nectar-feeder (*Anoura geoffroyi*) preferred sucrose over solutions of a single hexose (either fructose or glucose). He concluded that these bats preferred sucrose. The discrepancy between our study and that of Herrera (1999) could result from at least 2 factors. First, we allowed bats to choose between solutions containing mixtures of sugars rather than single sugars. This situation is what bats are most likely to encounter in nature, because few or no plants secrete nectars with only 1 sugar (Baker and Baker 1983). Second, we studied 2 species, both of which are nectarivores, 1 a specialized

TABLE 4.—Results of *t*-test comparing observed and expected slopes (i.e., caloric ratio values) for each species for each trial.

Concentration	Expected slope	Observed \pm SE	<i>t</i>	<i>P</i>
<i>Leptonycteris curasoae</i>				
SD:HD1				
20%:20%	−1.00	−0.74 \pm 0.10	2.60	0.01
27%:18%	−0.66	−0.58 \pm 0.07	1.14	0.26
18%:27%	−1.50	−0.35 \pm 0.08	14.4	<0.0001
HD2:HD1				
20%:20%	−1.00	−0.84 \pm 0.13	1.2	0.24
15%:18%	−1.20	−0.27 \pm 0.12	7.75	<0.0001
18%:15%	−0.83	−0.72 \pm 0.16	0.68	0.50
<i>Glossophaga soricina</i>				
SD:HD1				
20%:20%	−1.00	−0.72 \pm 0.09	2.89	0.007
27%:18%	−0.66	−0.78 \pm 0.10	1.20	0.24
18%:27%	−1.50	−1.40 \pm 0.11	0.89	0.38
HD2:HD1				
20%:20%	−1.00	−0.87 \pm 0.09	1.34	0.19
15%:18%	−1.20	−1.17 \pm 0.08	0.34	0.73
18%:15%	−0.83	−0.67 \pm 0.09	1.7	0.09

nectarivore (*L. curasoae*) and the other a generalist nectarivore (*G. soricina*). It is possible that differences exist between nectar- and fruit-eating bats in sugar preferences and because the study of Herrera (1999) used 2 frugivores and 1 nectarivore, this may have resulted in different conclusions. These potential differences remain to be investigated. In spite of these differences, our results contradict the hypothesis that nectarivores will prefer sugars most common in their natural diet (Martínez del Río et al. 1992). Bats did not prefer hexose-dominated solutions over sucrose-dominated solutions. The prevalence of hexose-dominated nectars among bat-pollinated plants in the New World does not appear to be a result of bats preferring hexose-dominated nectar. The predominance of hexose-dominated chiropterophilous flowers is an ecological pattern that remains to be explained.

Concentration preferences in bats and their implications.—Although bats did not exhibit preferences when offered nectars with different sugar compositions, *L. curasoae* preferred concentrated over dilute nectars in all trials. The nectar specialist, *L. curasoae*, appeared to be able to distinguish concentration differences even when the difference between 2 solutions was small (3%). The preference for more concentrated nectars also has been reported for the megachiropteran nectar specialist *S. australis* (Law 1993). It appears as if the more generalist nectarivore, *G. soricina*, only can distinguish between concentrations when the difference is large (9%). These results concur with those of Rocas et al. (1993), who found that *G. soricina* discriminated between sugar solutions with a large difference in concentration (20%). In our experiments, test solutions differed in concentration by only 3% and 9%.

Leptonycteris curasoae and *G. soricina* differed in their ability to discriminate between solutions with contrasting sugar concentrations. *L. curasoae* is more dependent on nectar than the more omnivorous *G. soricina*, and it seems that *L. curasoae*

has a better capacity to discriminate between solutions with different concentrations. We speculate that among bats, more-specialized nectarivores will be able to discriminate smaller differences in sugar concentration. Levey (1987) proposed a similar hypothesis for fruit-eating birds. He speculated that frugivores had finer discrimination abilities than insectivores (see also Schaefer et al. 2003). The potential correlation between the ability to discriminate small differences in sugar concentration and specialization to a nectar or fruit diet remains to be tested thoroughly in both bats and birds.

In the Neotropics, the nectar secreted by bat-pollinated plants is relatively dilute, ranging in concentration from 5% to 29% (w/v—Helvesen 1993). At our study site the flowers visited by bats secrete nectars that range from 3% to 33% with species averages ranging from 15% to 27%. (w/v—N. Rodríguez-Peña and K. E. Stoner, in litt.). If *L. curasoae* prefers more concentrated nectars, why is it that bat-pollinated plants secrete relatively dilute nectars? Nicolson (2002) reviewed the factors that might determine the prevalence of dilute nectars among flowers pollinated by passerines. She concluded that this prevalence was the result of 4 factors: hexose dominance, an open floral morphology, the secretion of a relatively dilute nectar, and production of copious nectar. In other words, the presence of hexoses in nectar may facilitate the secretion of a large volume at the expense of nectar concentration and may reduce evaporative water losses in open flowers (Nicolson 2002). These 4 factors also are present in bat-pollinated flowers, and may override the importance of the preferences of specialized pollinators.

Do bats perceive different sugars as energetically equivalent?—The results for energetic equivalence were variable both between experiments and bat species; nevertheless, in 68% of the trials bats perceived sugars as energetically equivalent. Given the result that bats showed no significant preferences between solutions with contrasting sugar compositions (previous section) how can we explain the discrepancy found in some of the trials if bats are perceiving sugars as energetically equivalent? One possibility is that the difference is a statistical artifact that results from points concentrated in a narrow range of one of the axes (Fig. 2; trial 3 in experiment 1 and trial 2 in experiment 2 for *L. curasoae*), or from using standard linear least squares regression in a situation in which there is error of the same magnitude in both the *x* and the *y* variable. Whenever the 2nd situation is encountered, statisticians advise using a reduced major axis regression (Bohonak and Van Derlinde 2004). Nevertheless, we opted not to use major axis regression estimates because they are derived assuming that all points in the regression are independent, whereas in our study repeated measurements on a single individual were used. For these reasons, our rejection of the null hypothesis of energetic equivalence must be tempered by the observation that the value of our estimates of slopes may be biased by an uneven distribution of points in our scatter grams, and by the biases introduced by standard linear least squares on data sets in which both the *x* and the *y* variable are measured with error. Further experiments conducted to assess whether different sugars are perceived as energetically equivalent by bats must control for these potentially confounding effects.

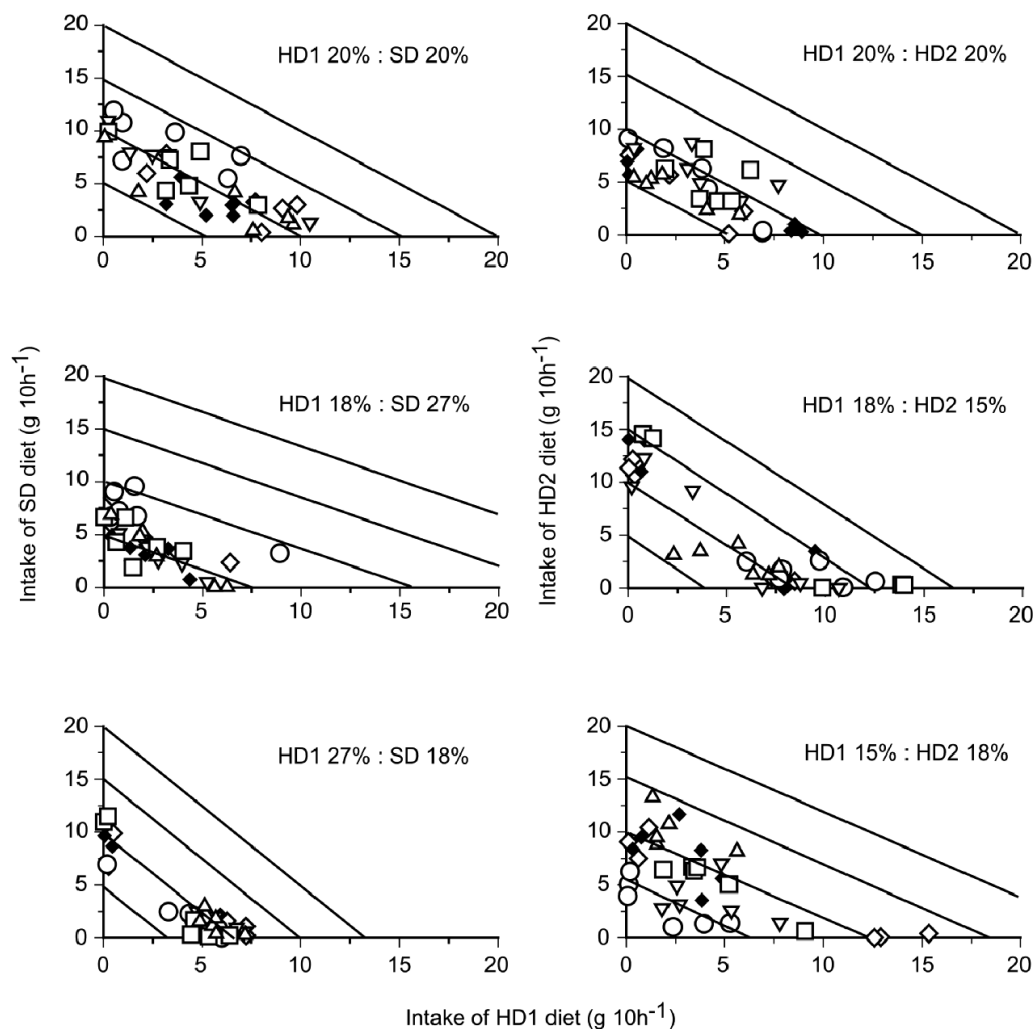


FIG. 3.—Energetic equivalence of test diets for *Glossophaga soricina*. The panels on the left represent experiment 1, whereas those on the right represent experiment 2. See Table 4 for observed and expected slopes.

In conclusion, our study rejects the hypothesis that nectar-feeding neotropical bats act as a selective pressure on nectar composition in chiropterophilous plants. Other possible explanation for the predominance of hexose in chiropterophilous flowers need to be evaluated. The result that bats prefer more concentrated nectar suggests that plants can use variation in this trait to attract bat pollinators, and possibly influence pollinator movements in a way that benefits the plant. Future studies should document the variation in nightly nectar production and relate this to bat pollinator visits to further evaluate this possibility. Finally, our results suggest that other factors than sugar composition influence preference within diets of neotropical bats.

RESUMEN

En el Neotrópico, las plantas polinizadas por murciélagos producen néctares relativamente diluidos y dominados por las hexosas (glucosa y fructosa), con pequeñas cantidades de sacarosa. Investigamos las preferencias en composición y con-

centración de azúcares en el néctar de dos murciélagos neotropicales nectarívoros (*Leptonycteris curasoae* y *Glossophaga soricina*; Phyllostomidae) con el fin de probar la hipótesis de que los murciélagos prefieren las características que de manera natural predominan en el néctar que suelen consumir. Ofrecimos individualmente a los murciélagos pares de dietas en grandes encierros artificiales inmersos en condiciones naturales, que permitían el libre forrajeo de los organismos. Preparamos néctares artificiales simulando la composición y concentración de azúcares de los néctares de flores visitadas por ambas especies de murciélagos en la zona de estudio. Contrario a lo esperado, los murciélagos no presentaron preferencias por ninguna combinación de azúcares, cuando éstas fueron ofrecidas a una misma concentración. Sin embargo, *L. curasoae* (nectarívoro especialista) consistentemente mostró preferencia por néctares concentrados sobre diluidos independientemente de la composición de los mismos, este mismo patrón no fue encontrado en el caso de *G. soricina* (omnívoro). Ambas especies de murciélagos percibieron las diferentes combinaciones de azúcares como energéticamente

equivalentes. Nuestros resultados contradicen la hipótesis de que los murciélagos nectarívoros neotropicales actúan como presiones selectivas que han determinado la composición del néctar en plantas quiropterofílicas. Se necesita evaluar otras posibles explicaciones para la predominancia de hexosas en las flores quiropterofílicas.

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