

SUGAR-TASTING ABILITY AND FRUIT SELECTION IN TROPICAL FRUIT-EATING BIRDS

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ABSTRACT.—The sugar-tasting abilities of four species of tanagers and two species of manakins were tested. Three tanager species were able to detect differences in diets containing 8%, 10%, and 12% sugar. In pairwise choice trials, they preferred the diet highest in sugar. Neither species of manakin discriminated among the three diets. This apparent difference in tasting abilities of tanagers and manakins may be a result of their fruit-handling techniques. Tanagers crush fruits in their bills, thereby releasing juices onto their tongues. Manakins swallow fruits whole; their tongues rarely encounter fruit juice. Hence, manakins' fruit-handling technique is poorly suited for sensing the taste cues in fruit juices. Variation in fruit sugar concentration is common within and among plant species and is great enough to be detected by birds. Birds probably have selected for sweeter fruits. *Received 17 April 1986, accepted 22 September 1986.*

SUGARS are one of the major and characteristic constituents of soft fruits (Hulme 1971). Sugar is likely to play an important role in fruit selection because it is a good energy source, birds can taste it (Duncan 1960), and its concentration varies within and among fruit species (White 1974, McDiarmid et al. 1977, Stiles 1980, Moermond and Denslow 1983, Wheelwright et al. 1984).

Previous studies have demonstrated that some birds can detect sugar (Kare et al. 1957, Duncan 1960, Gentle 1972, Kare and Rogers 1976, Stiles 1976). Many of these studies are difficult to interpret in an ecological context, however, because the species tested (e.g. Rock Doves, *Columba livia*; and chickens, *Gallus gallus*) seldom encounter sweet substances in the wild and were presented with seemingly arbitrary concentrations of sugar (Wenzel 1973). Taken together, the studies indicate that nectarivorous and frugivorous birds may be most likely to exhibit preferences for sweet substances (Kare and Rogers 1976).

We know very little about how taste sensitivity contributes to food selection by wild birds because few studies have combined laboratory taste experiments with complementary field observations (Stiles 1976, Brower and Fink 1985). I used field- and laboratory-collected data to determine experimentally if tropical fruit-eating birds can taste sugar. If so, do they prefer

sweeter substances, and can they discriminate between substances that differ only slightly in sugar concentration? Sugar concentrations used in the experiments reflected the natural range of fruit sugar concentrations found in locally available wild fruits.

METHODS

I worked at the La Selva Biological Station in northeastern Costa Rica (see Holdridge et al. 1971 for a site description). Birds were captured at La Selva and maintained in captivity for at least 5 months before beginning the experiments. They were kept separately in 1 × 1 × 0.5-m cages. All birds remained in good health throughout the study.

I selected six of the most common fruit-eating species at La Selva, four species of tanagers (Olive-backed Euphonia, *Euphonia gouldi*; Tawny-crested Tanager, *Tachyphonus delatrii*; Scarlet-rumped Tanager, *Ramphocelus passerinii*; and Palm Tanager, *Thraupis palmarum*) and two manakins (Red-capped Manakin, *Pipra mentalis*; and White-collared Manakin, *Manacus candei*). I ran replicate experiments on two individuals of each species.

I maintained birds on a diet that consisted primarily of mashed bananas and soy protein isolate in an agar base (Denslow et al. in press). I will refer to it as "banana mash." Its base sugar concentration was approximately 8%. When making the experimental diets, I dissolved sucrose in the boiling agar base to increase the sugar concentration to 10% or 12%. Concentrations were measured with a Bellingham and Stanley hand-held refractometer. The 8% sugar diet had little, if any, added sucrose. I used sucrose because fructose was not easily available. However, sucrose is a common constituent of tropical fruits (C. E. Freeman, H. and I. Baker pers. comm.).

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Every morning at approximately 0600 I presented each bird with two Petri plates of banana mash. I offered all three possible pairwise combinations of the three sugar concentrations (8% vs. 12%, 8% vs. 10%, 10% vs. 12%) over a 36-day period. Each pairwise choice trial lasted 12 days. Plates contained 49–51 g of the mash weighed to the nearest 0.1 g. Plates were reweighed at noon to determine amount eaten, and all birds were then given one plate of unadulterated mash (8% sugar) for the afternoon. Although the plates were equally accessible from any point on a perch (one plate was in front of the perch, the other behind), I reversed plate positions after the sixth day of a trial to avoid position-effect biases. A coin toss determined the initial position of the plates with respect to the perch.

To test for differences in amounts of banana mash eaten from each plate, I used Wilcoxon and Walsh tests. Both tests are nonparametric and based on the distribution of the difference in the amount eaten from the two plates on a given morning (Siegel 1956). After calculating differences for each individual on each of 12 days of a pairwise trial, I tested for differences between individuals of each species with Wilcoxon tests. Eighty-three percent (15/18) of these tests were nonsignificant ($P > 0.05$). The three significant tests were between individuals that showed preferences in the same direction, one bird with a much stronger preference than the other. Given this low individual variation, I averaged the daily differences in amount of mash eaten within each species on each day. I then used these 12 averages to test the null hypothesis of no difference in the amount eaten from the two plates. All tests were two-sided. In discussing the results of these tests I assume that a bird eats more of the banana mash it prefers.

I estimated sugar concentration in 73 species of common fruits at La Selva. This fruit sample included all the species most commonly eaten by the six species of captive frugivores. Fruit sugar in juice was estimated by readings with the refractometer. I selected only juicy fruits, avoiding dry or lipid-rich species, which give poor or inaccurate refractometer readings (White and Stiles 1985). I took readings on at least 10 fruits of each species to calculate the average solute concentration. The refractometer detects any solute; it is not specific for sugars. Thus, refractometry may overestimate sugar concentration in some fruits. The limitations of refractometry data in estimating nutritional rewards of fruits are discussed by White and Stiles (1985).

I examined within- and between-plant variation in fruit sugar content of a single species, *Hamelia patens* (Rubiaceae), a small, common secondary tree species. On each of 18 trees I sampled 20 ripe fruits for sugar analysis. Nine of the trees were growing in full sunlight, and 9 were in full or partial shade. To test for effects of infructescence position on berry sugar, I sampled fruits on exposed branch tips as well as

within the crown from 2 large *Hamelia* trees. Forty fruits were selected from each tree, 20 from exposed infructescences and 20 from shaded infructescences. Fruit volume was calculated by assuming the fruits were prolate ellipsoids.

RESULTS

There were marked differences among the bird species in their abilities to detect differences in the sugar concentration of their diet (Table 1). The manakins, considered as a group or by species, did not distinguish between the diets in any pairwise choice ($P > 0.5$, Wilcoxon statistic = 1,431, $n = 72$ paired choices; $P > 0.5$, Walsh tests, $n = 12$ days for each test; Table 1). In contrast, the tanagers, as a group, preferred the sweeter banana mash in pairwise choices ($P < 0.001$, Wilcoxon statistic = 8,064, $n = 144$ choices). Only one tanager species, *Tachyphonus delatrii*, failed to exhibit a preference for the sweeter diet. With one exception, the other three tanager species ate significantly more of the sweeter mash in all pairwise combinations ($P < 0.05$, Walsh tests, $n = 12$ for each test; Table 1).

Manakins and *Tachyphonus* may not have discriminated between the diets because they could not taste the sugar, could not discriminate between the two concentrations offered, or could taste the sugar but were indifferent to it. The three tanager species' ability to discriminate between diets may have been based on metabolic effects rather than on taste. I doubt this explanation for two reasons. First, during the first hours of a trial, tanagers always sampled from both plates and rapidly and consistently chose the sweeter diet. Second, if the birds selected the sweeter diet by plate position based on previous metabolic experience, they would have eaten more of the low-sugar diet on day 7, when plate position was switched. This did not happen. In 17 of 18 trials, the high-sugar diet was chosen on day 7 ($\chi^2 = 14.2$, $P < 0.01$). Furthermore, on the first day of the trials, the tanagers chose the high-sugar diet in 18 of 18 cases. These observations are inconsistent with the hypothesis that tanagers were selecting diets based on positive postingestional effects associated with plate position. The simplest explanation is that they were tasting sugar and preferred the sweeter diet.

Juicy fruits at La Selva averaged 8.7% sugar (SD = 3.8, $n = 73$ species). Hence, the range of

TABLE 1. The difference (g) in the amount of banana mash eaten from the two plates containing the indicated concentrations of sugar. The amount eaten of the mash with the lower concentration of sugar was subtracted from that eaten of the higher concentration; a positive number indicates the sweeter mash was preferred. Results from both individuals of each species were averaged for each day. P-values were calculated by Walsh tests.

Sugar concentration	Day												P
	1	2	3	4	5	6	7	8	9	10	11	12	
8% vs. 10%													
<i>Thraupis</i>	16.5	17.4	19.0	0.5	3.6	10.5	29.7	27.4	30.5	-24.6	-11.5	-20.1	NS
<i>Tachyphonus</i>	-11.5	-12.5	-0.6	2.6	3.0	-8.9	6.7	3.5	2.7	-2.2	-12.8	-6.1	NS
<i>Euphonia</i>	10.8	10.7	15.6	-6.6	-0.1	5.7	6.3	0.8	8.2	6.4	8.6	11.4	<0.01
<i>Ramphocelus</i>	4.0	10.8	6.9	8.4	11.3	3.7	26.5	16.9	19.2	5.9	-1.0	0.2	<0.001
<i>Pipra</i>	-0.5	4.6	7.5	-3.9	5.1	0.4	-15.2	-15.8	-0.5	16.5	8.5	13.6	NS
<i>Manacus</i>	-3.6	-3.2	-10.9	17.5	9.1	16.7	-4.9	4.1	-7.9	-2.6	14.6	10.1	NS
8% vs. 12%													
<i>Thraupis</i>	21.8	21.6	22.7	5.1	1.6	6.5	21.2	23.1	10.0	-19.8	-13.5	9.5	<0.03
<i>Tachyphonus</i>	-4.3	-3.2	8.0	-8.1	-2.4	-4.4	12.7	11.0	0.7	-7.8	-8.6	7.9	NS
<i>Euphonia</i>	10.0	5.2	15.1	11.8	10.7	1.1	2.2	13.7	3.6	6.5	6.1	-1.9	<0.005
<i>Ramphocelus</i>	5.8	9.4	12.0	-8.6	8.5	1.1	14.4	7.8	11.2	0.0	7.9	6.7	<0.005
<i>Pipra</i>	-8.8	-5.8	-1.1	0.4	8.0	15.7	-11.8	-7.3	1.0	0.7	4.2	-5.9	NS
<i>Manacus</i>	10.9	6.4	2.3	0.1	-4.9	-8.0	-6.6	2.5	-5.3	-7.1	10.6	9.7	NS
10% vs. 12%													
<i>Thraupis</i>	7.7	24.1	-5.2	25.0	-2.4	28.2	17.0	30.3	12.0	-4.1	5.1	-13.0	<0.03
<i>Tachyphonus</i>	-2.6	-6.0	3.4	2.6	3.3	4.5	7.3	7.1	11.4	-2.3	1.3	-9.0	NS
<i>Euphonia</i>	7.3	7.2	9.0	-8.6	3.2	10.8	1.9	5.0	6.1	-1.9	0.9	0.4	=0.05
<i>Ramphocelus</i>	6.0	10.9	11.3	7.6	6.2	13.7	-2.0	13.0	3.9	-5.3	9.2	-1.6	<0.005
<i>Pipra</i>	-3.3	-5.4	1.3	6.0	0.1	4.8	-4.8	5.3	-2.9	-9.6	1.5	6.8	NS
<i>Manacus</i>	6.4	6.4	5.0	-14.8	-8.6	-1.1	-6.2	-2.6	-8.4	5.4	3.2	0.1	NS

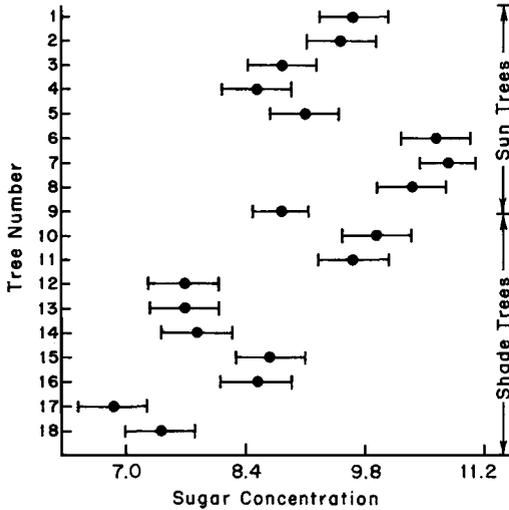


Fig. 1. Means and 95% confidence intervals of fruit sugar concentration of 18 *Hamelia patens* trees. The trees differed significantly in the sugar concentration of their fruits ($F = 22.5$, $df = 17, 342$, $P < 0.001$, ANOVA). The top nine trees were fully exposed to sun; the bottom nine were shaded.

sugar concentrations used in the experiments, 8–12%, was encountered commonly by birds in the field. Within each of the 73 species tested, the average standard deviation of sugar concentration was $0.97 (\pm 0.58)$. Thus, a 1–2% range in sugar concentration is common within as well as between species.

The 18 trees of *Hamelia* varied significantly in the sugar concentration of their fruits (Fig. 1). Trees in full sunlight bore sweeter fruits than did shaded trees ($F = 30.7$, $df = 1, 342$, $P < 0.001$, ANOVA). Similarly, on the two large trees, fruits on exposed portions of the tree were significantly sweeter than those shaded within the tree crown ($F = 22.9$, $df = 1, 76$, $P < 0.01$, ANOVA). Although fruits exposed to sun had higher concentrations of sugar than fruits in the shade, their total sugar content may not have been higher because shaded fruits were larger than sun-exposed fruits (volumes = $325.2 \pm 122.0 \text{ mm}^3$ and $234.2 \pm 89.9 \text{ mm}^3$, respectively; $n = 360$ fruits, $T = 7.59$, $P < 0.001$).

DISCUSSION

Fruit-eating birds can make fine-scale decisions in selecting among fruits (Moermond and Denslow 1983). Thus, slight differences in fruit composition or presentation may influence

which fruits they prefer (Howe and Vande Kerckhove 1980, Herrera 1981, Jordano 1984, Moermond and Denslow 1985). Such differences are common even within a species and affect how quickly individual fruits are removed and, presumably, seeds are dispersed (Howe and Vande Kerckhove 1980, Denslow and Moermond 1985). Rapid fruit removal is important to plants because ripe fruits quickly rot or are attacked by insects (Thompson and Willson 1978, 1979; Stiles 1980; Herrera 1982). Hence, small but detectable variation in fruit sugar concentration may influence fruit removal and, ultimately, dispersal success.

The *Hamelia* data show that detectable variation in fruit sugar concentration occurs within a species and is partially dependent on exposure to light. Other fruit species show a similar response to light; sunlit fruits tend to have higher sugar concentrations than shaded fruits (McDiarmid et al. 1977, Jordano 1984). In tropical forests, tree-fall gaps are areas of high light intensity (Chazdon and Fetcher 1984) and thus may contain sweeter fruits than the shaded understory. Fruits in gaps are removed more quickly than fruits in the neighboring understory (Thompson and Willson 1979, Denslow and Moermond 1982, Moore and Willson 1982). I suggest that a mechanism for these higher removal rates in gaps may involve birds tasting and preferentially selecting fruits high in sugar. Similarly, selective removal of fruits from different parts of a tree may be influenced by varying fruit sugar concentrations. However, other factors such as crop size, conspicuousness, and infructescence structure are also likely to influence removal rates (Denslow and Moermond 1982, Howe and Smallwood 1982, Morden-Moore and Willson 1982, Moermond and Denslow 1983, Santana C. and Milligan 1984).

Manakins feed primarily on fruit (Snow 1962a, b; Foster 1977; Worthington 1982), yet the two species I studied demonstrated no sugar-tasting ability. In contrast, most of the tanagers tested apparently could taste sugar. I propose that the apparent discrepancy between the sugar-tasting abilities of the tanagers and manakins could be related to their different fruit-handling techniques. Manakins swallow fruits whole with little or no mastication, whereas tanagers usually crush fruits in their bills, squeezing juices into their mouths (Snow 1962a, Moermond 1983, Moermond and Denslow 1985,

Levey in press). Because taste buds of manakins rarely come into contact with any part of a fruit except skin surface, manakins may not sense fruit juices as well as tanagers do. It does not necessarily follow that they have a more rudimentary sense of taste than tanagers; their fruit-handling technique simply is not well suited for detection of fruit taste cues. Further experiments and anatomical evidence are needed to determine how the difference in sugar-tasting ability of manakins and tanagers is related to taxonomy, morphology, and behavior.

The apparent difference in tasting abilities may lead to differences in fruit selection based not only on fruit sugar content but also on secondary compounds. Such compounds are common in fruit pulp and affect feeding preferences of frugivores (Herrera 1982). Sherburne (1972) and Sorensen (1983) demonstrated experimentally that birds actively avoid fruits containing known toxins. Manakins may be less deterred than tanagers by secondary compounds, especially if the compounds taste bad but do not inhibit nutrient assimilation. Whether a manakin or tanager feeds on fruits is important to many plant species because tanagers generally drop, and thus do not disperse, seeds larger than 4 mm (Levey in press). Large-seeded plants may discourage tanagers from feeding on their fruit and dropping their seeds by increases in the secondary-compound content of their fruit pulp. In this way a large-seeded plant may filter out poor dispersers and encourage frugivores most likely to disperse its seeds (Janzen 1979).

Tachyphonus delatrii was the only tanager species tested that lacked a sugar-tasting ability. In a pilot study, however, two individuals of this species ate significantly more of a banana mash containing 11% sugar than an identical diet with 8% sugar ($P < 0.05$, Walsh test, $n = 8$ days). Intraspecific variation in tasting ability has been noted previously (Ficken and Kare 1961). Fecal analysis (Levey unpubl. data) and the proportionately longer and narrower bill of *Tachyphonus* (see Herrera 1984) suggest it is probably more insectivorous than the other three tanager species. If fruit is less important in its diet, then its sugar-tasting ability may be less refined and more variable than other, more frugivorous tanagers.

How well *Rhamphocelus*, *Thraupis*, and *Euphonia* can discriminate among fruits of different sugar concentrations remains to be examined. I

did not determine the limit of sugar-tasting ability in these species. Because they consistently chose between artificial diets that differed by only 2% sucrose, they probably can detect even smaller differences in sugar concentration. Furthermore, natural fruits vary in both sugar concentration and composition. Glucose, sucrose, and especially fructose are common in tropical fruits (Chan and Kwok 1975, H. and I. Baker pers. comm.), and hummingbirds can distinguish among these sugars (Stiles 1976). The tanagers' ability to distinguish small differences in sucrose concentration suggests that they may also be able to taste other sugars.

Tropical fruit-eating birds can discriminate between synthetic diets that differ only slightly in sugar concentration. However, this ability may be restricted to those frugivores that crush fruits before swallowing. Because detectable sugar variation occurs naturally both within and between fruit species, birds may be an important factor in the evolution of sweet fruits.

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100 Years Ago in The Auk



From "General Notes" (1887, *Auk* 4: 167-168):

"What constitutes a Full Set of Eggs?—The question as to what constitutes a full set of eggs, and how to determine the number with any certainty, is a matter to which I desire to call attention, and, in doing so, will say that I have given the matter considerable thought, and have reached the conclusion, on account of the many nest robbers of the birds, that the larger number is the only safe one to enter as a full set. For example, say thirty nests of *first* sets of a species are found, with birds sitting, as follows: Four nests with four eggs in each; six nests with three eggs in each; ten nests with two eggs in each; and ten nests with one egg in each. In this case I would enter three and four—possibly two to four—as a full set. But in no case one to four, believing the undisturbed birds of a species do not vary much, if any, as to number of eggs laid. Say four eggs in first set, and three in the second; that is, in case the first set is destroyed, or the birds rear two or more broods in a season; for I find as a rule that the first set is the larger one.

"Many of the birds, especially the larger ones that breed in trees, as Hawks, Herons, etc., cannot hide their bulky nests; in fact, the branches overhead are more a protection to the thieves than to the nests when the parent birds are away; for all birds, however

watchful, will, during the early stages of laying and love making, steal away from their nests a short time, for a sail or flirtation, which affords the cunning Crows, Jays, squirrels, etc., an opportunity to come up from the lower limbs and steal the eggs unobserved, or before the parent birds can return to protect them. Such robberies, and the advancement of incubation, make the birds more watchful and closer sitters. But, with all their vigilance, I think to find a full set the exception and not the rule. It is to the interest of paid collectors and dealers in eggs to have the smaller as well as the larger number treated as full sets. But the oölogist at heart, whether a collector or not, can have but one desire, and that is to arrive at the facts in the case.

"In my 'Revised Catalogue of the Birds of Kansas,' I was governed in giving the dimensions and coloration of the eggs by the sets examined, but I did not venture to change the number when given by other writers, lest such changes, based on my limited observation, might prove erroneous or misleading; but the more I look the matter over, its importance to my mind increases. I therefore call attention to it, hoping to draw out, through 'The Auk' and other sources, the views of others.—N. S. Goss, *Topeka, Kans.*"