

PHYSIOLOGICAL BASIS AND ECOLOGICAL CONSEQUENCES OF SUGAR PREFERENCES IN CEDAR WAXWINGS

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ABSTRACT.—In paired preference tests Cedar Waxwings (*Bombycilla cedrorum*) preferred glucose, fructose, and a mixture of glucose and fructose over sucrose. Preferences for simple sugars were ranked as: glucose = glucose + fructose > fructose > sucrose.

To be absorbed by the brush border membrane, sucrose is hydrolyzed into its monosaccharide components, glucose and fructose. Because Cedar Waxwings preferred glucose and fructose over sucrose, we predicted that they would be sucrase deficient. We tested this by measuring the efficiency with which Cedar Waxwings absorbed glucose, fructose, and sucrose in vivo, and by directly assaying for sucrase in preparations of intestinal mucosa. Absorption efficiencies measured using a double isotope method falsified our prediction. Cedar Waxwings were able to absorb sucrose (absorption efficiency = $61\% \pm 1.2$), but absorbed glucose and fructose more efficiently (absorption efficiencies = $92\% \pm 1.5$ and $88\% \pm 3.5$, respectively). The presence of sucrase activity in Cedar Waxwings was confirmed in preparations of intestinal mucosa. Using a radioactively labeled inert marker, we found very short mean residence times of food particles in the gut of Cedar Waxwings (ca. 41 min). Because sucrose has to be hydrolyzed before it can be absorbed, the efficiency with which it is utilized may be hindered by the extremely fast passage rates in Cedar Waxwings.

We suggest that the preference of Cedar Waxwings for monosaccharides over sucrose is due to the relative inefficiency of sucrose absorption. However, absorption efficiencies cannot explain the strong preference of glucose over fructose. In consequence, neither the caloric value of the sugars nor the absorption efficiency was adequate to explain the sugar preferences exhibited by Cedar Waxwings. We conclude that the preferences for simple sugars appear to be determined by the complex interaction between digestive constraints, postingestional effects, and taste. Received 19 January 1988, accepted 10 August 1988.

THE disaccharide sucrose and the monosaccharide hexoses, fructose and glucose, are the most common simple sugars in fruit pulp and nectar (Chan and Kwok 1975; Baker and Baker 1983, 1986; Reid and Freeman MS). Hummingbird-pollinated plants produce nectars with a high proportion of sucrose whereas passerine-pollinated plants produce nectars with a low proportion of sucrose and high proportion of hexoses (Cruden and Toledo 1977; Baker and Baker 1982, 1983). Small bird-dispersed fruits, which are typically consumed by passerines, contain mainly hexoses, whereas cultivated fruits used for human consumption tend to have high sucrose contents (Baker and Baker 1986, pers. comm.). These differences in sugar composition remain largely unexplained. It has been postulated that chemical characteristics of nectar and fruit pulp evolved in response to the

preferences of pollinators and seed dispersers (Baker and Hurd 1968, Howell 1979, Levey 1987). With few exceptions (Hainsworth and Wolf 1976, Stiles 1976), the sugar preferences of birds that feed on nectar and fruit are unknown.

Glucose, fructose, and sucrose have different modes of intestinal transport, and produce different metabolic effects after ingestion and absorption (Sestoft 1983). Even though they are similar chemically and in caloric value, these sweet substances may not be biologically equivalent. The European Starling (*Sturnus vulgaris*) rejects sucrose solutions but readily accepts solutions of fructose and glucose (Schuler, 1983). Sucrose aversion in the Starling is associated with a deficiency of the intestinal enzyme sucrase which hydrolyzes sucrose into fructose and glucose (Martínez del Rio et al. 1988). Animals that lack sucrase cannot digest and absorb sucrose. Consequently, the presence of undigested sucrose in the intestine of these animals can cause severe osmotic diarrhea. In this way,

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the absence of intestinal sucrase can be associated with aversion for sucrose (Sunshine and Kretchmer 1964).

We studied the sugar preferences of the Cedar Waxwing (*Bombycilla cedrorum*), one of the most heavily frugivorous birds in temperate North America (Martin et al. 1951), and analyzed the influence of taste and postingestional factors on these preferences. Because most bird-dispersed fruits in temperate North America are hexose-dominated (I. Baker and H. G. Baker in litt.), we predicted that Cedar Waxwings would prefer glucose and fructose over sucrose. We also hypothesized that this preference would be a result of sucrase deficiency. We examined these hypotheses by simple choice tests; by estimating the efficiency with which the birds digested and absorbed sucrose, glucose, and fructose in vivo; and by assaying for sucrase in preparations of intestinal mucosa.

METHODS

We captured 10 Cedar Waxwings in Madison, Wisconsin, during October 1986 and housed them together indoors (cage size: $2 \times 2 \times 1$ m) for ca. 2 weeks. We then transferred them to individual cages ($40 \times 55 \times 55$ cm). They were fed a diet of mashed bananas and soy protein isolate ("banana mash") *ad libitum* (Denslow et al. 1987) and provided with water. The composition of simple sugars in this diet was 59% fructose, 38% glucose, and 3% sucrose (sugar analysis performed by I. Baker). The aviary had a 12D-12N-h light cycle and constant temperature of 23°C ($\pm 1^{\circ}\text{C}$).

Choice experiments.—Sugars were presented to birds in cubes made with 10 g agar (Difco Bacto-Agar), 150 g sugar (reagent grade), 2 ml red food-dye (McCormick & Co. Inc.), and 1,000 g boiling water. The resulting gel was cut into small cubes (ca. 0.6 cm^3 and 0.18 g, $\text{SD} = 0.06 \text{ g}$, $n = 50$). The sugar concentration used was within the range encountered in natural fruit (Moermond and Denslow 1985, White and Stiles 1985). Except where stated, sugar concentrations in the cubes are expressed as g sugar/100 g water. The cubes were presented in 2 plastic trays ($5 \times 3 \times 3$ cm) each containing cubes with one kind of sugar cube. Trays were attached to each side of a perch. The amount eaten from each tray was estimated as the difference between the weight of the tray before and after each experiment. To estimate weight loss from evaporation from cubes, 2 trays containing the same sugars used in the experiment were weighed, left inside the aviary for the duration of the trial and weighed again at the end. The loss by evaporation was minimal ($\bar{x} = 0.4 \pm 0.2 \text{ g}$, $n = 20$, about 3% of the total amount), and we used uncorrected weight values for analysis. We performed all choice experiments in

the aviary about 30 min after the lights were switched on (ca. 0800). Water was provided during the trials, but the banana maintenance diet was removed.

We performed 2 series of choice tests with 10 birds. In series 1 we tested preferences for glucose, fructose, sucrose, and a mixture of glucose and fructose (1:1 ratio) by offering the birds a choice between a tray containing agar cubes with sugar ("sugar" cubes) and a tray containing agar cubes made without sugar ("pure agar" cubes; 10 g agar, 2 ml food dye, and 1,000 g water). Preference for each sugar was calculated by dividing the mass of sugar cubes eaten by the total mass of both sugar and pure agar cubes that were eaten (Kare et al. 1957). To determine whether the birds could taste sugars, we observed 2-4 birds in each trial and recorded the number of cubes swallowed or dropped. Ten birds were tested in each trial. In all preference tests, we tested the null hypothesis that the mean preference of 10 birds, as defined above, was not significantly different from 0.5 (the indifference point where consumption of both sugars tested is equal) using one sample *t*-tests on arcsine $\sqrt{}$ transformed preference values. To compare consumption among trials we used sign tests.

In series 2 we compared preferences between sugars by presenting each bird with a choice between 2 trays. Each contained agar cubes made with a different sugar or sugar mixture. All possible pair-wise combinations of glucose, fructose, sucrose, and the mixture of glucose and fructose were tested. The position of the trays (left or right) was randomized for each bird in every experiment. We tested the null hypothesis that preference, as defined above, was not significantly different from 0.5 using one sample *t*-tests on arcsine $\sqrt{}$ transformed preference values. All trials lasted 1.5 h, with the exception of an experiment in which sucrose was paired with fructose. This experiment was repeated in both 1.5- and 3-h-long trials. The same 10 birds were used in all the preference experiments. We collected excreta samples from each bird after every experiment and measured the sugar concentration with a pocket refractometer. Although urates and other fecal contaminants with undetermined refractive properties make the refractometer readings imprecise (Inouye et al. 1980), we found different sugar concentrations in excreta of birds fed on different sugars.

Extraction efficiency and retention time.—To measure the efficiency with which Cedar Waxwings absorbed each sugar, we used a double-isotope method (Karsov et al. 1986). Agar cubes, labeled with ^{14}C (U) (uniformly labeled) sugar (D-glucose, fructose, or sucrose) and ^3H polyethylene glycol (PEG, molecular weight 4,000) as an inert marker that is not absorbed in the gut, were prepared by adding 20 μCi of ^{14}C (U) sugar and 75 μCi of ^3H PEG to 10 g of cubes. In each experiment, 6 birds were deprived of food for 15 min and then allowed to feed on these labeled cubes for 2 min. The mean weight of radioactively labeled cubes

TABLE 1. Series 1: Experiments pairing sugar cubes with pure agar cubes. Preference (the proportion of sugar cubes consumed) was calculated for each bird. The mean preference for the 10 birds was tested against the null hypothesis of no preference ($\bar{x} = 0.5$) using a one-sample *t*-test. All values \pm SD. The same 10 birds were used in all experiments.

	Glucose	Fructose	Sucrose	Glucose + fructose
Preference for sugar cubes	0.80 \pm 0.16*	0.76 \pm 0.10*	0.80 \pm 0.12*	0.81 \pm 0.06*
Total eaten (g)	11.5 \pm 3.3	14.6 \pm 5.4	23.6 \pm 7.8	10.8 \pm 3.6
Refractometer reading of excreta ^a	4.0 \pm 0.7	4.5 \pm 1.1	12.1 \pm 2.6	3.4 \pm 0.9

* Mean significantly greater than 0.5, $P < 0.005$, $n = 10$.

^a An estimate of percentage sugar in excreta.

eaten per bird was 0.23 g (SD = 0.06 g). After this period we allowed birds to eat banana mash *ad libitum*. Excreta were collected from plastic sheets at the cage bottoms at 15, 30, 45, 75, 135, 195, and 255 min. After 255 min, counts of ³H PEG in excreta were less than 4 times background. Recovery of the PEG marker ranged from 72–96% ($\bar{x} = 0.82 \pm 0.09$, $n = 18$). Excreta were counted for ³H and ¹⁴C using double-isotope procedures (see Karasov and Diamond 1983 for details). Extraction efficiency was calculated by the inert-indicator ratio method (Karasov et al. 1986) as

$$100 - 100[(\text{dpm}_{\text{PEG}}/\text{dpm}_{\text{sugar}})_{\text{food}} \times (\text{dpm}_{\text{sugar}}/\text{dpm}_{\text{PEG}})_{\text{excreta}}]$$

where dpm is counts per min in a scintillation counter.

Because all ingested PEG was excreted, an extraction efficiency of 100% was obtained if $(\text{dpm}_{\text{sugar}})_{\text{excreta}}$ equals zero, and an efficiency of 0 was obtained if the ratio $\text{dpm}_{\text{sugar}}/\text{dpm}_{\text{PEG}}$ had the same value in excreta as in food.

We obtained mean retention times for PEG by fitting the cumulative excretion as a function of time to the equation

$$Y(t) = 1 - \exp[-k(T_i - t)],$$

with a nonlinear least squares program (SAS procedure NLIN; SAS Institute). $Y(t)$ is the cumulative proportion of marker after time t ; T_i is the transit time for the leading edge of the bolus; and k is the rate constant for excretion. An estimate of the mean residence time of marker particles in the digestive tract was estimated by summing the estimated value of the reciprocal of k with the estimated value of T_i (Karasov et al. 1986, Penry and Jumars 1987). The reciprocal of the mean residence time is a measure of food passage rate (i.e. low mean residence times imply high passage rates). Six birds were used in this experiment.

Sucrase activity.—Three birds were anesthetized using metaphane. After the small intestines were excised the birds were killed. Small intestines were immediately chilled in ice cold 1.02% saline and scraped of mucosa with a glass slide. Mucosal samples for each bird were taken at proximal, medial, and distal sections of the small intestine. Mucosal scrapings were homogenized (0.3–0.5 g in 6 ml of 1.02% saline) using

a Brinkman Polytron homogenizer (25 s at setting # 6) and the resulting suspension was stored in liquid nitrogen. Just prior to sucrase assays, the homogenates were thawed at 22°C and kept on ice. The protein concentration of homogenates was measured using the Bio-Rad kit (Bio-Rad, Richmond, CA), with gamma globulin standards.

We assayed sucrase activities with a colorimetric method modified from Dahlquist (1984) and Trinder (1969). Briefly, the reaction was started by adding 33 μ l of thawed mucosal homogenate plus 33 μ l sucrose stock (sucrose dissolved in 0.1 M sodium maleate buffer pH 6.0 at various concentrations). After incubating at 39°C for 10 min, 1 ml stop/develop reagent stock was added to arrest the sucrase activity and to measure liberated glucose. Our stop/develop reagent was made by dissolving 1 bottle "Glucose (Trinder)-315-100" reagent powder (proprietary mixture of Sigma Chemical Co.) plus 50 ml 1.0 M Tris/HCl (pH 7.0) and 50 ml 0.5 M phosphate buffer ($\text{NaH}_2\text{PO}_4/\text{Na}_2\text{HPO}_4$, pH 7.0). Blanks were prepared by separately incubating 33 μ l mucosal homogenate at 39°C for 10 min, after which time 33 μ l sucrose stock plus 1 ml of stop/develop reagent was added. The arrested reactions were then allowed to stand at 22°C for 18 min, at which time the absorbances were measured at 505 nm using a Beckman DU-7HS digital spectrophotometer. Glucose standards (0–40 μ g in 66 μ l of 0.1 M sodium maleate buffer, pH 6.0) were also similarly reacted with the stop/develop reagent. Based on absorbance measurements, sucrase activities were subsequently calculated as $\mu\text{moles}/(\text{min} \cdot \text{g protein})$, or $\mu\text{moles}/(\text{min} \cdot \text{cm of intestine})$. We estimated maximal sucrose hydrolysis rates (V_{max}) and the binding constant for sucrase (K_m , the concentration of substrate at which the rate of hydrolysis equals $V_{\text{max}}/2$) using a nonlinear routine (SAS procedure NLIN; SAS Institute) to fit Michaelis-Menten equations. This analysis was performed for each bird and for each segment of intestine.

RESULTS

Choice experiments: series 1.—Birds strongly preferred sugar cubes over pure agar cubes (Table 1). Contrary to expectations, total consump-

TABLE 2. Series 1: Proportions of cubes dropped (\pm SD).

	Glucose	Fructose	Sucrose	Glucose + fructose
Pure agar cubes	0.85 \pm 0.05	0.88 \pm 0.01	0.71 \pm 0.03	0.98 \pm 0.03
Cubes with sugar	0.09 \pm 0.06	0.06 \pm 0.01	0.08 \pm 0.08	0.12 \pm 0.08
Number of birds observed	2	4	4	4

tion of cubes (sugar + pure agar cubes) was significantly higher for sucrose than for all the other sugars (sign tests, $P < 0.01$ in all cases; Table 1). The percentage of sugar in excreta was also significantly higher for sucrose than for all other sugars (sign tests, $P < 0.01$ in all cases; Table 1), suggesting a lower sucrose digestibility.

The birds picked up individual cubes and manipulated them in their bills, repeatedly touching the cubes with their tongues and then either swallowing or dropping them. Sugar cubes were almost always swallowed after having been picked from the tray, whereas pure agar cubes were almost always dropped (Table 2).

Choice experiments: series 2.—When given a choice between sugars, Cedar Waxwings significantly preferred glucose and the mixture of glucose and fructose over both fructose and sucrose (Table 3). Glucose was not significantly preferred over the mixture. In a 1.5-h trial, the birds appeared to show no preference between fructose and sucrose. When a longer trial (3 h) was used, however, the birds significantly preferred fructose over sucrose (preference for fructose = 0.59 ± 0.13 , $t = 2.31$, $P < 0.05$). The ranking of preferences therefore is:

$$\text{glucose} = \text{glucose} + \text{fructose} > \text{fructose} > \text{sucrose}.$$

As predicted, Cedar Waxwings preferred monosaccharides over sucrose.

In all tests involving sucrose vs. monosaccharides, the amount of sugar in excreta de-

creased significantly as the preference of monosaccharides increased (Fig. 1). This negative correlation suggests that birds preferring sucrose were assimilating less than birds preferring monosaccharides. The total amount of cubes eaten was significantly higher in those birds preferring sucrose over monosaccharides; the total amount of cubes consumed in each trial was correlated positively with preference for sucrose (Fig. 2).

Extraction efficiencies.—Extraction efficiencies by the 6 birds for both glucose ($92 \pm 2\%$) and fructose ($88 \pm 4\%$) were significantly higher than for sucrose, ($61 \pm 1\%$) (paired t -tests, $t = 6.28$ and $t = 4.51$, respectively, $P < 0.05$). The extraction efficiency of glucose appears higher than that of fructose, although the significance was marginal ($t = 2.52$, $P = 0.053$). Thus, extraction efficiencies were ranked in the same order as preferences. We had hypothesized that Cedar Waxwings would be sucrase-deficient and therefore unable to digest sucrose. This hypothesis was falsified by the estimated extraction efficiency found for sucrose; Cedar Waxwings were able to digest sucrose albeit less efficiently than glucose or fructose.

The averages of mean residence times of PEG, and thus of water soluble food particles in the gut, were 41.5 min (± 4.2 , $n = 6$) for the glucose experiment, 41.3 min (± 6.5 , $n = 6$) for the fructose experiment, and 39.1 min for the sucrose experiment (± 6.2 , $n = 6$). The frequency distribution of excreted PEG particles was a decreasing function of time and was adequately

TABLE 3. Preferences for sugars (left of matrix) over sugars available (top of matrix, series 2) in 1.5-h trials. Preference was the proportion of sugar (top of matrix) eaten. Preference was calculated for each bird and the mean preference for the 10 birds tested against the null hypothesis of no preference (i.e. a mean preference = 0.5) using one sample t -tests.

	Glucose	Glucose + fructose	Sucrose	Fructose
Glucose	—	0.54 \pm 0.19 ^{ns}	0.73 \pm 0.17*	0.72 \pm 0.09*
Glucose + fructose	—	—	0.67 \pm 0.14*	0.70 \pm 0.17*
Sucrose	—	—	—	0.55 \pm 0.19 ^{ns}

* Mean significantly different from 0.5, $P < 0.01$, $n = 10$.

^{ns} Mean not significantly different from 0.5, $P > 0.05$.

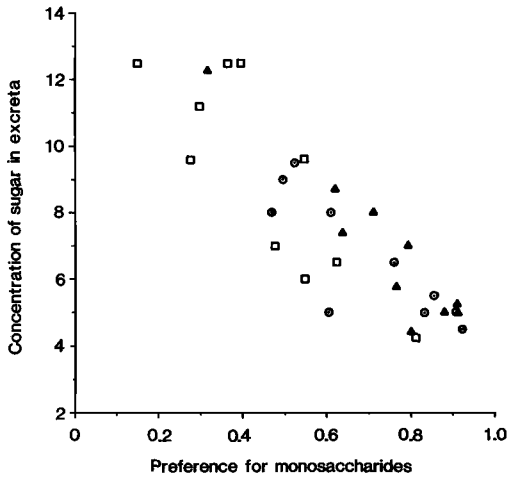


Fig. 1. Relationship between preference for monosaccharides over sucrose and sugar concentration in excreta. Data for 3 experiments in which glucose (circles, $r_s = -0.87$, $P < 0.01$), fructose (squares, $r_s = -0.80$, $P < 0.01$), and a mixture of glucose and fructose (triangles, $r_s = -0.78$, $P < 0.01$) were paired with sucrose. Each point represents an individual bird in 1 experiment (the same 10 birds were used in each experiment). Concentration is expressed as mass per unit mass of sucrose equivalents.

described by exponential density functions (the coefficient of correlation for individual trials ranged from 0.84–0.95) (Fig. 3).

Sucrase activity.—Because the extraction efficiency experiments indicated that Cedar Waxwings were capable of digesting sucrose, it was not surprising to find sucrase activity in the mucosal preparations. The affinity of this en-

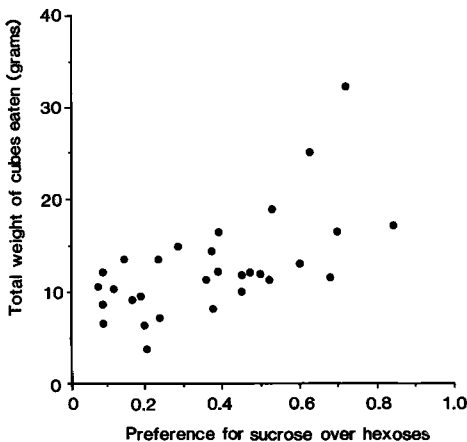


Fig. 2. Relationship between total mass of cubes consumed and preference for sucrose over monosaccharides ($r_s = 0.62$, $P < 0.001$).

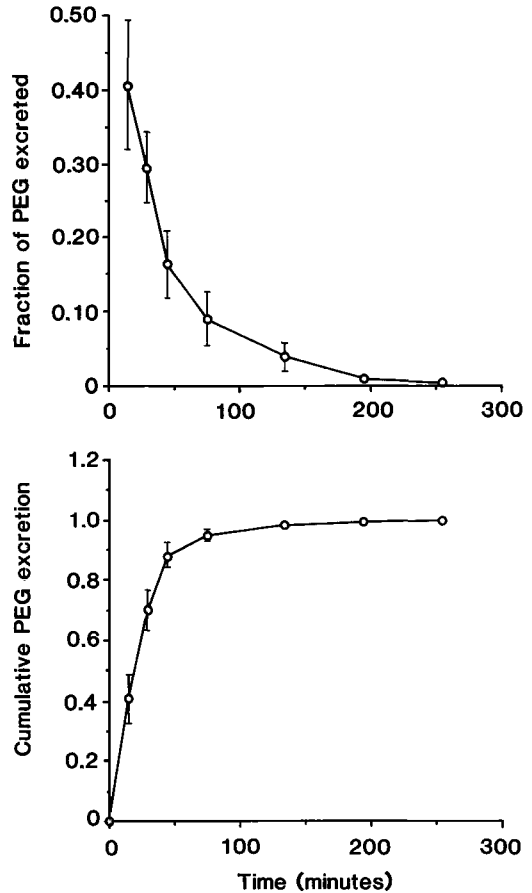


Fig. 3. Excretion of the inert marker PEG as a function of time. Top: fraction of total PEG excreted during the previous interval; bottom: cumulative excretion. Each point is the weighted mean of 3 experiments; bars are SEs. Six birds were used in each experiment.

zyme for sucrose as measured by K_m did not vary appreciably among the three birds examined or among the intestine segments (mean $K_m = 15.5$ mM, ranging from 15.2–15.7 mM). The maximal rate of sucrose hydrolysis (V_{max}) decreased from the proximal to the distal segments of the intestine regardless of whether sucrase activity was normalized to protein concentration or tissue length (Fig. 4). Sucrose hydrolysis increased with concentration in a typically decelerating fashion (Fig. 5).

DISCUSSION

Previous studies have shown that birds can detect sugars (Levey 1987 and references therein), but few have shown that taste is involved

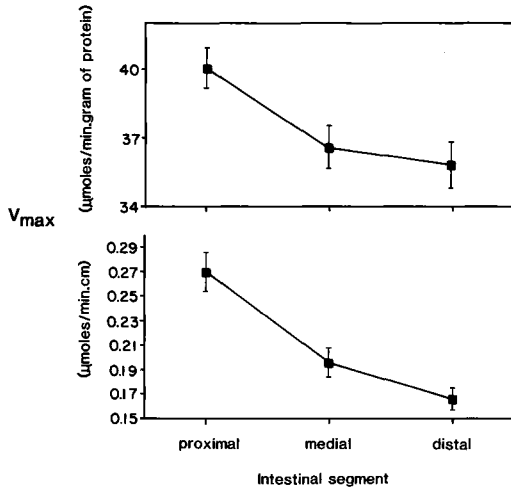


Fig. 4. Maximal sucrose hydrolysis (V_{max}) as a function of intestinal position in Cedar Waxwings. Hydrolysis is standardized to grams of protein in homogenate (top) and length of intestine (bottom). The value of V_{max} was estimated independently for each segment and each one of 3 birds using a nonlinear least squares routine. Bars are SEs.

in sugar detection (Kare and Mason 1986). Cedar Waxwings were able to distinguish between cubes with and without sugars before swallowing them. Taste, therefore, is probably involved in their recognition of sugars. In short-term trials (1.5 h), Cedar Waxwings were also able to differentiate among different sugars. The cues used by birds to achieve this are unknown. Taste may have been important, but position and the texture of the cubes made with different sugars may also have been involved. Jacobs et al. (1978) have suggested that flavors, as well as other cues, serve as markers for what animals have learned about food items (see also Brower 1984).

Total consumption of cubes was higher in the sucrose vs. pure agar trial than when hexoses were paired with pure agar; and preference for sucrose over monosaccharides was positively correlated with total consumption of cubes. These results indicate that birds feeding on sucrose or preferentially on sucrose were more stimulated to eat. Because sucrose is absorbed less efficiently than either glucose or fructose, the birds had to eat more to increase their absorbed energy intake.

Blood glucose level and its monitoring by brain glucose receptors have been implicated in many theories of food intake control (Le Maguen 1985). High levels of blood glucose are usu-

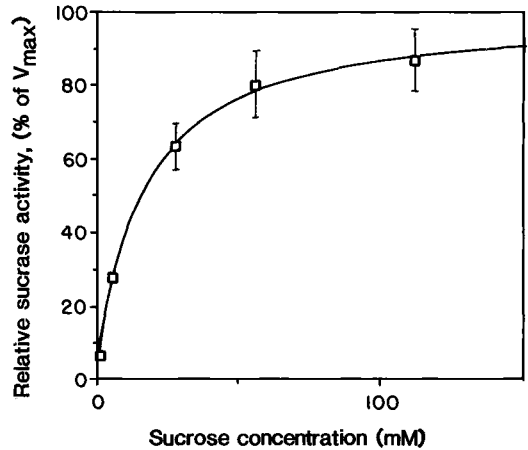


Fig. 5. Sucrase activity in mucosal homogenates of Cedar Waxwings as a function of sucrose concentration. Relative sucrose hydrolysis was calculated from values of V_{max} that were independently estimated for each intestinal segment and each bird. The curve is a Michaelis-Menten equation calculated using a V_{max} of 100% and a K_m of 15.5 mM; bars are SEs.

ally associated with lowered food intake. The rate at which circulating glucose increases in Cedar Waxwings is probably higher after a glucose (or a glucose + fructose) meal than after a sucrose meal of equal size. Glucose and glucose + fructose meals are probably more efficient at suppressing the feeding response ("hunger") than sucrose and are therefore preferred.

The difference in absorption efficiency between glucose and fructose was relatively small. Why Cedar Waxwings strongly preferred glucose and glucose + fructose over fructose is not clear. Rowland and Stricker (1979) have shown that intravenous infusions of fructose are less efficient than equicaloric infusions of glucose in suppressing insulin-induced feeding in rats. Fructose cannot cross the blood-brain barrier in mammals (Oldendorf 1971) and its effect in suppressing hunger may be less than that of glucose both in rats and in Cedar Waxwings. This hypothesis is supported by the observation that in 1.5-h trials, Cedar Waxwings did not prefer fructose over sucrose despite the more efficient absorption of fructose. The increase in blood glucose that follows the ingestion of fructose is delayed because fructose has to go through gluconeogenesis in the liver to be modified into glucose (Pontremoli and Grazi 1968, Sestoft 1983). The length of the delay in the blood glucose increase after a fructose meal is inversely

dependent on the levels of liver glycogen (Sestoft 1983, Novin et al. 1985). This lag may explain why fructose is preferred over sucrose in long-term (3 h) trials which permit glycogen accumulation but not in short term trials.

Cedar Waxwings are able to digest sucrose, although the digestive efficiency of sucrose is less than that of glucose and fructose. The reasons Cedar Waxwings absorb monosaccharides more efficiently than the disaccharide sucrose is also obscure. The estimated mean retention times for Cedar Waxwings were extremely short (grand mean of all the experiments = 40.73 min; see also Holthuitzen and Adkisson 1984). Even mean retention times (49 ± 3 min) in Rufous Hummingbirds (*Selasphorus rufus*) are longer (Karasov et al. 1986). The mass of Rufous Hummingbirds is ca. 3 g (Karasov et al. 1986) and that of Cedar Waxwings is about 30 g. In contrast with Cedar Waxwings, hummingbirds show extremely high extraction efficiencies (ca. 99%) when fed solutions of both monosaccharides and sucrose (Hainsworth 1974, Karasov et al. 1986). It may be that the extremely fast passage rates of food in Cedar Waxwings impede the efficient digestion of a substrate such as sucrose that has to be hydrolyzed before it is absorbed. Researchers have historically assumed that high food passage rates are a typical trait of frugivorous birds (Wetmore 1914, McKey 1975, Moermond and Denslow 1985). This assumption has received surprisingly little empirical support, and data that compare passage rates of frugivorous birds with those of birds with other feeding habits are scant (but see Herrera 1984). If high food passage rates are indeed typical of frugivores, and if fast passage rates hinder the digestion of sucrose relative to the digestion of hexoses, then we hypothesize that frugivorous birds are less efficient in digesting sucrose than in digesting glucose and fructose. Presumably, one consequence of the constraint imposed by high food passage rates is that frugivorous birds prefer the monosaccharides glucose and fructose over sucrose.

The patterns of sugar distribution in flowers and fruits are probably a result of the interaction between plants and the animals that pollinate them and disperse their seeds. By examining the mechanisms that govern the digestion of simple sugars and how they impinge on the behavioral preferences of birds, we may elucidate the factors that have produced these patterns.

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