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SUGAR PREFERENCES IN HUMMINGBIRDS: THE INFLUENCE OF SUBTLE CHEMICAL DIFFERENCES ON FOOD CHOICE[1]

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Abstract. The nectar secreted by hummingbird-pollinated flowers is rich in sucrose, whereas nectar secreted by passerine-pollinated plants contains a mixture of glucose and fructose. To test the hypothesis that sugar preferences and nectar composition are correlated, I examined the sugar preferences of three species of Mexican hummingbirds (*Amazilia rutila, Cynanthus latirostris,* and *Chlorostilbon canivetii*). As predicted, the three species preferred sucrose over glucose, fructose, and a mixture of glucose and fructose (hexose mixture) in paired preference tests. Preferences for simple sugars were ranked as: sucrose > hexose mixture > glucose > fructose. The preference of hummingbirds for sucrose was not reversed by feeding hummingbirds a hexose mixture as a sole diet for 20 days.

The preferences of hummingbirds for different sugars are puzzling because sucrose, glucose, and fructose have approximately the same energetic content. I hypothesized that sugar preferences were correlated with differences in the efficiency with which hummingbirds assimilated different sugars and/or in the time they required to process these sugars in the digestive system. Sucrose, glucose, and fructose, however, were assimilated by hummingbirds with equally high efficiency (>97%). Glucose solutions were processed by hummingbirds at a slower rate than hexose mixtures and sucrose solutions, and hence, were less profitable. Sucrose and hexose mixtures were processed at the same rate and therefore had the same profitability. Therefore, the preference of hummingbirds for sucrose over hexose mixtures cannot be explained by differences in assimilation efficiency or digestive handling time.

Sucrose must be hydrolyzed into its monosaccharide components, glucose and fructose, before it can be absorbed in the intestine and used as an energy source. Relative to other birds, hummingbirds exhibit highly specialized digestive traits, such as very high rates of intestinal sucrose hydrolysis and glucose transport, which allow them to use sucrose as efficiently as mixtures of glucose and fructose. Many passerine species, in contrast, use the more easily absorbed monosaccharides, glucose and fructose, more efficiently than sucrose. The distribution of nectar sugars among bird-pollinated plants seems to be the result of the evolutionary response of plants to two sets of pollinators with different degrees of digestive specialization.

Key words: Mexican hummingbirds; diet; nectar composition; food choices.

INTRODUCTION

In the process of feeding on nectar, hummingbirds transfer pollen from one flower to another (Trelease 1881). Hummingbird preferences for plants producing different types of nectar can result in changes in the frequency of preferred nectar in plant populations (Baker and Hurd 1968). Ecologists have generally assumed that the diversity of rewards that plants offer is a reflection of pollinator choice (Baker and Hurd 1968, Howell 1974), but there are few data demonstrating such preferences (see Hainsworth and Wolf 1976 and Stiles 1976 for hummingbirds, and Waller 1972 for bees).

Nectar is a dilute solution of different sugars containing small amounts of amino acids and electrolytes (Pyke and Waser 1981, Baker and Baker 1982, Hiebert and Calder 1983). The sugars most commonly encountered in nectar are sucrose, fructose, and glucose in varying proportions (Percival 1961). These sugars have approximately the same energetic content per unit gram (16.48×10^3 J/g, CRC Handbook of Chemistry and Physics 1979), but vary in their chemical structure. They differentially stimulate taste receptors (Pfaffmann 1975), and are digested, absorbed, and metabolized along different pathways by vertebrates (Alpers 1987). The distribution of these sugars in the nectars of plants pollinated by different groups of animals is a good example of the diversity of rewards usually assumed to be molded by the preferences of pollinators.

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Baker and Baker (1983) have shown that plants pollinated by hummingbirds produce sucrose-dominant (sucrose/[glucose + fructose] > 0.99) or sucrose-rich (0.5 < sucrose/[glucose + fructose] < 0.99) nectars. Plants pollinated by perching birds (a broad category including passerines of many Old and New World families, Stiles 1981), in contrast, secrete hexose-dominant nectars almost exclusively (sucrose/[glucose + fructose] < 0.1). This pattern has not received an adequate evolutionary explanation. Here I examine the sugar preferences of hummingbirds to determine if these preferences can indeed explain the differences in sugar constituents among these two groups of plants.

The effects of variation in energetic content on food preferences have been explored in detail by many studies (see Stephens and Krebs 1986 and references therein). Effects of the chemical nature of different energy sources on feeding preferences have received considerably less attention, however (Speakman 1987, Martínez del Rio et al. 1988). Nectar-feeding birds and the sugars they feed on are one of the simplest natural systems available to explore the effects of the chemical structure of food on feeding choices. Here I explore the effects of the subtle chemical differences among foods of equal energetic content (sucrose, glucose, and fructose) on the preferences of hummingbirds, the most specialized group of nectar-feeding birds (Stiles 1981).

I will describe a series of experiments conducted to measure the preferences of three species of Mexican hummingbirds (*Amazilia rutila, Cynanthus latirostris,* and *Chlorostilbon canivetii*) for sucrose, glucose, fructose, and a 1:1 mixture of glucose and fructose; I will also explore whether these preferences can be altered by a change in the birds' diets. I will then suggest a set of hypothetical proximal physiological mechanisms to explain the preferences found, and describe experiments conducted to examine them. Because the hypotheses examined in the second section depend on the results of the first, I present the methods and results of the two sections separately.

BIRD CARE AND HOUSING

I captured eight to 10 birds of each species with mist nets in the vicinity of the Estación de Biología Chamela UNAM, Jalisco, México. Birds were housed individually (50 × 50 × 50 cm cages) under ambient temperature and photoperiod (except during excretion measurements, see below) in a room illuminated with external light and two fluorescent lamps. Between experimental periods, birds were fed a 17.1% sucrose solution made with commercial table sugar and tap water. A vitamin supplement was added to the sucrose solution twice a week. Birds were provided with free-flying fruit flies at all times. The first week after capture most birds gained weight, to subsequently lose it to maintain body masses within 5% of those at capture. Mean body mass ± SD (*n*) for *C. canivetii, C. latirostris,* and *A. rutila* were: 2.2 ± 0.2 (10), 2.8 ± 0.2 (10), and 4.5 ± 1.0 (8), respectively.

SUGAR PREFERENCES

EXPERIMENTAL RATIONALE AND METHODS

With few exceptions, hummingbirds feed predominantly on nectars dominated by sucrose (Stiles 1976, Baker and Baker 1983). Remarkably few plants produce nectars containing glucose or fructose alone (Baker and Baker 1983). Thus, I predicted that the preferences of hummingbirds for equicaloric solutions would be ranked in the following order: sucrose > glucose + fructose > single hexoses (glucose or fructose). To test this hypothesis I presented hummingbirds with all possible pairwise combinations of sucrose, a 1:1 mixture of glucose and fructose (henceforth called hexose mixture), glucose, and fructose.

Two sugar solutions (17.1%, weight/total volume) were presented simultaneously in glass tubes. The tubes (i.d. = 7.6 mm) had a 42-cm vertical section and a lower 7-cm section that was bent upward at a 45° angle; the tip of the lower section was tapered into a hole (i.d. = 2.5 mm) from which the birds drank. Both tubes were at the same distance (ca. 30 cm) from a single perch and 5 cm apart. The solutions were prepared with distilled water and reagent grade sugars. Trials lasted 4 hr and were conducted from 08:00 to 12:00 and from 14:00 to 18:00. At the beginning of each trial the position of the tubes was randomized. At the end of each trial, consumption of solutions was measured to the nearest millimeter and then converted to volume units. Preference for sugar A over sugar B was calculated as the ratio of the consumption of sugar A divided by total consumption (A + B).

For each species and each pairwise comparison of sugars, I obtained an estimate of mean preference using six birds and six replicated trials per

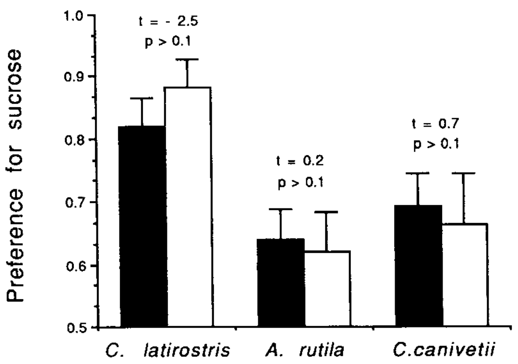

FIGURE 1. Effect of diet on sucrose preferences. Six birds of three species (*Cynanthus latirostris, Amazilia rutila,* and *Chlorostilbon canivetii*) were fed a sucrose maintenance diet for 20 days and then offered a choice between sucrose and glucose + fructose solutions (four 4-hr replicates per bird). Birds were then changed to a glucose + fructose maintenance diet for 20 days and after this period, offered a choice between sucrose and glucose + fructose solutions (four 4-hr replicates per bird). The mean preference of four replicates per bird was used as an estimate of sucrose preference, and the change in mean preference was tested using one-tailed paired t-tests. Closed bars are grand mean preferences for the sucrose diet, and open bars are grand mean preferences for the glucose + fructose diet. Error bars are interindividual standard deviations. Note that the trend in *C. latirostris* is in the opposite direction from that expected.

bird. The interindividual variance in preference (i.e., the variance among the six individual means) was used to construct a confidence interval for the mean preference of each species. I used this confidence interval to test the null hypothesis that preference was not significantly different from 0.5 (the indifference point where consumption of both sugars tested is equal) using one sample t-tests on arcsin$\sqrt{\ }$ transformed preference values.

Many hummingbirds feed on hexose-dominant nectars if these are available (Stiles 1976, Baker and Baker 1983, Gryj et al. 1990). Thus, the sugar composition of the current diet may influence the preferences of hummingbirds in the field. To examine whether shifting diets changed the preferences of hummingbirds, I fed six birds of each species a sucrose diet for 20 days and obtained an estimate of their preference for sucrose over a hexose mixture (four trials per bird). The same birds were then fed a hexose mixture for 20 days and retested (four trials per bird). I used one-tailed paired t-tests to detect increases in the preference for the hexose mixture.

RESULTS

All three species exhibited the following ranking in their preferences: sucrose > hexose mixture > solutions of single hexoses (Table 1). This ranking is the one predicted. In addition, all significantly preferred glucose to fructose solutions (Table 1). The preference for the hexose mixture did not increase significantly when the maintenance diet was changed from sucrose to a hexose mixture (Fig. 1). In fact, the preference of *C. latirostris* for the hexose mixture appeared to decrease after the diet change (Fig. 1).

DIGESTION OF SUGARS

EXPERIMENTAL RATIONALE AND METHODS

Items of identical caloric content but different chemical composition can have different profitabilities if they are assimilated in the digestive system with differing efficiencies and/or if they

TABLE 1. Preferences for sugars in three species of hummingbirds. Sugars were presented in solution (17.1% weight/volume) in paired drinking tubes (4-hr trials). Preference values for each combination of sugars are grand means (six individuals and six trials per individual) ± interindividual standard deviations. S = sucrose, G = glucose, F = fructose and G + F = 1:1 glucose + fructose mixture.

Species	Comparison					
	S vs. G + F	S vs. G	S vs. F	G + F vs. G	G + F vs. F	G vs. F
Chlorostilbon canivetii	0.69 ± 0.05 $t = 9.2$[a]	0.88 ± 0.06 $t = 14.2$	0.86 ± 0.05 $t = 15.2$	0.72 ± 0.20 $t = 2.7$	0.84 ± 0.10 $t = 7.6$	0.89 ± 0.06 $t = 15.26$
Cynanthus latirostris	0.79 ± 0.12 $t = 4.4$	0.93 ± 0.06 $t = 17.1$	0.88 ± 0.07 $t = 13.3$	0.91 ± 0.06 $t = 16.5$	0.79 ± 0.12 $t = 6.12$	0.88 ± 0.05 $t = 17.5$
Amazilia rutila	0.63 ± 0.07 $t = 4.5$	0.86 ± 0.09 $t = 9.7$	0.83 ± 0.13 $t = 6.7$	0.93 ± 0.06 $t = 17.0$	0.78 ± 0.10 $t = 7.2$	0.74 ± 0.22 $t = 2.7$

[a] $t_{0.05,5} = 2.6$.

are digested at different rates and hence vary in the digestive "handling time" required for assimilation (Speakman 1987, Martínez del Rio and Karasov 1990). To determine if sugar preferences in hummingbirds were correlated with differences in digestive processing, I measured the efficiency with which hummingbirds assimilated sucrose, glucose, and fructose, and compared the time required to process solutions of sucrose, glucose, and hexose mixtures in the digestive system.

ASSIMILATION EFFICIENCIES

I obtained estimates of digestive efficiencies for sucrose, glucose, and fructose by measuring apparent assimilated mass coefficients (AMC*, Karasov 1990) in 24-hr trials AMC* was calculated as:

$$\text{AMC*} = (\text{dry matter intake} - \text{dry matter excreted}) \div (\text{dry matter intake})$$

Because endogenous metabolic wastes are mixed with feces in the cloaca of birds, AMC* underestimates true assimilated mass coefficients (Robbins 1983). AMC*, however, permits a comparison of assimilation efficiency among different sugars.

Birds were fed ad libitum with sugar solutions (17.1%) and kept in cages with plastic sheets lining the bottom. Each cage had a single small perch (10 cm in length). Plastic sheets were removed and excreta was collected at hourly intervals. Most of the excreta produced fell directly under the perch and was readily collected with microcapillary tubes. Losses due to excreta adhering to the plastic sheets were minimized by frequent collection (1 hr). Birds were deprived of fruit flies 48 hr before each experiment, and to avoid contamination from the previous day's diet, birds were fasted overnight and for an hour after sunrise. Test solutions were offered 1 hr after sunrise, and excreta was collected at 1-hr intervals until sunset. Excreta produced during the night was collected the following morning. Birds were not fed for an additional hour the next day and all excreta produced in this interval was collected. Consumption of sugar solutions was measured at 1-hr intervals. Excreta was dried to constant weight at 60°C.

PROCESSING TIME

Digestive efficiencies are not sufficient to predict the rate of energy intake from digestion; the time required to process the energy obtained is also needed (Martínez del Rio and Karasov 1990). Because I found no differences in AMC* (see Results), I hypothesized that differences in processing rates could account for the preferences found. I predicted that the ranking in the time used to process sugar solutions in the gut would be the following: pure hexoses > hexose mixtures > sucrose. Chemical differences among sugars and their possible physiological consequences provide the mechanisms that can account for this ranking.

The hexoses, glucose and fructose, are transported across the intestinal membrane by independent carrier systems (Sigrist-Nelson and Hopper 1974). Consequently, solutions of these single monosaccharides that are absorbed by a single system working by itself should be absorbed at a slower rate than equicaloric solutions of mixtures that are absorbed by two independent carrier systems. It is assumed that most of the intestinal transport of monosaccharides in the hummingbird intestine is carrier mediated (Karasov et al. 1986, Martínez del Rio and Karasov 1990).

The osmotic pressure exerted in the intestinal lumen by a 1:1 mixture of glucose and fructose is twice as high as that of an equicaloric solution of sucrose. If the rate of delivery of food from the crop and stomach to the intestine is mediated by the osmotic pressure in the intestinal lumen (Gibson et al. 1968, McHugh et al. 1982), then sucrose may be processed at a faster rate than an equicaloric mixture of hexoses.

I compared processing times for sucrose, hexose-mixture, and glucose solutions at two concentrations (17.1% and 34.2%). As a processing time index (PTI) I used the reciprocal of the rate of excretion, because the time required to process one intestinal volume equals the ratio of intestinal volume/flow rate (Penry and Jumars 1987). If intestinal volume remains constant, the reciprocal of excretion rate (an index of intestinal flow rate) measures the time required to process each volume unit of digesta. The rationale and shortcomings of using PTI are discussed by Owen (1972, 1975) and Sibly (1981).

To obtain excretion rates, test solutions were presented at dawn to hummingbirds. After 2–3 hr of feeding, excreta was collected and measured in microcapillary tubes at 5-min intervals during 2 hr. Excreta was collected by removing the plastic sheets lining the bottom of the cages. Each 5-min interval measurement was used as a rep-

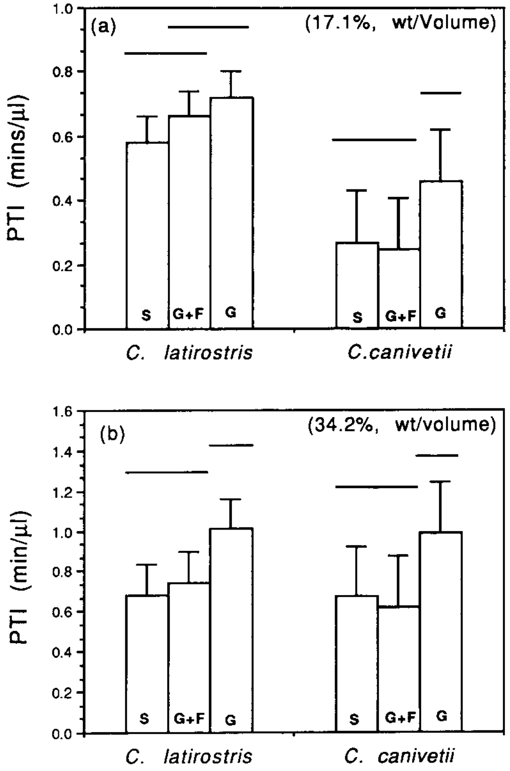

FIGURE 2. Processing times (PTI) for different sugars at two different concentrations: 17.1% (a) and 34.2% (b). A randomized-block design with 24 replicates per bird (five *Cynanthus latirostris* and four *Chlorostilbon canivetii*) was used to examine differences among sugars. Bars are means and error bars are 95% confidence intervals. The lines above the bars join means that are not significantly different at the 0.05 level (a priori *t*-contrasts). S = sucrose, G + F = 1:1 glucose + fructose mixture, G = glucose.

licate. To examine differences among the mean PTIs of different sugars, I used a randomized block design with 24 replicates per bird (five *C. latirostris* individuals and four *C. canivetii* individuals). Because I measured excretion rates in only two *A. rutila* individuals, I analyzed each individual separately using one-way analysis of variance (24 replicates per sugar solution). In all excretion rate experiments, birds were housed at 21°C (±2°C) and under a 12L:12D light cycle.

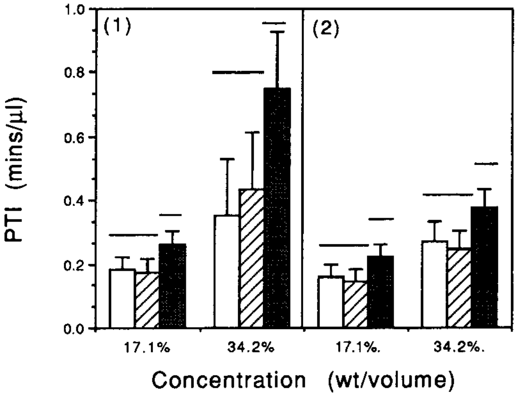

FIGURE 3. Processing times for different sugars in *Amazilia rutila.* Only two individuals were tested and were analyzed separately. Bars are means (n = 24) and error bars are 95% confidence intervals. The lines above the bars join means that are not significantly different at the 0.05 level (a priori *t*-contrasts). Sucrose = open bars, glucose + fructose = stippled bars, and glucose = solid bars.

RESULTS

Digestive efficiencies. Hummingbirds digested all sugars with extremely high and very similar efficiencies. AMC* for all sugars was ≥97% in all cases (Table 2) and not significantly different among sugars (paired *t*-tests, $P > 0.1$). Daily consumption of sugar solutions did not vary significantly among sugars (Table 2).

Processing times. In *C. latirostris* and *C. canivetii,* processing time indices were significantly different among sugars at both concentrations (17.1% and 34.2%, Figs. 2a and 2b). The two *A. rutila* individuals tested also exhibited significant differences in processing time indices among sug-

TABLE 2. Apparent assimilated mass coefficients (AMC*) and daily consumption of sugars in three species of hummingbirds (in parentheses). Sugar solutions had identical concentration (17.2%). Values are means ± SE.

	AMC* ± SE ([ml consumed/12 hr] ± SE)			
Species	Sucrose	Glucose	Fructose	*n*
Amazilia rutila	0.97 ± 0.01	0.99 ± 0.01	0.97 ± 0.02	4
	(6.6 ± 0.4)	(5.1 ± 0.5)	(6.2 ± 0.3)	
Cynanthus latirostris	0.99 ± 0.01	0.97 ± 0.02	0.98 ± 0.01	6
	(3.9 ± 0.5)	(4.0 ± 0.4)	(3.9 ± 0.2)	
Chlorostilbon canivetii	0.98 ± 0.02	0.99 ± 0.01	0.97 ± 0.03	5
	(4.2 ± 0.1)	(4.4 ± 0.2)	(3.8 ± 0.2)	

ars (Fig. 3). Contrary to my prediction, a priori t-contrasts (Kirk 1982) indicated no significant differences among mean processing time indices of sucrose and the hexose mixture. Significant differences between glucose and both sucrose and the hexose mixture were found in all but one experiment (Fig. 2b). As predicted, hummingbirds take longer to process glucose solutions than either hexose-mixture and sucrose solutions.

DISCUSSION

SUGAR PREFERENCES

The sugar preferences of hummingbirds have been examined in two previous studies (Hainsworth and Wolf 1976, Stiles 1976). These studies reported conflicting results: Stiles (1976) examined sugar preferences in four species (*Calypte anna, Selasphorus rufus, Archilocus alexandri,* and *Thalurania furcata*) and found that all of them significantly preferred sucrose over equicaloric solutions of single monosaccharides. When sucrose was paired with a mixture of glucose and fructose, sucrose was significantly preferred by two species (*C. anna* and *S. rufus*) but one species (*A. alexandri*) was indifferent. Thus, Stiles' results indicate strong preferences that agree with those presented in this study (Stiles 1976). In contrast, Hainsworth and Wolf (1976) found no strong preferences, and argued that in hummingbirds sugar composition has little effect on food choice.

Differences in test choice protocols can explain the discrepancy between these studies. Stiles (1986) and I exposed birds to test solutions in the same position for relatively long periods (12 and 4 hr, respectively), whereas Hainsworth and Wolf (1976) alternated the position of the feeders every 0.5 hr. Because hummingbirds take a relatively small number of meals in 0.5 hr (2.4 to 4.5, table VI in Wolf and Hainsworth 1977), this interval may be too short for sampling of both feeders and for the establishment of clear preferences.

Combining results from this study and that of Stiles, hummingbirds appear to show weak preferences among sugars in brief exposure tests, but strong preferences in long exposure tests. In long exposure tests the preference ranking of sugars in five species of hummingbirds is: sucrose > mixture of hexoses > glucose > fructose (Stiles 1976, this study). One species (*A. alexandri*) deviates from this ranking in that it appears to show no preference for sucrose over mixtures of glucose and fructose.

The preferences that hummingbirds show for different sugars contrast with those exhibited by Cedar Waxwings (*Bombycilla cedrorum*) and European Starlings (*Sturnus vulgaris*). These two passerines strongly prefer mixtures of glucose and fructose over sucrose (Martínez del Rio and Stevens 1989, Martínez del Rio et al. 1989). The variation in sugar preferences among bird species indicates that the sugars, sucrose, glucose, and fructose, are not equivalent for different species of birds even though they are quite similar chemically.

PRE- AND POSTINGESTIONAL CORRELATES OF SUGAR PREFERENCES

The preingestion handling time of sugar solutions depends on nectar viscosity and surface tension (Pyke and Waser 1981, Kingsolver and Daniel 1983). In the range of concentrations used in these preference tests, the differences among sucrose, glucose, and fructose solutions in viscosity and surface tension are extremely small and have little effect on the rate of intake (Heyneman 1983). Hence, preingestion handling times are unlikely to generate differences in profitabilities that can account for the sugar preferences exhibited by hummingbirds.

I hypothesized that postingestional variation in the digestion and absorption of different sugars by hummingbirds could explain their preferences. I was unable, however, to find differences in the efficiency with which hummingbirds assimilated different sugars. Hummingbirds assimilated sucrose, glucose, and fructose with the same and extremely high efficiency (see also Hainsworth 1974). I was also unable to find differences between the rate at which hummingbirds processed sucrose and 1:1 mixtures of glucose and fructose solutions in the digestive system. Apparently the preference of hummingbirds for sucrose over a mixture of hexoses cannot be explained by differences in processing rate in the digestive system.

Hummingbirds processed glucose solutions at significantly slower rates than solutions of sucrose and 1:1 mixtures of glucose and fructose. This result is consistent with the existence of two independent transport systems for glucose and fructose in the small intestine (Sigrist-Nelson and Hopper 1974). Solutions of single monosaccharides (glucose or fructose) that are absorbed by a single system working by itself, should be absorbed at a slower rate than equicaloric solutions of 1:1 mixtures that are absorbed by two independent carrier systems working simultaneously. Sucrose and hexose-mixture solutions probably have higher profitabilities for hummingbirds than solutions of single hexoses.

Hummingbirds showed a very strong preference for glucose over fructose (see also Stiles 1976). Cedar Waxwings also prefer glucose over fructose, suggesting that this preference may be widespread among birds (Martínez del Rio et al. 1989). The metabolic responses of animals to glucose and fructose meals are very different and may explain the preference of birds for glucose over fructose. Fructose meals can be followed by hypoglycemia (Roudybush 1970, Shafir 1985) and fructose does not cross the blood-brain barrier and therefore cannot be oxidized by the brain (Oldendorf 1971). Glucose meals, in contrast, cause postprandial hyperglycemia (Hazelwood 1986) and glucose freely crosses the blood-brain barrier (Oldendorf 1971). Consequently, glucose may be more efficient than fructose at stimulating the cerebral chemoreceptors responsible for suppressing hunger (Stricker et al. 1977, Stricker and Rowland 1978). Thus, the preferences of birds for simple sugars may be influenced by physiological events that occur after sugars are tasted, ingested, and absorbed in the digestive system.

WHY DO HUMMINGBIRDS PREFER SUCROSE?

A digestive mechanism seems an unlikely explanation for the preference of hummingbirds for sucrose over mixtures of glucose and fructose. Sucrose and 1:1 hexose-mixture solutions appear to be equally profitable and to cause similar postprandial physiological effects in hummingbirds. Then why do hummingbirds prefer sucrose? Studies on the feeding preferences of a variety of vertebrates and invertebrates have indicated that foods experienced early in life are preferred over those experienced later (Hess 1964, Dethier and Goldrich 1971, Bronstein et al. 1975). Hess (1964) has called this phenomenon "food imprinting." Maybe nestling hummingbirds become "imprinted" to the sucrose-rich nectars regurgitated by their mothers (Dickey 1915, Bent 1964, Carpenter and Castronova 1980). I hypothesize that the preference of hummingbirds for sucrose is acquired at an early age, and that the preference of hummingbirds for sucrose over equicaloric hexose mixtures is mediated by flavor (preingestional sensory perception) rather than by differences in postingestional digestion handling.

I attempted unsuccessfully to reverse the preferences of hummingbirds for sucrose by exposing them to the nonpreferred diet, a hexose mixture. My results attest more to the strength of the preferences of hummingbirds than to their lability (see Fig. 1 and Stiles 1976). Although food imprinting appears not to be as irreversible as filial imprinting can be (Jacobs et al. 1978), the preferences acquired in early life can strongly influence later decisions (Burghardt and Hess 1966, Rabinowitch 1969).

SUGAR PREFERENCES IN HUMMINGBIRDS AND THE SUGAR CONSTITUENTS OF NECTAR

Hummingbird-pollinated plants produce nectars with a high proportion of sucrose, whereas passerine-pollinated plants secrete nectars with a balanced mixture of glucose and fructose, and extremely low amounts of sucrose (Baker and Baker 1982, 1983). Martínez del Rio and Stevens (1989) hypothesized that the preferences of birds are the selective pressure responsible for maintaining the sugar composition in the rewards that plants offer. I have argued, however, that sucrose and hexose-mixture solutions appear to be equally profitable for hummingbirds. I have also hypothesized that the preference of hummingbirds for sucrose is a result of food imprinting with sucrose-dominated nectars—that sucrose preference in hummingbirds is the consequence rather than the cause of the chemical composition of nectar.

Sucrose is the major form in which energy is translocated in most plant species (Hawker 1985), and it is probably cheaper for plants to secrete sucrose directly from the phloem than to hydrolyze it in the nectaries into glucose and fructose (Frey-Wyssling 1955). It is likely that in the absence of pollinator selection against sucrose, sucrose producing phenotypes are advantageous. Hummingbirds are perhaps the most specialized nectar-feeding birds (Stiles 1981), and their digestive systems are extremely well suited to digest and absorb a sucrose diet efficiently. Hummingbirds have the highest rates of carrier-mediated intestinal glucose transport reported among vertebrates (Karasov et al. 1986) and their rates of intestinal hydrolysis of sucrose are extremely high (Martínez del Rio 1990). These digestive traits allow them to use sucrose as efficiently as hexose mixtures. The digestive adaptations of hummingbirds allow hummingbird-pollinated plants to secrete sucrose-dominated nectar. Passerine-pollinated plants, in contrast, are visited and pollinated by a diverse group of relatively unspecialized species (Oatley and Skead 1972, Stiles 1981, Gryj et al. 1990), some of which cannot use sucrose as efficiently as the readily assimilable monosaccharides, glucose and fructose (Martínez del Rio 1990). In these plants the presence of sucrose in nectar can act as a floral filter that excludes valuable potential pollinators. The distribution of floral nectar sugar constituents in bird-pollinated plants appears to be the result of the evolutionary response of plants to two sets of pollinators with contrasting degrees of digestive specialization.

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