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PHYSIOLOGICAL CORRELATES OF PREFERENCE AND AVERSION FOR SUGARS IN THREE SPECIES OF BIRDS[1]

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We studied preferences of red-winged blackbirds, common grackles, and European starlings for the disaccharide sucrose and the monosaccharides glucose and fructose. We also tested the hypothesis that sucrose preference is correlated with activity of sucrase, the intestinal enzyme that hydrolyzes sucrose. All species preferred a 1:1 mixture of glucose and fructose over water at concentrations > 0.75 M. Starlings rejected concentrated solutions of sucrose and lacked sucrase activity. Red-winged blackbirds preferred sucrose solutions at intermediate concentrations (0.35 M) but rejected concentrated ones, whereas common grackles preferred sucrose at all the concentrations offered. Sucrase activity was higher in grackles than in red-winged blackbirds. Blood glucose levels were measured after a meal of a mixture of glucose and fructose or of sucrose. Blood glucose concentration increased in all species after the monosaccharide meal and peaked after about 30 min. In starlings the concentration of glucose in blood remained constant after a sucrose meal, whereas in the other species there was an increase similar to that observed after a monosaccharide meal. Because starlings are mainly insectivorous and blackbirds and grackles are granivorous, we hypothesize that relative activity of intestinal sucrase and hence the preference for sucrose are related to the proportion of complex carbohydrates in a bird's diet.

INTRODUCTION

It has been commonly assumed that preference for substances perceived as sweet by humans is ubiquitous among vertebrates (Frings 1951). This preference, however, has been demonstrated experimentally for only a few species (Jacobs, Beauchamp, and Kare 1978). Another common assumption having little experimental support is that this preference is based on sweet taste (Hellekant 1979). Very different sugars are often considered equivalent, and preference for "sweet" substances is inferred from preference experiments using only one sugar (Hamrum 1953; Warren and Vince 1963; Brindley 1965; Levey 1987). Some experimental evidence suggests that preference for simple sugars in vertebrates may not be so widespread (Jacobs et al. 1978). Preferences for simple sugars in many species may be mediated not only by taste but also by nutritional state and postingestional effects (Shuford 1959; Kare and Ficken 1963; Kare and Maller 1967; Tomljenovic-Borer 1967). Species showing a strong preference for one sugar may exhibit aversion to another (Schuler 1983).

Kare and Mason (1986) and Levey (1987) have suggested that nectarivorous or frugivorous bird species are more likely to prefer sugars than granivorous or insectivorous species and that sugar concentration and composition of fruits and nectar may influence fruit and flower choice. Currently these ideas cannot be substantiated because we know very little of the comparative biology of sugar preferences in birds. Except for Stiles's (1976) work on hummingbirds and Schuler's (1983) research on European starlings (*Sturnus vulgaris*), few species have been tested with a variety of sugars. Especially relevant are the monosaccharides glucose and fructose and the disaccharide sucrose contained in

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fruits and nectars (Chan and Kwok 1975; Baker and Baker 1983).

Rogers and Maller (1973) showed that red-winged blackbirds (*Agelaius phoeniceus*) were indifferent to dilute sucrose solutions but rejected concentrated ones. These authors did not test preference for monosaccharides. Schuler (1983) examined the preferences of *S. vulgaris* for sucrose and the monosaccharides glucose and fructose and found that European starlings strongly rejected sucrose solutions but avidly drank solutions of glucose and fructose. Why might both red-winged blackbirds and starlings reject sucrose solutions? Absorption of the monosaccharides derived from sucrose (i.e., glucose and fructose) requires the hydrolysis of sucrose by the intestinal enzyme sucrase (Semenza 1968). Perhaps avian preference for sucrose is correlated with the presence or absence of sucrase activity. We examined the influence of sucrase activity on preferences of birds for simple sugars. We investigated the preferences of three species of omnivorous birds (European starlings, red-winged blackbirds and common grackles [*Quiscalus quiscula*]) for the disaccharide sucrose and for its constituent monosaccharides (glucose and fructose). We then tested the hypothesis that sucrose averse birds were sucrase deficient by measuring blood glucose changes after a sucrose or a monosaccharide meal, and by quantifying the activity of intestinal sucrase in preparations of intestinal mucosa. We predicted that intestinal sucrase activity in the three species examined would be ranked in the same order as preference for sucrose.

MATERIAL AND METHODS

We captured test birds at least 3 mo before the experiments and acclimatized them to 1.3 × 1.3 × 2-m outdoor cages at a density of 25 birds per cage. Processed chicken feed (Purina Layeena) and water were provided ad lib. during that period. During experiments, birds were housed in a covered aviary under natural temperature and photoperiod conditions. Each was caged individually (cage size: 48 × 48 × 72 cm) and isolated visually. A 5-day acclimation period during which food and water were presented ad lib. preceded each experimental trial. Adult males and females of *Sturnus vulgaris* and *Quiscalus quiscula,* and adult males of *Agelaius phoeniceus,* were used in the experiments. We conducted all experiments during July and August 1986 at the facilities of the Denver Wildlife Research Center, Gainesville Field Station.

PREFERENCE TESTS

Solutions were prepared 12–24 h before the experiments and presented to the birds in closed glass drinking tubes (50 cm long, internal diameter: 1.1 mm). The tubes consisted of a 42-cm vertical section and a lower 7-cm section that was bent upward at a 45° angle; an elliptical hole (2 × 1.5 cm) in the top wall of this last section provided access to the solutions.

Each trial spanned 2 days. On day 1 birds were trained to use the drinking tubes by exposing them in sequence to a tube containing the test solution for 1 h and then for another hour to a tube containing distilled water. Test solution and water drinking tubes were marked with different colored tapes wrapped just above the drinking holes. Color was used because a preliminary set of experiments suggested that the birds had difficulty distinguishing between solutions and water when only positional (left and right) cues were given (see also Schuler 1983). On day 2, test solution and water tubes were presented simultaneously but separated by 10 cm. Colors were alternated systematically between left and right to minimize positional bias. After each trial, consumption was measured to the nearest millimeter and subsequently transformed to volume units. Food and water were removed from the cages during trials.

We used a completely randomized factorial design (2 × 3) with two colors and three osmolarities of test solutions (0.175 M, 0.35 M, and 0.7 M) in all experiments. Eight birds were randomly assigned to each cell (color and concentration combination). The variable used for preference was the amount of test solution consumed divided by total fluid consumption.

A two-way ANOVA was conducted on preference values to determine interactions between color and concentration. If no significant interactions were found (*P*

> .05), the null hypothesis that preference at each concentration was not significantly different from 0.5 (indifference point) was tested using multiple contrasts (Chew 1976; Kirk 1982).

We conducted two experiments with each species. Experiment 1 tested preference for mixtures of glucose and fructose (1:1 ratio) against water; red and green were used to mark the drinking tubes in this experiment. Experiment 2 tested preference for sucrose against water, and white and blue were used to mark the drinking tubes.

BLOOD TESTS

Fifteen birds of each species were used in each test. The birds were fasted overnight and randomly assigned to five groups of three individuals. In one group, birds were sham-intubated while the rest were gavaged with 3 g per kg of bird mass of a 1:1 mixture of glucose and fructose administered in a 1.66-M solution. Blood was obtained from the sham-intubated birds 1 min after intubation. Blood was obtained from birds in each of the remaining groups at 15, 30, 60, or 90 min after intubation. Blood collection and treatment followed Cohen (1966). Samples were centrifuged for 3 min in an International Micro-capillary Centifuge, plasma was separated from cellular elements, and blood glucose concentration (BGC) was measured using a glucose oxidase method (Worthington Statzyme, Cooper Biomedical).

After 10 days we randomly reassigned the same birds to five groups of three individuals and the same procedure was repeated, using a 0.87-M solution of sucrose.

SUCRASE ACTIVITY

Birds were anesthetized using metaphane. The small intestines were excised, chilled in ice-cold 1.02% NaCl, and scraped of mucosa using 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% NaCl) using a Brinkman Polytron homogenizer (25 s at setting 6), and the resulting suspensions were stored in liquid nitrogen. Just prior to sucrase assays, the homogenates were thawed at 22 C and kept on ice. Protein concentration of homogenates was measured using the Bio-Rad kit (Bio-Rad, Richmond, Calif.), with gamma globulin standard.

We assayed sucrase activities with a colorimetric method modified from Dahlquist (1984) and Trinder (1969). Briefly, the reaction was started by adding 33 µl of thawed mucosal homogenate plus 33 µl of sucrose stock (0.056 M sucrose in 0.1 M sodium malate buffer pH 6.0). After incubating at 39 C for 10 min, 1 ml of stop/develop reagent stock was added to arrest the sucrase activity and to measure liberated glucose. Our stop/develop reagent was made by dissolving one bottle of "Glucose (Trinder)-315-100" reagent powder (proprietary mixture of Sigma Chemical Co.) plus 50 ml of 1.0 M Tris/HCl (pH 7.0) and 50 ml of 0.5 M phosphate buffer (NaH_2PO_4/Na_2HPO_4, pH 7.0). Blanks were prepared by separately incubating 33 µl of mucosal homogenate at 39 C for 10 min, after which time 33 µl of 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 µg in 66 µl 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 µmol/min·mg protein. In preliminary tests of the assay, we found that sucrose hydrolysis increased linearly for absorbances lower than 0.8. Incubation times of 10 min consistently gave absorbance values in the linear range.

RESULTS

PREFERENCE TESTS

We found no significant interactions between concentration and color in any of the experiments ($0.09 \leq F \leq 2.63$, df = 2, 47, $P > .05$). All species significantly preferred solutions containing glucose and fructose at 0.35 M and 0.7 M concentrations (fig. 1), but were indifferent to 0.175-M solutions.

Starlings significantly rejected the most

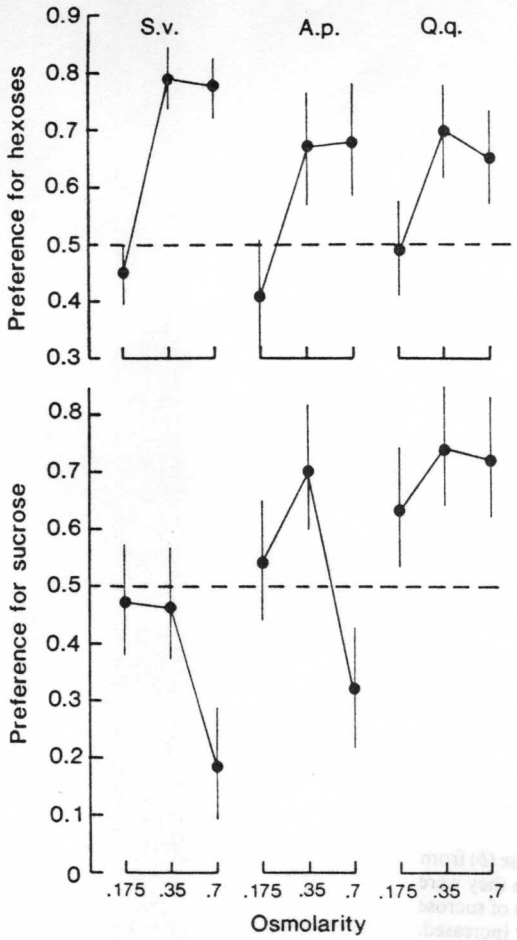

FIG. 1.—Comparative preferences for a mixture of glucose and fructose (above) or sucrose (below) against water. Bars are 95% confidence intervals, and the dashed line at 0.5 indicates no preference. *S.v.* is *Sturnus vulgaris*, *A.p.* is *Agelaius phoeniceus*, and *Q.q.* is *Quiscalus quiscula*.

concentrated of the sucrose solutions (0.7 M) and were indifferent to 0.175-M and 0.35-M solutions (fig. 1). Regardless of concentration, the amount of sucrose solution consumed in day 2 was significantly less than the amount consumed on day 1 ($P < .01$, sign test, fig. 2). In contrast consumption of glucose + fructose solutions by *Sturnus vulgaris* increased significantly for the most concentrated solution (0.7 M) from day 1 to day 2 ($P < .05$, sign test), and was not significantly different for 0.175-M and 0.35-M solutions (fig. 2).

Red-winged blackbirds were indifferent to 0.175-M solutions of sucrose, significantly preferred 0.35-M solutions, and rejected 0.7-M solutions (fig. 1), showing a typical indifference-preference-aversion curve (Harriman and Kare 1966). This result contrasts with Rogers and Maller's (1973) report of a continuously decreasing preference-concentration curve. Common grackles significantly preferred sucrose solutions over water at all concentrations (fig. 1).

BLOOD TESTS

A sharp increase in BGC followed the administration of the glucose-fructose mixture in all species. BGC peaked at about 30 min after intubation and declined thereafter (fig. 3). Red-winged blackbirds and common grackles showed qualitatively similar BGC curves after a sucrose load (fig. 3). These curves are only slightly lower than the ones obtained after a glucose and fructose load. In starlings no elevation in BGC was found after administration of sucrose.

ENZYME ACTIVITY

We measured how sucrose enzymatic hydrolysis varied with position along the small intestine in three individuals of each species (fig. 4). Sucrose hydrolysis per unit milligram of protein decreased distally in common grackles but remained relatively constant in red-winged blackbirds. Sucrase activity was consistently higher in common grackles than in red-winged blackbirds. We were unable to detect any sucrase activity in starlings.

DISCUSSION

This study demonstrated that interspecific differences in preferences for sucrose occur among birds and that these preferences are correlated with relative sucrase activity. The three species studies can be ranked with regard to these preferences as sucrose prone (preferring sucrose to water at all concentrations tested; common grackles); sucrose tolerant (preferring intermediate concentrations of sucrose over water but rejecting concentrated ones; red-winged blackbirds), and sucrose intolerant (rejecting concentrated solutions and developing a conditioned aversion to even diluted concentrations; starlings). Sucrase activity was, as predicted, ranked in the same order as preference for sucrose solu-

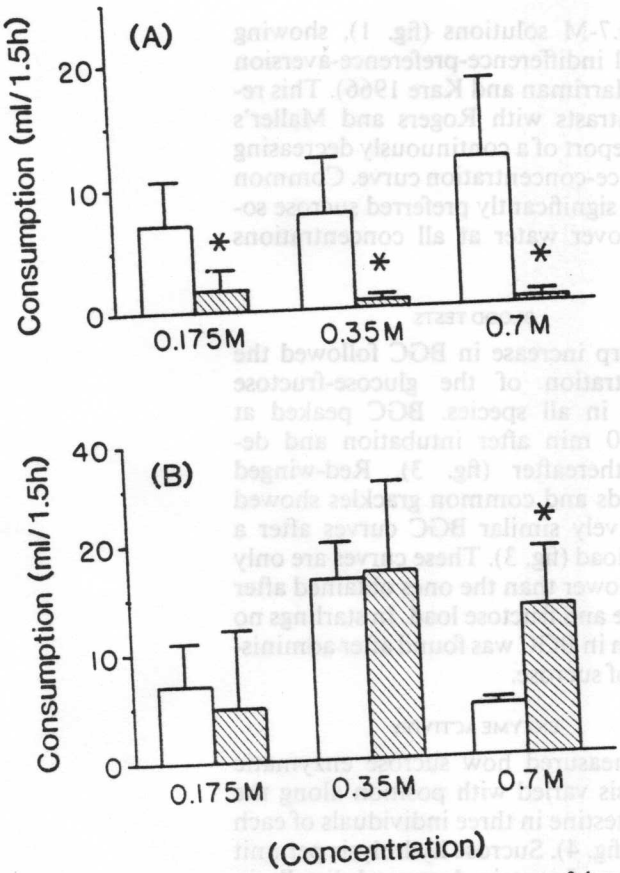

FIG. 2.—*Sturnus vulgaris* changes in consumption of sucrose (*a*) or a mixture of glucose and fructose (*b*) from day 1 (open columns) in which solutions were presented singly and day 2 (stipled columns) in which they were presented paired with water. Bars are standard errors. Note that there was a decrease in consumption of sucrose from day 1 to day 2 but that the consumption of the glucose and fructose either remained equal or increased. Asterisks indicate a significant change in test solution consumption from day 1 to day 2 ($P < .05$, sign tests).

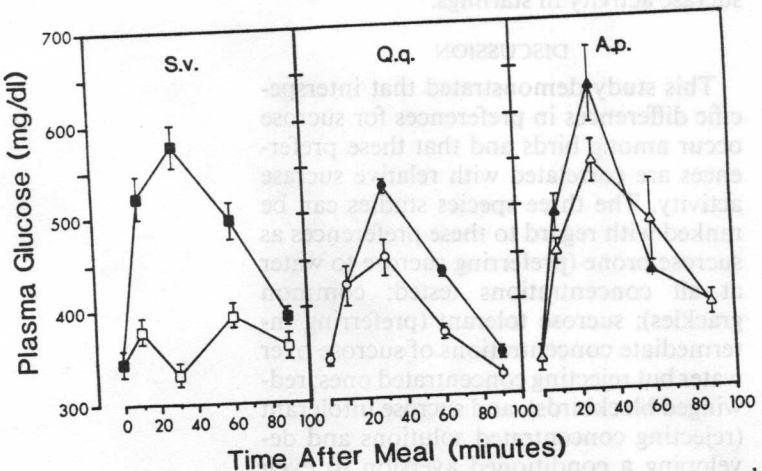

FIG. 3.—Temporal changes in blood glucose concentration after intubation with monosaccharides (closed) or sucrose (open) for *Sturnus vulgaris* (*S.v.*), *Quiscalus quiscula* (*Q.q.*), and *Agelaius phoeniceus* (*A.p.*). Bars are standard errors.

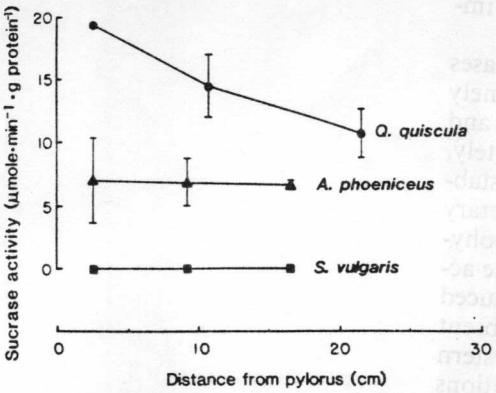

FIG. 4.—Sucrase activity as a function of intestinal position in three species of birds. Activity is normalized to mg of mucosal protein. Points are means, and bars are standard errors.

tions, with common grackles showing the highest activity, red-winged blackbirds intermediate levels, and starlings lacking detectable activity. In animals with disaccharidase deficiencies, the ingestion of substrates is accompanied by both osmotic and fermentative diarrhea (Sunshine and Kretchmer 1964; McMichael, Webb, and Dawson 1965). The development of an aversion for sucrose solutions shown by starlings is probably a result of the effects caused in the intestine by a substrate that can be neither digested nor absorbed.

In contrast to the results reported by Rogers and Maller (1973), we did not find that preference decreased as sucrose concentration increased. Instead, red-winged blackbirds were indifferent to sucrose solutions at low concentrations, significantly preferred 0.35-M solutions over water, and rejected concentrated solutions. The discrepancy between our results on red-winged blackbirds and those reported previously by Rogers and Maller (1973) may be due to differences in the source populations or differences in diets during the acclimation period before the experiments. Rogers and Maller's birds were captured in Maryland, whereas the birds we used were captured near Gainesville, Florida. It is conceivable that there is interpopulation variation in preference resulting from variation in diets. Rogers and Maller fed their birds Purina Game Bird Flight Conditioner (PGBFC), while we fed ours Purina Layeena (PL). PGBFC is a high-protein diet (>30% crude protein) and does not include molasses products (containing sucrose) in its composition, whereas PL contains less protein (>16%) and includes molasses products (data from the feed bags). Rosenweig et al. (1968) and Stifel et al. (1968) have shown that dietary levels of carbohydrates result in changes in jejunal glycolytic enzymes in humans and rats, and Karasov et al. (1983) showed that a high-carbohydrate diet induces intestinal monosaccharide transport. It is very likely that the adaptive processes taking place whenever an animal changes its diet will result in preference changes. However, since all the birds used in our experiments were fed exactly the same diet for an extended period of time, the interspecific enzyme activity differences found are not just physiological adaptations to a particular diet but probably possess a strong genotypic component.

Hanson and Parsons (1976) and Riesenfeld et al. (1980) have shown in the chicken (*Gallus gallo*) that part of the glucose absorbed after a meal is converted to lactate in the intestinal wall. The observed increase in BGC after a glucose-containing meal, therefore, is not an absolute indicator of the amount of glucose that is absorbed, and the technique is useful only for comparative purposes. As shown by the data, it serves only to distinguish sucrose digestors (species or individuals) from nondigestors (see Newcomer et al. [1975] for the performance of a similar technique used to detect lactase deficiency in humans).

The variations in sucrase activity found among European starlings, common grackles, and red-winged blackbirds may be correlated with their feeding habits in nature. Although the three species used in the experiments are largely omnivorous, the proportions of insects, grain, and fruit they eat vary widely among them. Common grackles and red-winged blackbirds include large amounts of grains and seeds in their diets, especially during the winter and fall (Beal 1900; Martin, Zim, and Nelson 1951), whereas European starlings are much less granivorous and have insects and fruit as the main components of their diets, consuming only small amounts of grain or grain products during the winter

(Martin et al. 1951; Kalmbach and Gabrielson 1921). Starlings show lower levels of activity of other intestinal carbohydrases such as maltase and isomaltase than the other two species (Martinez del Rio and Stevens, unpublished data) and have been shown to fare poorly on high-carbohydrate grain diets (Taitt 1973; Thompson and Grant 1968). Berthold (1976) has suggested that many temperate bird species use fruit as a nutritional supplement to either insects or grain (see also Martin et al. 1951). The pulp of most bird-dispersed fruits is rich in glucose and fructose but contains only small amounts of sucrose (whereas fruits used for human consumption tend to be richer in sucrose; Baker and Baker 1986). Starlings can include many species of fruits in their diets precisely because fruits either lack sucrose or contain only small amounts of it. By acting as discriminating consumers, birds may have influenced the sugar composition of the fruits they consume and whose seeds they disperse. The preferences of fruit-eating birds for different sugars and the distribution of sucrase among them may have important coevolutionary consequences.

The distribution of disaccharidases among mammals and birds is extremely heterogeneous (see Semenza 1968; and Vonk and Western 1984). Unfortunately, too few species have been assayed to establish a clear relationship between dietary habits and the activity of various carbohydrases. Data suggest, however, that the activities of specific enzymes are reduced when their substrates are rare or absent from an animal's diet (Vonk and Western 1984). Our results indicate that variations in sucrase activity, presumably resulting from genotypic adaptations to dietary differences, are correlated with the preference of birds for sucrose. It can be hypothesized that insectivorous and carnivorous birds have low levels of sucrase and, therefore, are sucrose averse. Granivorous birds, in contrast, probably have higher sucrase activities and are sucrose tolerant or sucrose prone.

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