

SUCROSE REPELLENCY TO EUROPEAN STARLINGS: WILL HIGH-SUCROSE CULTIVARS DETER BIRD DAMAGE TO FRUIT?¹

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Abstract. European Starlings (*Sturnus vulgaris*) are often pests in commercial fruit crops in North America and Europe. Because starlings lack the digestive enzyme sucrase and cannot digest sucrose, they may develop an aversion to high-sucrose fruits. In water-tube drinking trials, we tested captive starlings with aqueous solutions of 15% (mass/volume) mixed sugars to identify the level of sucrose required to develop a conditioned feeding aversion when digestible sugars are present. In one-tube tests, starlings decreased intake of 11.25 and 15% sucrose solutions relative to their pretest intake of a 15% glucose-fructose mixture. In two-tube tests with sucrose solutions paired against a digestible glucose-fructose solution, starlings decreased preferences for the sucrose solutions as sucrose concentrations increased. These data suggest that the presence of digestible nutrients mitigates the effect of sucrose in sucrase-deficient birds and that a fruit cultivar would require $\geq 11.25\%$ sucrose to repel starlings.

Key words: bird damage; digestion; European Starlings; fruit; integrated pest management; sucrose; vertebrate pest control.

INTRODUCTION

Fruit damage

Some fruit-eating birds, such as European Starlings (*Sturnus vulgaris*) and American Robins (*Turdus migratorius*), are considered agricultural pests because they seasonally feed in ripening fruit orchards and fields. The agricultural damage caused by fruit-eating birds can be significant seasonally and locally (Mott and Stone 1973, Stone 1973, Crase et al. 1976, DeHaven et al. 1974). For example, assessments in early-ripening blueberries in Florida reveal that birds damage 17–75% of the crop by plucking or pecking berries (Nelms et al. 1990); damage to the entire North American blueberry crop may be 10% (Avery et al. 1992). Similarly, 60–100% of early-ripening cherries in the Hudson Valley of New York are subject to bird damage;

yet only 1–12% of late-ripening cherries are affected by birds (Tobin et al. 1991).

Methods to deter birds from feeding in orchards range from visual and aerial scare devices to exclusion, but the effectiveness and economy of these methods are in question (Tobin et al. 1988). Chemical repellents, such as methiocarb, are not available for use in fruit crops because of the potential for hazards to nontarget species (Tobin and Dolbeer 1987, Avery et al. 1993). Agricultural losses to birds are expected to increase in coming years because of increased conversion of land to human uses, increased demand for fresh fruits, and lack of effective means to prevent or reduce bird-feeding activity in orchards and fields. Clearly, an economical, effective, and environmentally safe method to deter fruit-eating birds is needed.

Avian digestive constraint

Robins and starlings are widely distributed in North America, yet are unusual in that they share a common digestive constraint. Neither species can digest the disaccharide sucrose. Lack of the activity of the digestive enzyme, sucrase, occurs in European Starlings (Martínez del Río et al. 1988), American Robins and possibly Gray Catbirds (*Dumetella carolinensis*, Karasov

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and Levey 1990), Rufous-backed Robins (*T. rufopalliatu*), and Orange-billed Nightingale Thrushes (*Catharus aurantirostris*, Martínez del Rio 1990). Perhaps lack of intestinal sucrase activity is a phylogenetic character of the avian families Turdidae, Sturnidae, and Mimidae (Martínez del Rio 1990). When these birds consume sucrose, digestive upset and osmotic imbalance ensue (Schuler 1983, Martínez del Rio and Stevens 1989). Correlated with lack of sucrase activity is expression of a conditioned avoidance of foods that contain sucrose (Schuler 1983, Martínez del Rio et al. 1988, Brugger and Nelms 1991, Brugger 1992).

The digestive constraint may offer a physiological limitation that could be exploited by agriculturalists to prevent or reduce bird damage to fruits. At maturity, small-berried fruits such as grapes, blueberries, cherries, and strawberries contain equal proportions of the sugars glucose and fructose, yet these fruits have very little sucrose (Lee et al. 1970). Although carbohydrates are translocated in the phloem from leaf to fruit in the form of sucrose, the disaccharide is metabolized to glucose and fructose by one or several enzymes during fruit maturation, resulting in minimal sucrose in the ripe berry (Willenbrink 1982). If high-sucrose fruit cultivars could be developed, then perhaps the cultivar would have bird-deterrent qualities (Brugger and Nelms 1991).

In aviary tests, American Robins avoided drinking 15% sucrose solutions, but readily consumed a mixed sugar solution of 7.5% sucrose + 7.5% glucose and fructose (Brugger 1992). To define more clearly the sucrose-deterrent level and extend our knowledge to another species, we quantified the responses of starlings to aqueous mixtures of the three sugars that predominate in small fruits: glucose (G), fructose (F), and sucrose (S). We reasoned that, although food avoidance learning may occur rapidly in sucrase-deficient birds when only sucrose is present, the presence of the digestible nutrients glucose and fructose might mitigate any negative digestive effects associated with sucrose, perhaps by reducing the osmotic gradient between body and gut tissues.

METHODS

Sugar

We prepared five test solutions in glassware with distilled water. Each solution was made of a predetermined proportion of sucrose (S) and a complementary proportion of a 1:1 glucose:fructose (GF) mixture to equal a total sugar concentration of 15% (mass/volume, Bolten et al. 1979). We mixed solutions of 0% S + 15% GF, 3.75% S + 11.25% GF, 7.5% S + 7.5% GF, 11.25% S + 3.75% GF, and 15% S + 0% GF each day prior to testing. We used a control solution (15% GF) to identify baseline consumption of digestible sugars. We obtained fructose (CAS number 57-48-7), glucose (CAS number 50-99-7), and sucrose (CAS number 57-

50-1) from Sigma Chemical Company, St. Louis, Missouri, USA.

Birds

We trapped European Starlings in Alachua County, Florida, in March 1991 and transported them to the research station. Starlings were acclimated to captivity in large outdoor cages (1 × 1 × 1.3 m) that held up to 20 birds. Cages were suspended under a roof yet exposed to ambient air temperatures. Starlings were fed ad libitum a maintenance poultry diet (Flint River Mills Game Bird Starter) and water.

Drinking tests

For testing in each of two experiments, we housed 40 birds in individual cages (dimensions: 61 × 61 × 122 cm). We assigned starlings to treatment groups based on body mass in an attempt to equalize initial masses and therefore baseline consumption among groups (Mason et al. 1989). Mean body mass of starlings was 77.8 ± 4.9 g (mean ± 1 SD, *n* = 80).

We tested each concentration of sucrose with separate one- and two-tube experiments. In each experiment, we used a 5 × 2 completely randomized factorial design, with five sucrose concentrations and two test periods (pretreatment and treatment), to test for starling responses to mixed sugars. We tested eight birds per sucrose concentration.

The one-tube test consisted of offering solutions in only one glass tube. This procedure tests for physiological tolerance by starlings for each of the sugar solutions. The two-tube test consisted of offering starlings two tubes placed 10 cm apart at the back of the cage. One tube contained a test solution and the other contained a control solution of the 15% GF mixture. The position of the sucrose-containing tube was arbitrarily assigned and held constant among days of testing (Pick and Kare 1962). We reasoned that the position of fruit cultivars would be constant on a farm, thus the method of allowing birds to associate treatment with position was relevant to this test. This procedure tests for relative preferences for one solution over the other. We calculated a sucrose solution preference ratio (Kare et al. 1957) for individual starlings with the equation,

$$\text{preference ratio} = \frac{(\text{consumption of sucrose solution})}{(\text{consumption of both solutions})}$$

In each experiment we allowed 6 d for the birds to acclimate to the new cage and test regime. Thereafter, we conducted a 4-d pretreatment drinking test to obtain baseline consumption. This was followed by a 4-d treatment drinking test to obtain repeated measures of drinking responses to sugar solutions. The protocol was similar among training, pretreatment, and treatment days. At 0800 (1.5 h after sunrise), we removed food and water from the cage to encourage drinking during the test. At 0900 we attached clean tubes to the cages and then filled each with a sugar solution. Starlings

were allowed to drink from the tubes for 3 h. We recorded fluid consumption hourly (to within ± 1 mm) and later transformed the value to volume units (± 0.1 mL).

In the one-tube experiment we measured the solute concentration in feces with a pocket refractometer (Hainesworth 1974) during one pretest day and all test days. One hour after testing began we sampled three fecal samples per bird that were collected from an aluminum pan beneath each cage. The pans were not sampled after the 1st h because we could not be sure which droppings were fresh. In both experiments we replaced maintenance food and water in the cages by 1300.

As a cautionary note, refractometer readings include not only the concentration of sugars, but other substances such as salts, lipids, and uric acid (Inouye et al. 1980, White and Stiles 1985). We assumed that the concentration of nonsugar components remained constant among fecal samples, thus interpreted the measurement as an index to fecal sugar concentrations, or an estimate of the proportion of nonabsorbed sugar. The unit of measurement for refractometers is degrees Brix, which corresponds to percentage calculated as mass: mass (Bolten et al. 1979). This differs from the calculation of sugar percentages in test solutions, which uses mass: volume. No correction was applied to refractometer readings to reference fecal sugars to test solutions.

Osmotic concentration

In August 1992, the osmotic concentration of test solutions and the plasma of four European Starlings fed the maintenance diet and water (no sucrose) were determined. Two replicates per bird and three replicates per sugar solution were analyzed. Starling blood was drawn from a clipped toenail into a heparinized microhematocrit tube and centrifuged at 48 000 m/s^2 for 10 min. Test solutions and plasma samples were vaporized in a Wescor 5100B osmometer. The test sugars are nonionizing molecules, thus osmotic concentrations of the test solutions can be calculated directly from molecular masses. Predicted osmotic concentrations of the sugar solutions were calculated from molecular masses of glucose (180.16 g/mol), fructose (180.16 g/mol), and sucrose (342.3 g/mol) and the amounts used in each test solution.

Statistical analyses

We analyzed two response variables per experiment (Experiment 1: total volume of fluid consumed and fecal sugar concentration; Experiment 2: total volume of fluid consumed and sucrose preference ratio). We tested response variables for equality of variances using Bartlett's test (Sokal and Rohlf 1981). To obtain homogenous variances among treatment groups to meet assumptions of statistical tests, we transformed consumption data with the \log_{10} transformation, and sucrose preference ratios with the arcsine transformation.

No transformation improved heteroscedasticity of fecal sugar concentrations.

In both experiments, we predicted that total consumption would decrease with increasing sucrose concentration. We used a two-way repeated-measures ANOVA with sucrose concentration (0, 3.75, 7.5, 11.25, and 15%) and test period (pretest vs. test) as factors to test for the effects of sucrose concentration on the repeated measures of fluid intake by individual starlings. In the one-tube experiment, we predicted that fecal sugar concentrations would increase with increasing sucrose concentration. We used Kruskal-Wallis one-way ANOVA to test the latter prediction. In the two-tube experiment, we predicted that starlings would avoid sucrose solutions, thus the sucrose-solution preference ratios would decrease with increasing sucrose concentration. We used a single-sample *t* test to test the null hypothesis that mean sucrose-solution preference did not differ from 0.5.

RESULTS

One-tube tests

Five birds did not drink fluid consistently during the pretreatment period. These data were eliminated from analyses, resulting in unequal sample sizes ($n = 6$ for 0%; $n = 5$ for 3.75%; $n = 8$ for all others). Total fluid intake (in millilitres per 3 h) varied significantly as an effect of sucrose concentration ($F_{12,153} = 3.36$, $P < .001$), test period ($F_{3,58} = 3.5$, $P = .02$), and an interaction of sucrose concentration and test period ($F_{12,153} = 3.75$, $P < .001$). Starlings consumed an average (mean ± 1 SE) of 18.4 ± 0.9 mL/3 h of the digestible glucose and fructose solutions (0% S) in the pretest period. During the test period, mean intake by birds in the 11.25 and 15% S treatment groups declined to $< 30\%$ baseline by the 2nd d of testing (Fig. 1A). It is worth noting that, in both the 11.25 and 15% treatment groups a single bird drank above-average amounts during the test period, thus increasing the mean responses.

Starlings that drank the 0% solution had average fecal sugars of $1.13 \pm 0.73\%$ solutes (mean ± 1 SE; Fig. 1B). Fecal sugars increased with sucrose treatment in the first ($H = 18.9$, $df = 4$, $P = .001$) and second ($H = 19.6$, $df = 4$, $P = .001$, Fig. 1B) days of testing, but not linearly. Starlings that drank $\geq 7.5\%$ sucrose solutions had fecal sugars up to 12%. By the 3rd d of testing mean fecal sugars dropped below 10% in all groups. Sample sizes declined in the final days of testing because several starlings drank little sugar solution and did not defecate.

Two-tube tests

Total fluid intake varied as an effect of test period ($F_{3,68} = 3.06$, $P = .03$), but not sucrose concentration ($F_{12,180} = 0.69$, $P = .76$), or an interaction of sucrose concentration and test period ($F_{12,180} = 1.16$, $P = .35$). In the 0, 3.75, 7.5, and 15% treatment groups, intake

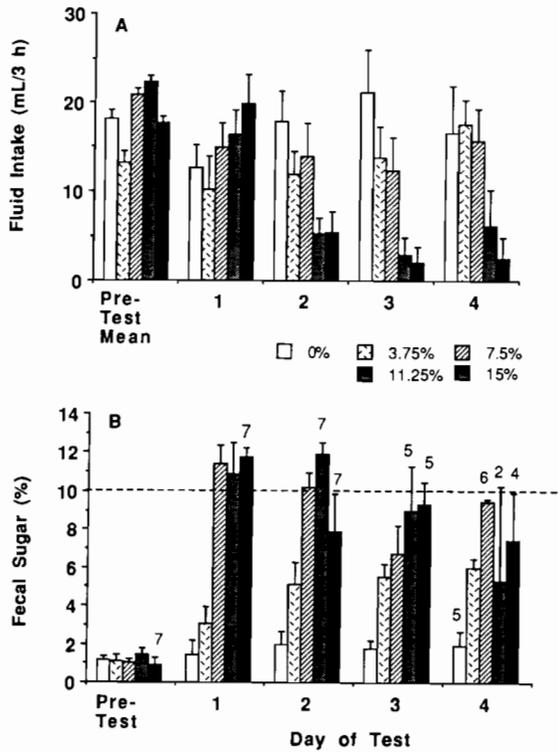


FIG. 1. Results of one-tube drinking tests with European Starlings given 1 of 5 mixed sugar solutions, each totalling 15% sugar (mass/volume). All data are means and 1 SE. (A) Total fluid intake during the pretest period (calculated from 4 d of testing per sugar treatment group) and each of 4 d of testing. (B) Fecal sugar concentrations (% calculated as mass/volume) for one pretest day and four test days. Sample sizes are given (above error bars) when they deviate from those reported in the text.

increased slightly from pretest to test periods (Fig. 2A). In the 11.25% treatment group, intake decreased slightly from pretest to test period (Fig. 2A). On average, starlings consumed 20.4 ± 1.1 mL/3 h (mean \pm 1 SE) in the two-tube experiment.

During the pretest period, sucrose preference ratios did not differ from a null value of 0.5 in each treatment group (Fig. 2B). Mean preference ratios of starlings in the 7.5% group were significantly lower than 0.5 on the 4th d of testing; those of starlings in the 11.25 and 15% treatment groups were significantly lower than 0.5 during each test day. On the final test day, mean preference ratios declined linearly with increasing sucrose concentration (Fig. 2B).

Osmotic concentrations

Osmotic concentrations of the blood of starlings was 348 ± 1.6 mmol/kg of water (mean \pm 1 SE, $n = 4$). Calculated and observed osmotic concentrations of test solutions are given in Table 1. Differences between the two could be due to mixing errors or to machine bias.

DISCUSSION

In both one- and two-tube drinking experiments, European Starlings consistently expressed an aversion to mixed sugar solutions that contained $\geq 11.25\%$ sucrose. In the one-tube test, birds decreased intake of 11.25 and 15% sucrose solutions and in the two-tube test, starlings clearly avoided these sucrose solutions. Our results corroborate previous work with American Robins, which showed an aversion to 15%, but not 7.5%, sucrose solutions (Brugger 1992). Our results also suggest that the presence of digestible carbohydrates (glucose and fructose) mitigate the effects of sucrose. For example, European Starlings avoided 6% sucrose when it was offered in water solutions with no food in the test cages (Martínez del Río et al. 1988), yet readily consumed the 7.5% sucrose when it was offered with digestible glucose and fructose. Additionally, our results suggest that a fruit cultivar would require at least 11.25% sucrose to deter starlings. Many commercial fruits contain a total sugar content of 10–20% fresh mass (Lee et al. 1970), thus the threshold concentration of 11.25% (mass/volume) sucrose is within an attainable range in agriculturally important fruit crops.

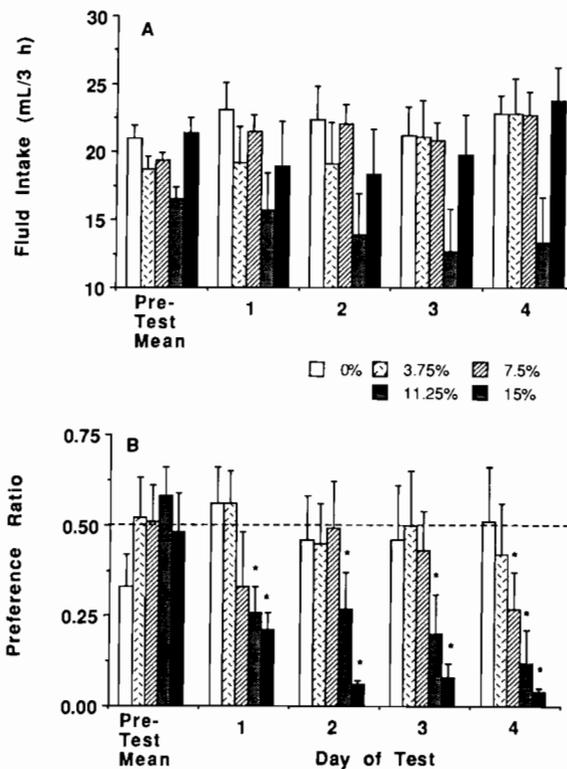


FIG. 2. Results of two-tube drinking tests with European Starlings given 1 of 5 sucrose solutions paired with a 1:1 (mass/volume) mixture of 1:1 glucose:fructose. All data are means and 1 SE. (A) Total fluid intake during the pretest period (calculated from 4 d of testing per sugar treatment group) and each of 4 d of testing. (B) Preference ratios for the sucrose solutions during the pretest period (calculated from 4 d of testing per sugar treatment group) and each of 4 d of testing.

How do laboratory results transfer to feeding behavior in the field? Development of a conditioned feeding aversion is related to the intensity of the stress that an animal experiences and the animal's ability to identify the source of the stress. Osmotic imbalance is probably the primary stress associated with consumption of sucrose by birds that lack sucrase (Martínez del Río et al. 1988). Osmotic imbalance occurs because undigested sucrose molecules increase the osmotic potential within the intestine, thus draw water from the body across intestinal wall into the lumen (Dahlqvist 1962). The bird becomes dehydrated, yet experiences intestinal bloating and malaise. The intensity of osmotic stress might increase with rate of sucrose ingestion, total amount ingested, or availability of drinking water, which could mitigate osmotic imbalance. The contribution of each factor to osmotic stress may change depending on the bird's state of hunger and availability of other food or water resources in a foraging setting.

To exceed the osmotic concentration of starling blood, an aversive solution must be > 350 mmol/kg of solute. Assuming glucose and fructose are absorbed by the gut of starlings, then only the partial osmotic pressure of sucrose will affect the development of an osmotic imbalance between gut and body tissues. For sucrose, a 12% (mass/volume, or 10% mass/mass) solution is sufficient to exceed 350 mmol/kg. Indeed, starlings in the 15% S, one-tube test reduced intake from ≈ 20 mL on the 1st d of testing to 6 mL by the 2nd d, thereby reducing the rate and total amount of sucrose ingested. By the 2nd d, fecal sugar concentrations decreased in this group to a level below the body's osmotic pressure.

Will robins and starlings avoid eating high-sucrose fruits in an agricultural setting? Where high-sucrose fruits are widely planted (little alternative food) and little free water is available, crop protection by a high-sucrose cultivar might be good. However, in a situation where few high-sucrose cultivars are planted, crop protection might be poor if robins and starlings cannot identify the different bushes. In this setting, crop damage even might increase if birds repeatedly peck fruits to identify the high-sucrose cultivars. The ability of starlings and robins to identify the source of sucrose is problematic and needs further research. In laboratory tests starlings, but not robins, distinguished drinking tubes that contained sucrose; the relationship of laboratory responses to field responses by hungry birds is not known. Seasonal nutritional status of the bird (Wheelwright 1988) and nutrient content of the fruit (Herrera 1982, Jones and Wheelwright 1987), the bird's prior feeding experience with different fruit species, availability of alternative foods (Snow 1971, McPherson 1987), accessibility of the fruits (Moermond and Denslow 1983), and social factors (Powell 1985) may affect the bird's feeding responses. Thus the context in which a feeding aversion develops in wild birds foraging in an agricultural setting can be complex and difficult to predict.

Is it reasonable to pursue development of a high-

TABLE 1. Calculated and observed osmotic concentrations of sugar solutions (S = sucrose; GF = a 1:1 glucose-fructose mixture) and the normal blood of European Starlings fed maintenance diet and water.

Sample	Calculated*		Observed total*	
	Total (mmol/kg)	Sucrose (mmol/kg)	\bar{X}	SD
European Starling	348	1.6
Sugar solutions†				
0% S + 15% GF	833	0	806	6.0
3.75% S + 11.25% GF	734	110	724	5.5
7.5% S + 7.5% GF	635	219	651	5.9
11.25% S + 3.25% GF	537	329	552	7.2
15% S	438	438	464	4.6

* Osmotic concentrations are given as millimoles of solvent per kilogram of solute.

† S = sucrose; GF = 1:1 glucose : fructose mixture.

sucrose cultivar with the specific goal of deterring birds in fruit crops? First, the genetic resources are available to develop a high-sucrose cultivar through traditional breeding practices or bioengineering. Variation in the proportion of sucrose in mature fruits has been identified among cherry cultivars (Lee et al. 1970) and blueberry species (K. Koch, R. Darnell, P. Lyrene, University of Florida, Gainesville, unpublished data), suggesting that variation exists in the activities of sucrose-metabolizing enzymes among cultivars and species. Thus, we think that development of a high-sucrose cultivar is an attainable goal.

Second, there is substantial economic incentive to develop high-sucrose, bird-deterrent cultivars. Annual losses to birds in blueberries exceeds \$8.5 million in the United States (Avery et al. 1992); in cherries and grapes annual losses to birds clearly exceed \$1 million (Besser 1985). However, we cannot fully address the question of economics without more information concerning the agricultural impact of fruit-sugar replacement and the genetic systems that express glucose and fructose over sucrose. For example, replacement of glucose and fructose by sucrose may affect economically important characters such as disease resistance, ripening patterns, or storage quality. Without such information, a benefit/cost analysis of fruit-sugar replacement cannot be performed.

It must be noted that we do not expect high-sucrose cultivars to eliminate bird damage to small fruit. These hypothetical cultivars represent a potentially important means for reducing the value of fruit as a food source for robins and starlings. Combined with other crop protection methods, high-sucrose cultivars should result in substantial reductions in bird damage. Despite the obvious data needs, we think that increasing the sucrose content of small-berried fruits is a promising integrated pest management technique for three reasons. Humans prefer the taste of sucrose to that of glucose or fructose (Vettorazzi and MacDonald 1988)

and can easily digest the disaccharide to its constituent molecules (Dahlqvist 1962). Because natural variation in sucrose concentration occurs in some small-berried fruits (Lee et al. 1970), it is reasonable to suggest that plant breeders aim for selection of high-sucrose cultivars. Most important, if effective in a field setting, a high-sucrose cultivar represents an important element in an overall strategy of nonlethal control of bird damage to fruits.

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