Sucrose as a Feeding Deterrent for Fruit-Eating Birds

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ABSTRACT

Economic losses due to bird damage to small fruits such as blueberries, grapes, and cherries can be very high and are expected to increase in the future. The primary sugars in these fruits are glucose and fructose. Sucrose is present in very low concentrations only. Our research has unveiled a physiological trait common to many fruit-eating species in the phylogenetically related families Muscicapidae, Mimidae, and Sturnidae. These birds are unable to digest sucrose because they lack the intestinal enzyme sucrase which hydrolyzes sucrose into glucose and fructose prior to absorption. In cage tests these birds prefer glucose and fructose to sucrose solutions and reject concentrated sucrose solutions and artificial gel fruits made with sucrose. Is it reasonable and feasible to attempt development of highsucrose cultivars with the goal of deterring birds in fruit crops? Variation in the proportion of sucrose in mature fruits is present among strawberry, cherry, and blueberry cultivars. Consequently, genetic resources are available to develop high-sucrose cultivars through traditional breeding practices or bioengineering. We suggest that major fruit-depredating species, such as American robins and European starlings, will avoid eating high-sucrose fruits in an agricultural setting provided that (1) sucrose concentration in these fruits is sufficiently high, (2) there is alternate food available, and (3) high-sucrose fruits are planted in relatively large stands. Despite the obvious need for more data, we believe that increasing the sucrose content of small-berried fruits is a promising direction in integrated pest management research that can result in substantial reductions in bird damage.

KEY WORDS

digestion, digestive enzymes, fruit-eating birds, sugars

INTRODUCTION

Fruit-eating birds, such as European starlings (*Sturnus vulgaris*), American robins (*Turdus migratorius*), and cedar waxwings (*Bombycilla cedrorum*), feed seasonally on cultivated fruits and can cause significant economic damage (e.g., Brown 1974, Mott and Stone 1973). In Florida, 17-75% of the early blueberry crop is damaged by birds (Nelms et al. 1990, Avery et al. 1992); and in the Hudson Valley of New York, 60-100% of the early ripening cherries are damaged by the plucking or pecking of fruit-eating birds (Tobin et al. 1991). Bird damage to blueberries, cherries, and other fruit is expected to increase substantially in the United States due to increased conversion of land to human uses and lack of effective and environmentally safe methods to deter fruit-eating birds. Currently, no chemical repellent is registered for use against birds in fruit crops (Tobin and Dolbeer 1987, Avery et al. 1993a), and the effectiveness and economic feasibility of scare methods and exclusion techniques is questionable (Tobin et al. 1988). It is clear that an economical, effective, and environmentally safe method to deter fruit-eating birds from feeding in orchards is needed.

Research on the digestive physiology and feeding preferences of fruit-eating birds has provided a potential alternative to current available methods to deter fruit-eating birds. Briefly, this research has unveiled a large amount of variation in the preferences of birds for the simple sugars contained in fruit (glucose, fructose, and sucrose). Many fruit-eating species appear to strongly prefer the monosaccharides glucose and fructose over sucrose. Furthermore, the variation in sugar preferences among fruit-eating birds can be explained by relatively simple physiological mechanisms. These results gave rise to the idea of modifying the relative sugar composition of cultivated fruit to reduce its monosaccharide content and increase its sucrose content as a means to reduce bird depredation on cultivated fruits (Brugger and Nelms 1991). Here we review the data on avian sugar preferences, outline the mechanisms that can account for this variation, and use these to evaluate the concept of increasing the sucrose content of small-berried fruits as a management technique to reduce bird damage.

The work reviewed is the result of the interaction between two research groups with contrasting, but complementary, goals. The basic work on sugar preferences and their ecological and physiological correlates was conducted in Martinez del Rio's laboratory with the intent of solving a problem in evolutionary comparative biology (outlined in following sections). Some of the basic themes originally developed were then elaborated by Brugger and Avery for possible management application. Throughout this article we emphasize the usefulness that this interaction between applied and basic perspectives has had on the development of our respective research programs. We use our research as an example of the potential utility and power of adopting a comparative evolutionary perspective in the creation of wildlife management approaches.

ECOLOGICAL CORRELATES OF SUGAR PREFERENCES IN BIRDS

Patterns in the Sugar Composition of Food Plants

The three most common sugars in nectar and fruit pulp are the disaccharide sucrose and the monosaccharides glucose and fructose (Hawker 1985). Analyses of the nectar sugar constituents of over 200 species of bird-pollinated plants revealed that plants pollinated by different groups of birds have contrasting compositions: hummingbird-pollinated plants secrete predominantly nectar containing sucrose, whereas plants pollinated by many (but not all) passerine species secrete nectars containing glucose and fructose (Baker and Baker 1983). This dichotomy is extremely well supported by analyses that control for plant phylogenetic affinity (Martínez del Rio et al. 1992, Bruneau 1995).

Baker et al. (1995) analyzed the sugar content in fruit and discovered a similar pattern. They discovered that the pulp of most bird-dispersed fruits is rich in glucose and fructose but contains only very small amounts of sucrose. With some exceptions, cultivated fruits used for human consumption and mammal dispersed fruits contain significantly higher sucrose proportions (Baker et al. 1995, Freeman and Worthington 1989). The exception to this pattern is significant for the theme of this article: most of the cultivated small juicy fruit cultivars depredated by birds (e.g., grapes [*Vitis*], blueberries [*Vaccinium*], cherries [*Prunus*], blackberries and raspberries [*Rubus*], strawberries [*Fragaria*], and currants and gooseberries [*Ribes*]) are derived from bird dispersed wild species and contain primarily glucose and fructose (Lee et al. 1970).

Why do nectar and fruit-pulp of different plants contain different kinds of sugars? Conventional ecological wisdom suggests that the chemical composition of the rewards that plants offer should be the result of selection by pollinators and seed dispersers that vary in their preferences (Baker and Baker 1983). Natural selection probably molded the characteristics of fruit-pulp to make it attractive to birds. Intense bird depredation of cultivated fruits that retain most of the traits of their bird-dispersed ancestors should not be a surprise to evolutionary-minded biologists!

The limited available data on bird sugar preferences supports the above hypothesis. The known preferences of nectar and fruit-eating birds seem to nicely mirror the composition of their food plants. Many frugivorous birds appear to prefer glucose and fructose (Martínez del Rio et al. 1988, 1989), whereas many frugivorous primates (including humans) strongly prefer sucrose. Hummingbirds strongly prefer sucrose over glucose and fructose, whereas several New World nectar-feeding birds prefer glucose and fructose (Martínez del Rio and Restrepo 1993). Recent evidence suggests that the preferences of Old World nectar-feeding birds may not support the hummingbird/sucrose preference-passerine/monosaccharide preference dichotomy, however. Lotz and Nicolson (1995) reported that a South African sunbird (Nectarinia *chalybea*) strongly preferred sucrose over glucose and fructose. They also reported high sucrose contents in the nectar of some of the Protea flowers that these birds visit and presumably pollinate. It is clear that we need more data on the sugar preferences of Old World nectar- and fruit-eating passerines.

DIGESTION AND THE SUGAR PREFERENCES OF FRUIT-EATING BIRDS

Why Should Fruit-Eating Birds Prefer Glucose and Fructose to Sucrose?

The variation in sugar preferences among frugivores is puzzling. Why should animals show marked preferences among what are often considered readily assimilable sugars which have very similar energetic content? Here we emphasize only a small part of this question: why should fruit-eating birds prefer glucose and fructose to sucrose? The physiological details of sugar assimilation provide an answer to this question. Sucrose is a disaccharide that has to first be hydrolyzed by intestinal enzymes into its monosaccharide constituents, glucose and fructose, in order to be assimilated (Alpers 1987). Glucose and fructose, in contrast, are absorbed intact in the intestine (Semenza and Corcelli 1987). Fruit-eating birds appear to be relatively inefficient at assimilating sucrose, but are extremely efficient at assimilating glucose and fructose (Martinez del Rio and Restrepo 1993).

Two physiological mechanisms seem to account for the relatively inefficient sucrose assimilation in avian frugivores: lack of functional intestinal sucrase activity and extremely fast food passage rates (Karasov and Levey 1990). Some fruit-eating birds lack intestinal activity of sucrase, the enzyme responsible for the hydrolysis of sucrose into glucose and fructose in the intestinal brush-border membrane (Martínez del Rio 1990). Lack of functional sucrase activity has been reported in several fruit-eating passerines (Figure 1). All the species reported lacking intestinal sucrase activity are in the families Sturnidae, Mimidae, and Muscicapidae (Martinez del Rio 1990, unpubl. data). Molecular evidence established that these three families are closely related and form part of a single monophyletic lineage (Sibley and Ahlquist 1984, 1990; Figure 1). Because these families include a very large number of fruit-eating species worldwide (Snow 1981), their evolutionary impact on fruitbearing plants is probably important (Martínez del Rio et al. 1992).

Lack of sucrase activity seems to be a shared derived trait of the lineage which includes robins, starlings, and catbirds (the sturnid-muscicapid lineage sensu Sibley and Ahlquist 1984). This finding highlights the predictive values of phylogenetic data and the importance of evolutionary biology to applied biologists. The physiological and behavioral traits of a large number of birds can be predicted from their taxonomic affiliation (assuming of course that taxonomy accurately reflects phylogenetic affinities, Malcarney et al. 1994). In following sections we will argue that the success of increasing sucrose in fruit as a management technique depends on the degree to which it reduces the palatability of fruit to birds. Thus, knowledge about the phylogenetic affinities of the birds towards which this method is targeted is important.

Lack of sucrase activity is an extreme physiological trait that leads to the complete inability to assimilate sucrose. Some fruit-eating birds show intestinal sucrase activity and hence are able to assimilate sucrose albeit inefficiently. The fast passage rates of these frugivores (Karasov and Levey 1990) may preclude the efficient hydrolysis and absorption of sucrose relative to the hexoses glucose and fructose (Martínez del Rio et al. 1989, Levey and Grajal 1991). Afik and Karasov (1995) provide a good example of the tradeoff between the assimilation of complex

substrates and food passage rate. These authors acclimated omnivorous yellow-rumped warblers (*Dendroica coronata*) to either an insect or a fruit diet and then measured retention time and the efficiency with which birds assimilated glucose and sucrose. They found significantly shorter food retention times and lower sucrose assimilation efficiency in birds feeding on a fruit diet than in birds feeding on an insect diet. Glucose assimilation efficiency was high (~90%) regardless of diet (Figure 2).

Behavioral and Physiological Consequences of Sucrose Assimilation

The difference between "asucrotic" birds which are unable to assimilate sucrose and birds which can assimilate it, albeit inefficiently, is relevant in the context of management to reduce bird damage to cultivated fruits. In this section we outline some of the differences in the behavioral and physiological responses of these two groups of birds when confronted with sucrose-containing food. To highlight these differences, we compared the responses of gray catbirds (*Dumetella carolinensis*) and cedar waxwings to a combination of behavioral and physiological tests designed to diagnose deficiency of intestinal sucrase activity in birds (Malcarney et al. 1994). Catbirds lack intestinal sucrase activity (Malcarney et al. 1994),

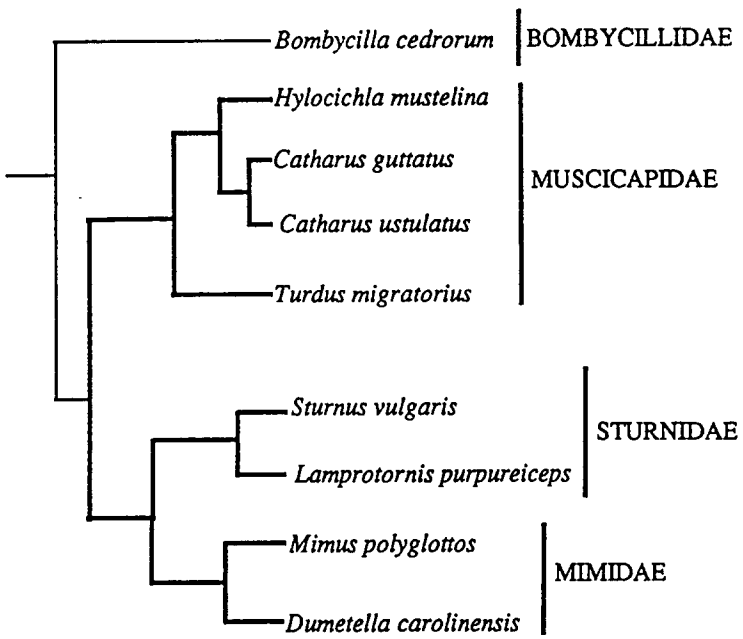

FIGURE 1. Schematic representation of phylogenetic relationships of bird species in the superfamily Muscicapoidea after Sibley and Ahlquist (1990). The phylogeny includes only those species for which the ability to assimilate sucrose has been examined (see text for references). All species in the families Muscicapidae, Sturnidae, and Mimidae examined so far are unable to assimilate sucrose. Cedar waxings can assimilate sucrose.

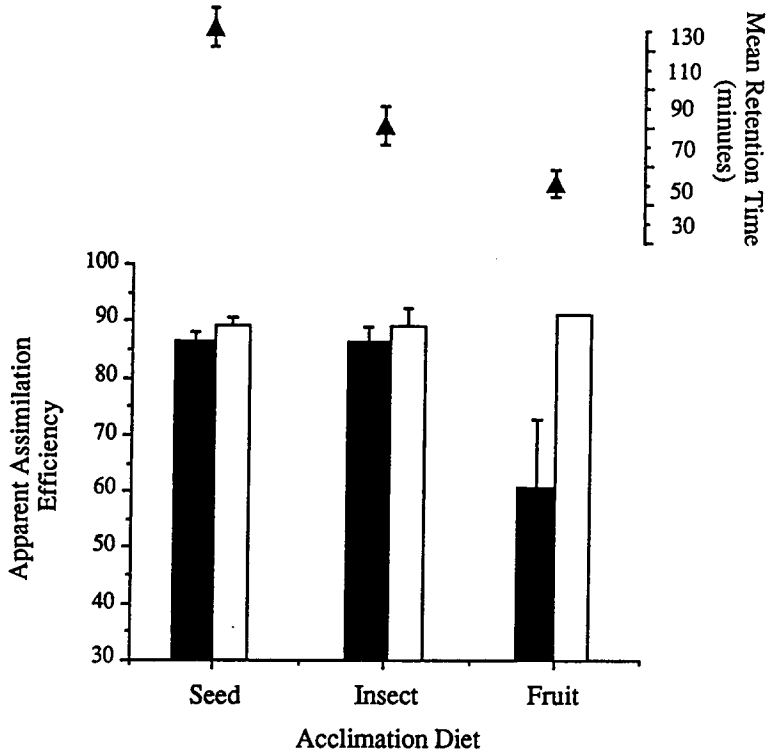

FIGURE 2. Apparent assimilation efficiency of a monosaccharide (glucose; open circles) and the disaccharide sucrose (closed circles) for three different diets which are associated with different retention times of food in the gut of yellow-rumped warblers (*Dendroica coronata*). Note the decreased assimilation efficiency of sucrose at the low mean retention times associated with the fruit diet. After Afik and Karasov (1995). Values are means and error bars are standard errors.

and cedar waxwings can assimilate sucrose (Martínez del Rio et al. 1989). The first set of tests asked whether birds develop an aversion to sucrose. Birds were exposed for 2 consecutive days to food containing 1: 1 glucose and fructose (15% mass/volume; either in solution or in artificial agar cubes) for 2 hr; and in the third day, they were shifted to food in which glucose and fructose had been substituted by equicaloric sucrose (i.e., isomolar in terms of glucose equivalents; Malcarney et al. 1994). Catbirds showed high consumption of glucose and fructose but significantly decreased consumption of sucrose (Figure 3). In contrast, cedar waxwings showed a slight increase in consumption or no significant change when shifted from glucose and fructose to sucrose (Figure 3).

The second test involved measuring the increase in plasma glucose levels (PGL) after birds were challenged with an oral dose of sucrose (3 g/kg). For reference, birds were also challenged with an equicaloric 1:1 glucose:fructose mixture. Sucrose intolerant birds should show nil increases in plasma glucose relative to fasting PGL (Isokosi et al. 1972, Krasilnikoff et al. 1975). Both gray catbirds and cedar waxwings showed an increase in PGL after feeding on glucose and fructose. In contrast, after feeding on sucrose, gray catbirds showed no significant change in PGL relative to fasting levels. Cedar waxwings showed a significant increase (paired t-test, $P<0.001$)

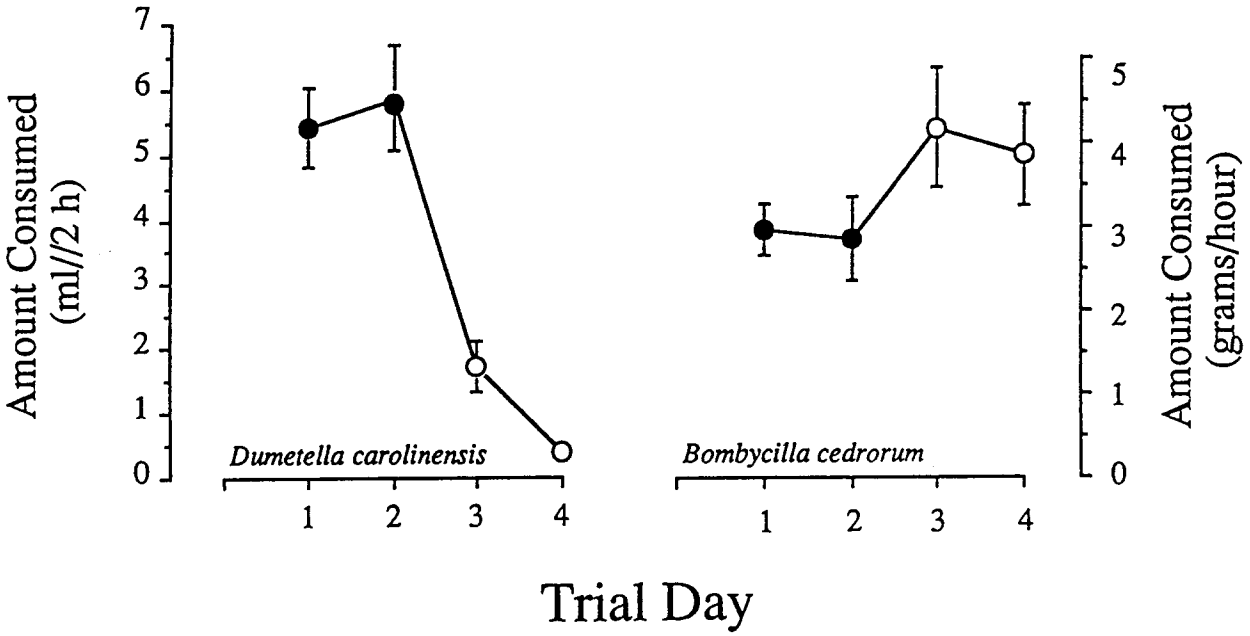

FIGURE 3. Contrasting behavioral responses of sucrose intolerant gray catbirds (*Dumetella carolinensis*) and sucrose tolerant cedar waxwings (*Bombycilla cedrorum*) to one-choice experiments in which food containing a 1:1 mixture of glucose and fructose (closed circles) is substituted by equicaloric sucrose (open circles). Data from Malcarney et al. (1994) and Martínez del Rio (unpubl.). Values above dashed lines are means + standard errors.

after feeding on sucrose, but this increase was lower than that elicited by the glucose and fructose test meal (Figure 4). Results of similar experiments conducted with European starlings, purple-headed glossy starlings (*Lamprotornis purpureiceps*), and American robins indicate that the behavioral and physiological responses of gray catbirds to sucrose are typical of birds lacking intestinal sucrase activity (Brugger 1992, Brugger et al. 1993, Malcarney et al. 1994).

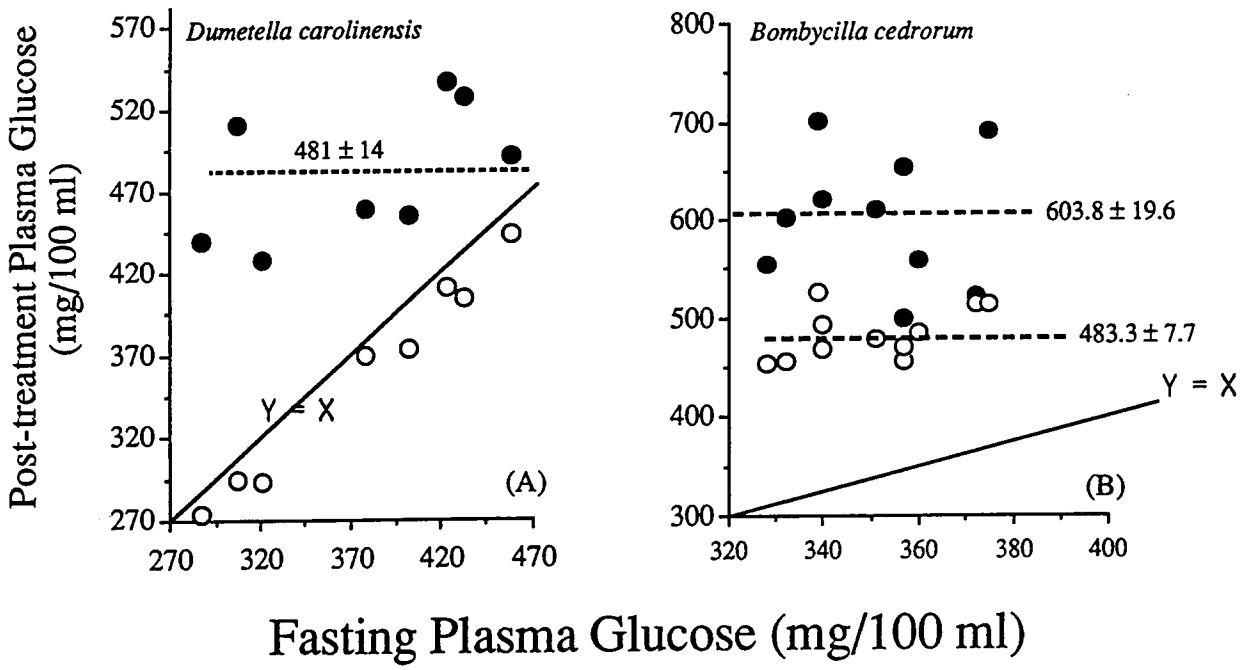

FIGURE 4. Contrasting physiological responses of sucrose intolerant gray catbirds (*Dumetella carolinensis*) and sucrose tolerant cedar waxwings (*Bombycilla cendrorum*) to a single dose of either sucrose (open circles) or equicaloric 1:1 glucose and fructose (dose was 3 g/kg in a 15% weight/total volume solution). Post-treatment plasma glucose was measured after 30 min, when the glycemic response peaks (Martínez del Rio et al. 1988). Data for this figure are from Malcarney et al. (1994) and Martínez del Rio (unpubl.).

The differences in the response of the sucrose-intolerant gray catbirds, and the sucrosetolerant cedar waxwings points out at a clear limitation to the use of sucrose as a deterrent for fruit-eating birds. The method is likely to work only for sucrose intolerant birds. Cedar waxwings assimilate sucrose and do not develop an aversion for it after being exposed to a test meal of concentrated sucrose. Data on the natural diet of cedar waxwings clearly indicates that they are capable of utilizing and regularly feed on sucrose-containing food such as tree sap and flower parts (Witmer 1995).

Mechanism of Sucrose Aversion in Sucrose Intolerant Birds

Understanding why birds lacking intestinal sucrase activity develop an aversion for sucrose-containing food is pertinent from a management perspective. Disaccharide intolerance (e.g., lactose and sucrose intolerance) is a common condition in humans (Semenza and Auricchio 1987). The discomfort produced by the ingestion of disaccharides in humans is produced by osmotic and fermentative diarrhea (Buller and Grand 1990). In small passerine birds with reduced

fermentative capacity in the gastrointestinal tract, the presence of undigested sucrose probably causes only osmotic diarrhea and dehydration. The symptoms exhibited by sucrose-intolerant birds after feeding on sucrose support this hypothesis. American robins increase water consumption when fed sucrose-containing artificial fruits (Brugger and Nelms 1991), and the development of sucrose aversion in sucrose intolerant birds is strongly concentration dependent (Brugger et al. 1993). Birds do not develop an aversion when fed food containing dilute sucrose concentrations, i.e., containing less than 350 mM (Brugger et al. 1993).

Because the effect of sucrose on gastrointestinal function is through osmotic imbalance, its effect depends on the presence of other food constituents with which sucrose is ingested. Provided that the concentration of sucrose is high enough, sucrose solutions and artificial fruits cause a reduction in feeding intake after a single exposure in many sucrose-intolerant species (Martinez del Rio et al. 1988). In contrast, European starlings fed on dry food laced with sucrose do not develop an aversion even when the sucrose content is high (Clark and Mason 1993). The osmotic effects of a solute within the GI tract depend strongly on the water and fiber content of food (Binham 1987). Because sugars in fruit are present in solution or in a gel matrix and because sugars are the primary nutrient in berries, assessing the aversive effects of sucrose as a component of dry food is of questionable ecological relevance.

DEVELOPING A HIGH SUCROSE BERRY: UNDER WHAT CONDITIONS WILL IT REDUCE BIRD DAMAGE?

Will birds avoid eating high-sucrose fruits in an agricultural setting? The research described above provides some answers to this question and a guide to the kind of research needed to answer it. In this section we will first review the possible limitations of the management method and then assess the conditions under which it may work. Finally we describe further experiments needed to properly evaluate the performance of the approach in the field.

What Kinds of Birds Will be Deterred by a High-Sucrose Cultivar?

A high sucrose berry will not reduce the damage done by bird pests that are sucrose tolerant. Although cedar waxwings and other sucrose tolerant fruit-eating birds prefer glucose and fructose to sucrose (Martínez del Rio and Restrepo 1993), they can ingest and assimilate sucrose without any damaging effects (Avery et al. 1995). In short-term feeding trials, cedar waxwings tolerate sucrose well and thus may not be deterred by high sucrose fruit in the field. The strategy is likely to be most successful for crops and geographic locations where the main agents of damage are species belonging to the families Mimidae (catbirds, mockingbirds, and thrashers), Muscicapidae (robins and thrushes) and Sturnidae (starlings).

A high sucrose content cultivated fruit is likely to deter feeding by birds in the sturnid-muscicapid lineage for two interrelated reasons. Sucrose is not assimilated by these animals and consequently (1) its presence in the gastrointestinal tract causes osmotic imbalance, dehydration, and discomfort; and (2) it does not provide an energetic reward to birds and dilutes the nutrient

content of the fruit. The osmotic imbalance and dehydration caused by sucrose are severe enough to deter feeding only at relatively high concentrations (≥350 mM; Brugger et al. 1993). These concentrations are at the high end of the sugar concentrations found in fruit (Witmer 1995a). Selecting for a berry that can deter feeding by birds should have as a goal not only shifting the sugar composition from fructose and glucose to sucrose but also to increase its overall sugar content. Reducing damage by starlings and robins, however, may not require "creating" a fruit that produces aversion in birds. It may be sufficient to make a fruit useless to birds from a nutritional/energetic perspective. This can be achieved by shifting its composition from the readily assimilable sugars glucose and fructose to the unasssimilable sucrose. This fruit would not be avoided because it produces a severe adverse physiological reaction, but because it provides no net benefit.

The Effect of Alternative Food and Suqar Mixtures in Fruit Pulp

To date, research on sugar selection by birds has been conducted in the laboratory in situations where birds have access to either a choice between two sugar-containing foods (typically hexoses versus sucrose; Martínez del Rio et al. 1989, Brugger et al. 1993, Avery et al. 1995) or when they are presented with a single sugar. In the wild, birds encounter fruits that contain mixtures of sugars, and typically they have a choice between fruit and other alternative foods. Furthermore, breeding for high sucrose will probably yield cultivars that retain a small amount of glucose and fructose. We currently lack the information needed to evaluate the reaction of birds to these more realistic mixed sugar situations. Figure 5 shows a conceptual model that explores the relationship between fruit profitability and fruit intake with the fraction of the total sugar in fruit that is comprised by sucrose. The remaining sugar fraction in fruit pulp is assumed to be a completely assimilable 1:1 mixture of glucose and fructose. In what follows we use this simple model to generate hypotheses to be tested in the laboratory as well as to examine the possible effect of introducing cultivars of variable sucrose content to the field.

For a sucrose intolerant bird, the profitability of fruit decreases linearly as the relative sucrose content of fruit pulp increases. Paradoxically, the effect of this decrease in fruit profitability is to increase fruit consumption. As the content of assimilable energy in fruit is decreased, birds have to increase consumption in order to meet daily energy needs (see Witmer 1995b). Fruit consumption decreases as a function of increased relative sucrose content only when the profitability of fruit drops below the profitability of other food items available in the environment (Stephens and Krebs 1986). Fruit consumption probably decreases very rapidly if the sucrose content of fruit pulp exceeds the concentration that causes osmotic discomfort (~350 mM; Brugger and Nelms 1991).

Several features of the model described above deserve emphasis. First, increasing sucrose content slightly can have the paradoxical effect of increasing fruit damage by birds. Second, the shift to altemative foods depends on the availability and relative profitability of alternative foods in the environment. The profitability of a food item includes not only its energy content, but also the time required to find it and handle it (Charnov 1976, Daneke and Decker 1988, Avery et al. 1993b). Cultivated fruits are very profitable to birds because the clumped distribution of the crop

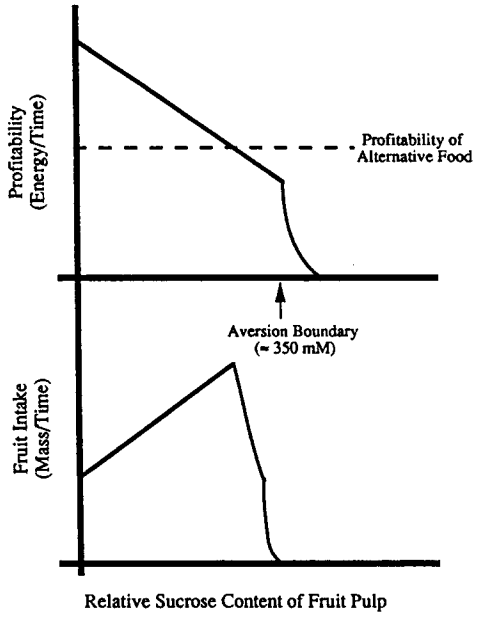

FIGURE 5. Hypothetical relationship between the profitability for birds and their intake rate of fruits containing a mixture of sugars as a function of the relative content of sucrose in fruit.

minimizes the birds' handling and search times. The point at which birds will shift from fruit to an alternative food depends not only on the characteristics of fruit but also on the nature and distribution of alternate food sources (e.g., "spoil crops" planted around orchards, Brown 1974). Third, the reduction in fruit intake caused by increasing fruit pulp sucrose content is due to two complementary mechanisms: (1) a reduction in the profitability of fruit resulting from a decrease in the assimilable content of fruit at low sucrose contents (< 350 mM) and (2) an aversive effect if the sucrose concentration of fruit-pulp is sufficiently high (> 350 mM). We emphasize that we currently lack the experimental data needed to support the details of this model. Some of the qualitative features of our model can be tested in the laboratory. Its relevance for field situations, however, requires providing unrestricted birds with choices at large spatial scales more akin to the conditions experienced by birds in the field. Large spatial scales are needed because the rules used by birds in choosing foods are mediated by the costs of traveling and searching between food patches which, in turn, are dependent on the distance among patches (Pyke 1983).

Is it Possible to Develop High Sucrose Fruits?

Our previous discussion was predicated on the assumption that current horticultural methods can be used to develop high sucrose fruits from high hexose varieties. How realistic is this assumption? Recent research on the sugar metabolism of fleshy fruits indicates significant genotypic variation in the type of sugars accumulated and stored in fruits. For example, some tomato lines store hexoses primarily, whereas others store sucrose (Yelle et al. 1988, 1991). Sucrose accumulation in tomato (*Lycopersicon* spp.) fruits appears to be controlled by one

recessive gene and is associated with low levels of the enzyme acid invertase which hydrolyses sucrose into glucose and fructose in plant tissues (Klann et al. 1993). Recent crosses have introduced the sucrose accumulating trait into low sucrose varieties (Klann et al. 1993). A similar situation has been reported in blueberries (*Vaccinium* spp.), a crop intensely damaged by birds. Darnell et al. (1994) reported significant variation in sucrose content both within and among blueberry species. Furthermore, these authors reported an interspecific negative correlation between sucrose content in fruit pulp and the activity of soluble acid invertase (Figure 6). Substantial variation in sugar content and composition exists in strawberry (*Fragaria* spp.) also (R. L. Darnell, unpubl. data), but the enzymatic basis for sucrose accumulation in this crop remains to be defined. The extent of sucrose accumulation in fruits and the degree of variability for this traits in Vaccinium, Fragaria, and Lycopersicon supports the feasibility of developing high sucrose fruits. To our knowledge no similar studies exploring the genetic variability in sugar types have been done on other cultivated species subject to bird damage.

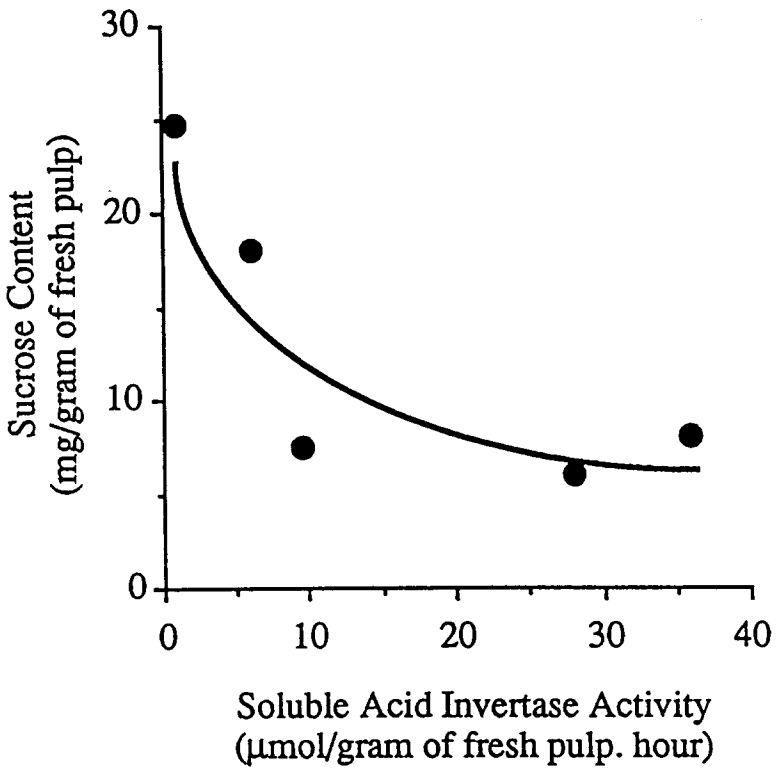

FIGURE 6. Relationship between the sucrose content and the activity of soluble invertase in the pulp of ripe fruit of five *Vaccinium* species. After Darnell et al. 1994. Each point represents the mean value for several determinations.

MANAGEMENT IMPLICATIONS

Humans prefer the taste of sucrose to that of glucose and fructose (Vatorazzi and MacDonald 1988) and can easily digest the disaccharide to its constituent monosaccharides (Alpers 1987). Some bird species that cause serious damage to cultivated small fruits are unable to assimilate sucrose and develop an aversion to it at high concentrations. Natural variation in sucrose content occurs in small-berried fruits. Despite an obvious need for more data on both birds and fruits, it is reasonable to suggest that selection for high sucrose cultivars may represent an important element in an overall strategy of nonlethal and environmentally safe control of bird damage to fruits. We reiterate that increasing sucrose content in fruits by selective breeding is not a magic bullet that will eliminate all bird damage to small fruit. Some species of birds (e.g., cedar waxwings and grackles, *Quiscalus* spp.) will probably not be deterred by high-sucrose fruits, and development of other deterrent methods is essential (Clark and Mason 1993, Cummings et al. 1995). Developing a sucrosebased strategy to reduce bird damage will require more data on the behavior of sucrose depredating birds at spatial scales that are much larger than those used routinely in behavioral experiments. It will also require detailed knowledge about the physiological and genetical determinants of sugar composition of fruit, and the creation of selective breeding programs on chosen cultivars. These research programs are not easy nor cheap. The potential payoff is a long-term reduction of bird damage with minimal environmental impact and with no costs associated with the maintenance of a bird deterrence program.

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