The Auk 112(2):436-444, 1995

COLOR, SIZE, AND LOCATION OF ARTIFICIAL FRUITS AFFECT SUCROSE AVOIDANCE BY CEDAR WAXWINGS AND EUROPEAN STARLINGS

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ABSTRACT.—Fruit choice by birds is affected by many factors, but the interactions between sensory and postingestive cues has received little experimental study. To evaluate how postingestive responses to fruit sugars relate to color and other visual cues, we offered individually caged Cedar Waxwings (*Bombycilla cedrorum*) and European Starlings (*Sturnus vulgaris*) artificial red and green fruits containing 12.8% (g/g) sucrose or hexose (1:1, glucose : fructose) sugars. In 1-h trials with 6-mm-diameter fruits, waxwings preferred hexose to sucrose fruits, regardless of color. Birds given only sucrose fruits ate more than other groups. With 11-mm fruits, patterns of consumption were the same, but clear preferences for hexose over sucrose showed only in 3-h trials. Waxwings given red-hexose and red-sucrose fruits or green-hexose and green-sucrose fruits in two-cup tests learned to prefer the hexose fruits from positional cues. Starlings that initially preferred green learned to prefer red-hexose over green-sucrose fruits after two 3-h trials. Similarly, starlings that initially preferred red learned to prefer green-hexose fruits when paired with red-sucrose fruits. These preferences persisted through three posttreatment trials when both red and green fruits had only hexose sugars. In contrast to Cedar Waxwings, starlings given all-sucrose fruits ate the least, and two of four birds in the all-sucrose group stopped eating fruits altogether. At the level tested, sucrose was a strong associative repellent for starlings, probably because of induced postingestional distress due to their inability to digest sucrose. In contrast, waxwings can digest sucrose, but appear unable to maintain positive energy balance feeding solely on high-sucrose fruits. Development of high-sucrose cultivars may alleviate depredation to fruit crops by sucrose-deficient species like the European Starling, as well as by inefficient sucrose-digesting species like the Cedar Waxwing. *Received 27 January 1994, accepted 2 July 1994.*

VARIOUS STUDIES have demonstrated the importance of readily detectable visual cues such as color, size, and position on fruit selection by birds (Moermond and Denslow 1983, Levey et al. 1984, McPherson 1988, Willson et al. 1990, Avery et al. 1993, Sallabanks 1993). In addition, fruit selection can be affected by postingestive factors such as seed load (Jordano 1984, Levey 1987, Levey and Duke 1992), potentially harmful secondary compounds (Sherburne 1972, Sorensen 1983), or nutrient composition (Schuler 1983, Martínez del Rio et al. 1988, 1989). There is little information, however, on how visual cues interact with postingestive factors to affect frugivore feeding behavior.

Although European Starlings (*Sturnus vulgaris*; Schuler 1983, Martínez del Rio et al. 1988) and Cedar Waxwings (*Bombycilla cedrorum*; Martínez del Rio et al. 1989) may detect the presence of sugar by taste, neither species seems to discriminate among fructose, glucose, and sucrose on that basis. Rather, in these species, preference for hexose sugars (fructose and glucose) over sucrose seems to reflect postingestive effects.

European Starlings lack the intestinal enzyme necessary for hydrolysis and digestion of sucrose (Martínez del Rio and Stevens 1989). Consequently, sucrose ingestion by starlings results in an osmotic imbalance that is distressful or even fatal (Schuler 1983, Martínez del Rio et al. 1988). Birds that experience intestinal distress from ingesting sucrose learn to avoid it thereafter. Cedar Waxwings are able to digest sucrose, but they do it inefficiently, probably because of rapid gut passage rate (Martínez del Rio et al. 1989). The less-efficient digestion of sucrose keeps their blood glucose level low and, consequently, birds that consume sucrose remain hungry. Thus, in choice tests, waxwings learn to prefer hexose sugars over sucrose (Martínez del Rio et al. 1989).

In this study, we examined the interaction between preingestive (color, size, position) and postingestive (sugar composition) cues in fruit selection behavior of Cedar Waxwings and European Starlings. Specifically, we hypothesized that waxwings and starlings would learn to associate sucrose with either red or green artificial fruits, and would reject the appropriate color. For waxwings, we expected that this ability would not be affected by fruit size and, when there was no color difference between hexose and sucrose fruits, waxwings would then discriminate by location. For starlings, we expected, that when sucrose was no longer present in the fruits, the birds would revert to their pretreatment color preference.

We selected Cedar Waxwings and European Starlings because they have been well studied (Schuler 1983, Martínez del Rio et al. 1988, McPherson 1988, Avery et al. 1993), are economically important because they damage cultivated fruit crops (Nelms et al. 1990, Avery et al. 1992, Brugger et al. 1993), and have different physiological responses to dietary sugars (Martínez del Rio and Stevens 1989, Martínez del Rio et al. 1989). Manipulation of fruit sugar composition represents a potentially effective, long-term approach to bird depredation management in berry and fruit crops (Brugger et al. 1993).

Methods

We housed birds by species in communal 1.4 × 1.4 × 1.8 m cages in an outdoor aviary in Gainesville, Florida. The Cedar Waxwings were mist netted in a local blueberry field in April 1993 and tested during May-June 1993. Starlings were decoy-trapped in February 1993 and tested during September-October 1993.

In captivity, waxwings initially received fortified banana mash (Denslow et al. 1987) supplemented with fresh blueberries. The birds were gradually switched from the fruit diet to a dry diet (Kaytee Exact, Kaytee Products, Chilton, Wisconsin) on which they were maintained for the balance of the study. We maintained starlings on F-R-M Layer Crumbles (Flint River Mills, Bainbridge, Georgia).

We prepared artificial fruits according to methods described by Levey and Grajal (1991). Hexose berries were made by mixing 7.5 g of glucose and 7.5 g of fructose with 2 g of agar in 100 ml of boiling water. We added several drops of red or green food coloring and reduced the heat. The warm solution was then injected into pellet molds 6 mm and 11 mm in diameter, allowed to set, and the excess trimmed from the berries. We prepared sucrose berries in the same way, using 15 g of sucrose instead of the hexose sugars. The sugar concentration of 12.8% (g/g) was slightly higher than the total sugar concentration in five blueberry (*Vaccinium*) species (9.3 to 11.8%; Darnell et al. 1994). We determined fruit colors by comparing them to standard charts (Smithe 1975). Red berries corresponded to color 210 (Pratt's ruby), and green berries to color 62 (Spectrum green).

We checked sugar content of the artificial fruits with a hand-held refractometer prior to and just after presenting the fruits to the birds. We also measured fecal sugar concentrations to verify differences in digestibility between sucrose and hexose. We obtained three measurements per bird from each test session and used the median of these readings for comparison. Because refractometer readings reflect a variety of nonsugar constituents (White and Stiles 1985), we regard the readings from fecal samples as only an index to the actual fecal sugar concentrations (Brugger et al. 1993).

Generally, we analyzed actual numbers of fruit eaten. For clarity, however, we calculated preference scores (Kare et al. 1957), and presented these in some figures and tables to illustrate comparisons among treatment groups. For example, a preference for green fruits was the number of green fruits eaten divided by the total number eaten. Preference scores range from 0 (total rejection) to 1.0 (total acceptance). In several cases, we applied two-tailed t-tests to determine if preference scores differed ($P < 0.05$) from the no-preference value of 0.5.

Experiment 1.—We individually caged 24 naive Cedar Waxwings in visually isolated 45 × 45 × 45 cm cages and assigned them randomly to four groups: red hexose versus green hexose (RHGH); red hexose versus green sucrose (RHGS); red sucrose versus green hexose (RSGH); and red sucrose versus green sucrose (RSGS). After five days of acclimation to the test cages during which the standard maintenance food was provided, we presented the birds with 11-mm artificial fruits during 0900–1000 and 1200–1300 EST on each of two consecutive days. Then, after a two-day break when only maintenance food was offered, we repeated the procedure using 6-mm fruits. We presented test fruits (8 red and 8 green of the 11-mm berries, or 20 of each color for the 6-mm fruits) to each bird in a clear plastic cup. Birds were deprived of food for 30 min prior to receiving the test fruits. After 60 min, we scored the number of red and green fruits left in each bird's cup, as well as the number in spillage pans below each cage. We then collected fecal samples and replaced the birds' maintenance food.

We assessed consumption in three-way analyses of variance (ANOVA) with group as the independent factor and trial and color as repeated measures. A separate analysis was made for each size class. Tukey HSD tests (Steel and Torrie 1980) were used to isolate differences among means ($P < 0.05$). Based on previous findings, we made several predictions. We assumed that Cedar Waxwings would initially select red fruits over green (McPherson 1988). Therefore, we expected that birds receiving red fruits with hexose (glucose and fructose) sugars would show the least tendency to eat green fruits, regardless of the green-fruit sugar. Because Cedar Waxwings digest sucrose less efficiently than they do hexoses, however, we anticipated that birds that received red fruits with sucrose would eventually prefer green fruits with hexoses. We predicted that waxwings receiving red-sucrose and green-sucrose fruits would consume the most of any group because they would have to eat more to compensate for less efficient energy extraction.

Experiment 2.—We evaluated the responses of 16 naive Cedar Waxwings to the same four color-sugar combinations as in Experiment 1, but over 3 h instead of 1 h. We used only 11-mm fruit (15 of each color), and conducted one trial daily (0730–1030) for four consecutive days. We reasoned that with longer exposure the birds might discriminate between the two colors of large berries more readily than in the shorter time span of Experiment 1. There were four birds per group, but in all other respects this trial was conducted the same as Experiment 1.

Experiment 3.—Twelve naive Cedar Waxwings were individually caged and randomly assigned to receive 11-mm artificial fruits that were red hexose and red sucrose (RHRS), or green hexose and green sucrose (GHGS). The test procedure was the same as in Experiment 1, except that each bird received two cups placed 36 cm apart instead of one. Prior to the initial feeding trial, we randomly assigned one cup (left or right) in each cage to hold the hexose fruit, and the positions were fixed in each cage for the duration of the four trials.

Although hummingbirds distinguish among types of sugars by taste (Stiles 1976), no such ability has been found in Cedar Waxwings (Martínez del Rio et al. 1989). We expected, therefore, that waxwings would not initially differentiate between hexose and sucrose fruits of the same color. After experiencing both types of sugars, however, the birds would use positional cues to select hexose over sucrose fruits. We tested this in a three-way ANOVA with repeated measures over trials and cups.

Experiment 4.—We tested 12 European Starlings for two days to determine their individual responses to red-hexose and green-hexose berries. We removed maintenance food at 0600 and, at 0700, we gave each bird a plastic cup with 20 red-hexose and 20 green-hexose 6-mm fruits. We recorded the number of fruits in each cup and spill pan after 3 h. We then returned the maintenance food to the birds. We assigned the four birds that ate the most green fruits to the RHGS group. The four starlings that ate the most red fruits comprised the RSGH group, and the remaining four birds received RSGS fruits. Assignments were made systematically rather than randomly to ensure that each starling would consume fruits made with sucrose preferentially at the beginning of the experiment. We conducted the feeding trials on days 3 and 4 as on prior days except that instead of receiving RHGH fruits, the birds received artificial fruits with the newly assigned color-sugar combination. After a two-day break, during which only maintenance food was provided, the birds again received their assigned treatment during trials 5 and 6. We then examined the robustness of any learned avoidance acquired during the birds' exposure to sucrose by offering each bird 20 red-hexose and 20 green-hexose fruits for 3 h on each of three consecutive mornings.

We analyzed berry consumption in a three-way ANOVA with group as the independent factor and repeated measures across color and trials. We did not know how starlings would respond to red and green fruit, but expected that, as birds learned to associate the appropriate fruit color with reward, initial fruit color biases would be overcome. Birds in the RHGS group would learn to prefer red fruits while those in the RSGH groups would learn to prefer green. Color choices of the RSGS group would show little variation. Although we expected that Cedar Waxwings given RSGS fruits would increase berry consumption to compensate for digestive inefficiency, starlings exposed to all-sucrose fruits should decrease consumption due to intestinal distress resulting from their inability to digest sucrose.

RESULTS

Experiment 1.—In 1-h trials, we examined responses of Cedar Waxwings to artificial fruits of two size classes. We expected total consumption to be greatest in the RSGS group because of compensatory feeding due to digestive inefficiency. Total consumption of 11-mm berries by Cedar Waxwings did not differ among groups ($F_{3,20} = 2.07$, $P = 0.137$); however, means ranged from 5.3 fruits per bird ($\pm$SE of 0.4) in the RHGH group to 7.2 (± 0.7) in the RSGS group. Consumption of red berries (4.6 ± 0.2 per bird) exceeded ($P < 0.001$) that of green (1.5 ± 0.2 per bird). There was no group $\times$ color interaction ($P = 0.721$).

Total consumption of 6-mm fruits varied among groups ($F_{3,20} = 3.41$, $P = 0.037$) and across trials ($F_{3,60} = 7.27$, $P < 0.001$; Fig. 1). The RSGS group ate the most fruits (35.8 ± 1.5 per bird), whereas the RHGH birds ate the fewest (24.4 ± 1.6 per bird). The interaction between group and color ($F_{3,20} = 4.76$, $P = 0.012$) was apparent (Fig. 2A). The greatest consumption of red fruits occurred in the RHGS ($\bar{x} = 19.7 \pm 0.1$) and RSGS

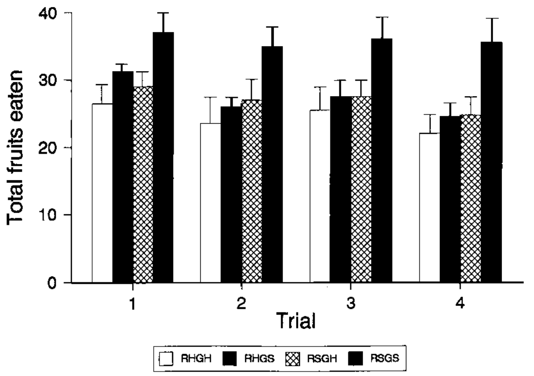

Fig. 1. Mean number of 6-mm artificial fruits eaten by individual Cedar Waxwings (n = 6/group) during four successive 1-h feeding trials. Each bird received 20 red (R) and 20 green (G) fruits that contained 12.8% (g/g) hexose (H) or sucrose (S). Whiskers indicate 1 SE.

($\bar{x}$ = 19.7 ± 0.1) groups, while the RSGH group exhibited the lowest red-fruit consumption ($\bar{x}$ = 10.2 ± 1.5). The three-way interaction ($F_{9,60}$ = 3.96, P = 0.001) reflected the increasing divergence of the RHGS and RSGH groups across trials as the birds learned to associate colors with sugars (Fig. 2A). In each trial, the green preference score of the RHGS group differed from 0.5 (P = 0.017 to 0.02), as did RSGH on trial 4 (P = 0.019). No other score differed from the no-preference level.

Experiment 2.—Here, we extended the daily trial period to 3 h to determine if prolonged exposure to 11-mm fruits would increase the birds' ability to associate colors and sugars. Cedar Waxwings in the RSGS group ate more (24.4 ± 1.4 per bird) than did those in the other groups ($F_{3,12}$ = 2.86, P = 0.081). The interaction ($F_{3,12}$ = 7.80, P = 0.004) between groups and color (Fig. 2B) reflected that the RHGS group ate almost twice as many red fruits ($\bar{x}$ = 12.0 ± 0.7) as green fruits ($\bar{x}$ = 6.3 ± 1.2), while the RSGH group ate an average of 6.3 ± 1.1 red fruits and 11.2 ± 0.5 green fruits per bird. The birds in this test displayed a pattern of preferences similar to that with 6-mm fruits in Experiment 1 (Fig. 2A); however, only the preference score for the RHGS group in trial 3 differed (P = 0.047) from 0.5. Birds in both the RHGS and RSGH groups displayed preferences for hexose, whereas in the 1-h trials (Experiment 1) only the RHGS group did (Table 1).

Experiment 3.—In this experiment, we tested

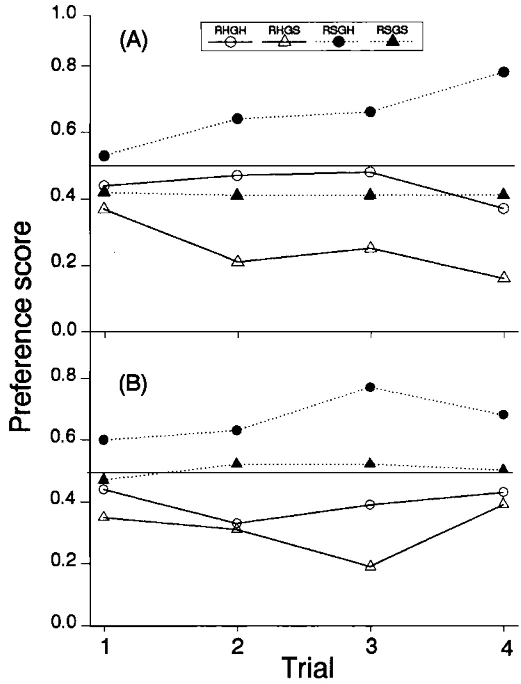

Fig. 2. Preference scores (number green fruits eaten/total eaten) of individually caged Cedar Waxwings exposed to: (A) 6-mm artificial fruits during four 1-h trials; or (B) 11-mm fruits during four 3-h trials. Each bird received red (R) and green (G) fruits that contained 12.8% (g/g) hexose (H) or sucrose (S). A value of 0.5 indicates indifference; lower values suggest a preference for red fruits while higher scores suggest preference for green.

the assumption that without color cues Cedar Waxwings would be able to discriminate hexose fruits from sucrose fruits using positional cues. Overall, waxwings ate equal numbers of red and green fruits (P = 0.781), and consumption did not vary (P = 0.053) among trials. Waxwings ate more hexose berries ($\bar{x}$ = 4.7 ± 0.3) than sucrose ($\bar{x}$ = 2.4 ± 0.3; $F_{1,10}$ = 10.81, P = 0.008). Over time, selection of hexose fruits increased ($F_{3,10}$ = 3.53, P = 0.027) regardless of color (Fig. 3).

Experiment 4.—The ability of European Starlings to associate fruit color with sugar type was examined in this experiment. We anticipated that starlings would readily learn to avoid fruits containing sucrose, regardless of color. Total berry consumption did not differ ($F_{2,9}$ = 0.67, P = 0.534) among groups or between colors ($F_{1,9}$ = 2.77, P = 0.131), but varied ($F_{8,72}$ = 13.37, P < 0.001) among trials (Fig. 4). The lack of a treat-

TABLE 1. Preference scores of Cedar Waxwings given 11-mm-diameter artificial berries in various color ([R] red, [G] green) and sugar ([H] hexose, [S] sucrose) combinations during 1-h and 3-h trials.

Color-sugar combination	Color[a] 1 h	Color[a] 3 h	Sugar[b] 1 h	Sugar[b] 3 h
RHGH	0.22	0.40	—	—
RHGS	0.16	0.31	0.84	0.69
RSGH	0.30	0.67	0.30	0.67
RSGS	0.25	0.50	—	—
RHRS	—	—	0.71	—
GHGS	—	—	0.68	—

[a] Number of green berries eaten divided by total number eaten.
[b] Number of hexose berries eaten divided by total number eaten.

ment × trial interaction ($F_{16,72} = 1.65$, $P = 0.079$) indicated that the groups responded similarly over time. Nevertheless, consumption by RSGS group, highest during the two pretreatment trials, was lowest among the three groups during the treatment period (Fig. 4).

Treatment groups responded differently ($F_{2,9} = 9.64$, $P = 0.006$) to the colors, and the three-way interaction ($F_{16,72} = 7.42$, $P < 0.001$) reflected the divergence in color preference across trials (Fig. 5). Preference scores for each group during days 1 and 2 did not differ ($P > 0.05$) from 0.5 (Table 2). During days 3–6, however, preference scores for RHGS and RSGS reflected avoidance ($P < 0.001$) of green berries (Fig. 5).

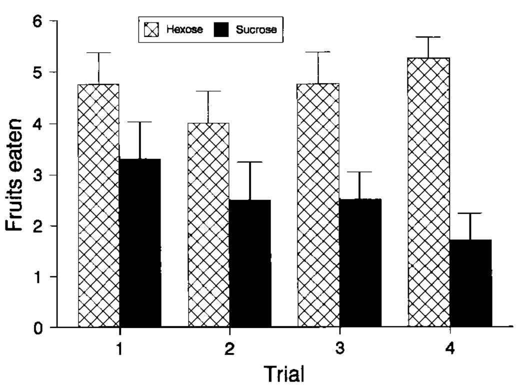

Fig. 3. Mean number of 11-mm hexose and sucrose fruits eaten by individual Cedar Waxwings during four successive 1-h feeding trials. Each bird received either red or green fruits in two cups, one with eight hexose fruits and the other with eight like-colored sucrose fruits. As no difference between colors was found, combined data for red and green groups are presented. Whiskers indicate 1 SE.

Starlings in the RSGH group showed the opposite response, but scores did not differ ($P = 0.53$) from 0.5.

Contrary to expectations, when we presented only hexose fruits during trials 7–9, the RHGS and RSGH groups maintained their learned color preferences ($P < 0.001$) and did not revert to initial values (Fig. 5). Although RHGS birds increased total fruit consumption in the posttreatment period, neither group approached pretreatment levels (Fig. 4).

Total numbers of fruits eaten by RSGS birds varied greatly among individuals (Fig. 6). Bird 2 gradually reduced consumption during the four treatment trials, while birds 3 and 4 stopped eating almost completely. During the three-day posttreatment period, birds 1 and 2 rapidly returned to pretreatment consumption levels but birds 3 and 4 continued to avoid the artificial fruits.

Fecal sugar.—We obtained 136 fecal sugar measurements from 34 Cedar Waxwings and 35 from 12 European Starlings. There were overall differences in fecal sugar among groups in both waxwings ($F_{3,132} = 39.8$, $P < 0.001$) and starlings ($F_{3,31} = 12.21$, $P < 0.001$), reflecting differential absorption of sucrose and hexose sugars (Fig. 7). Among waxwings, fecal sugar concentrations in RHGH and RHGS groups were similar and differed ($P < 0.05$) from the RSGH and RSGS groups which in turn differed from one another. Among starlings, pairwise comparisons showed that RHGH readings differed ($P < 0.05$) from RHGS and RSGS, while RSGH differed ($P < 0.05$) from RSGS only.

DISCUSSION

Cedar Waxwings are able to detect the presence of sugar and to distinguish between artificial fruits with and without sugar, but there is no evidence of their responding to taste differences among sugars (Martínez del Rio et al. 1989). Similarly, Schuler (1983) found no evidence that European Starlings responded to taste differences in selecting among fructose, glucose, and sucrose solutions.

In our trials, waxwings selected fruits initially by color and, as in previous studies, preferred red over green (McPherson 1988). The birds were able to adjust their choices, however, based upon postingestional feedback, so that hexoses were preferred to sucrose, regardless of color.

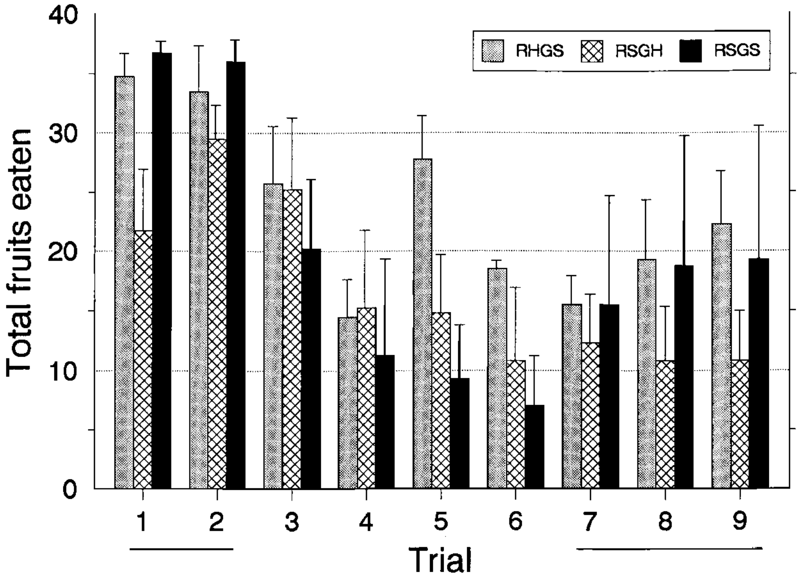

Fig. 4. Mean number of 6-mm artificial fruits eaten by individual European Starlings during nine daily 3-h feeding trials. Each bird received 20 red and 20 green fruits in 1 cup. During trials 3-6, test groups (n = 4/group) received the color-sugar combination indicated. For example, the RHGS group received red-hexose and green-sucrose fruits. During trials 1-2 and 7-9, the fruit contained only hexose sugars. Whiskers denote 1 SE.

The shift in preference to green-hexose fruits over red-sucrose fruits (treatment RSGH) by waxwings was gradual and accomplished more readily with 6-mm fruits than with 11-mm fruits. In 1-h trials (Experiment 1), mean preference scores for 11-mm green-hexose fruits did not exceed 0.36, whereas with 6-mm fruits waxwings displayed a definite preference (0.78) for green-hexose by the fourth trial (Fig. 2A).

At this time the reason for the birds' differential response with fruits of different sizes is not clear. Fecal sugar readings did not differ with fruit size, so waxwings apparently digested fruits of both sizes with equal efficiency. Perhaps the absolute number of fruits eaten, as opposed to the total mass or surface area of the food items, affects a bird's ability to associate physiological responses with fruit color and to alter its food selection behavior accordingly. For birds in the RSGH group, the number of large fruits eaten in 1 h averaged 7, compared to 27 of the smaller fruits. In Experiment 2, RSGH birds averaged 18 fruits eaten over 3 h which permitted adjustments in intake to be manifested, and the birds' performance resembled that with the smaller fruits in Experiment 1 (Fig. 2).

When waxwings were deprived of color as a cue for discriminating between sucrose and hexose fruits, they were able to use position instead. They were equally adept with red and

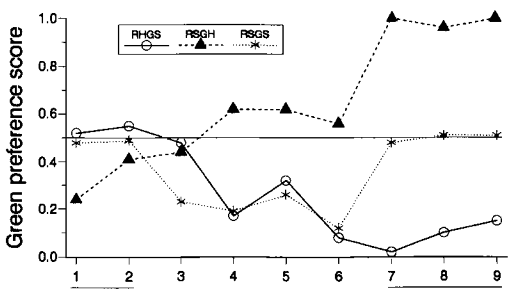

Fig. 5. Mean preference scores (number of green fruits eaten/total number eaten) of European Starlings given 20 green and 20 red 6-mm artificial fruits during nine daily 3-h trials. In trials 3-6, test groups (n = 4/group) received fruits with the color-sugar combination indicated. For example, the RHGS group received red-hexose and green-sucrose fruits. During trials 1-2 and 7-9, fruits contained only hexose sugars. A value of 0.5 indicates indifference; lower values indicate preference for red fruits, while higher values suggest preference for green fruits.

TABLE 2. Green preference scores ($\bar{x}$ ± SE; number of green fruits eaten divided by total number eaten) of European Starlings during pretreatment, treatment, and posttreatment periods. Fruit contained sucrose (S) during treatment period only; otherwise, only hexose (H) sugars were used.

	Treatment group[a]		
Period	RHGS	RSGH	RSGS
Pretreatment (days 1-2)	0.53 ± 0.03	0.32 ± 0.08	0.48 ± 0.01
Treatment (days 3-6)	0.26 ± 0.05	0.56 ± 0.09	0.21 ± 0.06
Posttreatment (days 7-9)	0.09 ± 0.05	0.99 ± 0.01	0.49 ± 0.01

[a] Letter codes: (R) red; (G) green; (H) hexose; (S) sucrose. For example, RHGS refers to presenting red-hexose versus green-sucrose fruits.

green fruits in learning which of two cups held hexose fruits. This level of discrimination was not achieved by waxwings given red-sucrose and green-hexose fruits in the same cup (Table 1). It appears that for waxwings it is more difficult to associate green with hexose than it is to discern which of two locations contains hexose fruits.

Starlings responded rapidly and strongly to artificial fruits having 12.8% (g/g) sucrose. Birds that had initially displayed a preference for red or green shifted to preferring the other color after experiencing sucrose fruits of their initially preferred color. The newly acquired color preferences showed no sign of deterioration even after three trials without sucrose in the fruits. Furthermore, two of four starlings exposed to only sucrose fruits during four 3-h trials stopped eating the fruit completely and did not resume eating during three posttreatment, no-sucrose trials. For starlings, sucrose appeared to act as a strong associative repellent, presumably because of postingestional distress (Brugger et al. 1993). In some birds, avoidance was established in two or three trials, and suppression of consumption persisted even after sucrose was removed.

Our findings support the contention that the development of high-sucrose fruit cultivars may be an effective tool in reducing crop damage (Brugger and Nelms 1991, Brugger 1992). Sucrase-deficient species, such as European Starlings and American Robins (*Turdus migratorius*), should readily learn to avoid feeding on high-sucrose fruits because of the postingestional distress produced (Brugger 1992, Brugger et al. 1993). Furthermore, our demonstration of conditioned avoidance of colored artificial fruits paired with sucrose suggests that the full potential of sucrose as an associative repellent may be exploited by using colors or other conditional stimuli (Clark and Mason 1993).

The increased consumption of all-sucrose fruits by waxwings indicates, however, that

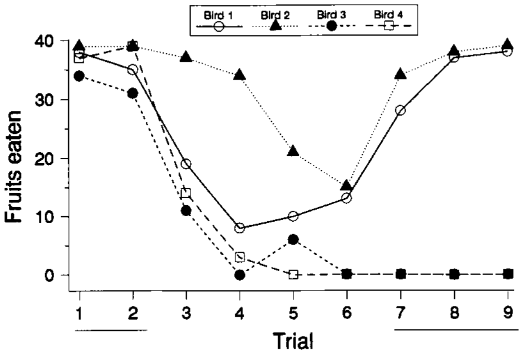

Fig. 6. Total consumption of 6-mm artificial fruits by four European Starlings in the RSGS treatment group during nine 3-h trials. Each bird received one cup with 20 red and 20 green fruits. All fruits contained hexose sugars (12.8% g/g) during trials 1-2 and 7-9, and sucrose (12.8% g/g) during trials 3-6.

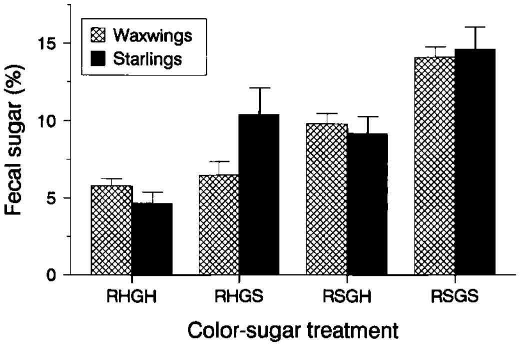

Fig. 7. Estimated sugar concentration (%, g/g) of fecal samples from refractometer readings of 34 Cedar Waxwings and 12 European Starlings fed red (R) and green (G) artificial fruit containing 12.8% (g/g) hexose (H) or sucrose (S). For example, group RHGS received red-hexose and green-sucrose fruits. Whiskers denote 1 SE.

high-sucrose cultivars might receive increased damage by this and similar species that compensate for inefficient sucrose digestion by increasing their fruit intake. This raises the question of whether waxwings can overcome limitations on processing rates (Levey and Grajal 1991) to acquire sufficient energy from high-sucrose fruits.

To maintain constant mass, captive Cedar Waxwings require approximately 100 kJ per day (Holthuijzen and Adkisson 1984). Sucrose and hexose sugars yield approximately 16.7 kJ/g (Mathews and van Holde 1990). Among the waxwings we trapped for this study, several regurgitated recently eaten berries ($\bar{x} = 0.57 \pm 0.04$ g/berry, $n = 20$). Blueberries contain approximately 100 mg sugar/g fresh berry (Darnell et al. 1994). Thus, for a 0.57-g berry, approximately 1 kJ is available. Waxwings are 90% efficient in extracting hexose sugars and 60% efficient with sucrose (Martínez del Rio et al. 1989). Therefore, feeding solely on blueberries, a waxwing would have to eat approximately 111 berries containing hexose or 167 berries containing sucrose to acquire 100 kJ of energy daily.

The berries regurgitated by captured birds averaged 10.8 ± 0.3 mm in diameter ($n = 20$). In Experiments 1 and 2, we recorded feeding rates of 7.2 and 8.1 berries/h, respectively, by waxwings offered 11-mm, all-sucrose fruits. If birds feed for 12 h per day, we estimate maximum consumption by a single waxwing to be 90 to 100 berries per day. Combined with their inefficient digestion of sucrose, this apparent limitation on the birds' rate of processing fruit (Levey and Grajal 1991) suggests that Cedar Waxwings could not maintain a positive energy balance feeding solely on high-sucrose fruits. Long-term feeding trials with captive birds will be needed to evaluate the Cedar Waxwing's physiological and behavioral responses to high-sucrose fruits.

Acknowledgments

We thank K. E. Brugger, E. P. Hill, D. J. Levey, and J. R. Mason for review comments. L. A. Whitehead assisted in preparation of the manuscript, and K. L. Roca supervised care and maintenance of the birds.

Literature Cited

Avery, M. L., K. J. Goocher, and M. A. Cone. 1993. Handling efficiency and berry size preferences of Cedar Waxwings. Wilson Bull. 105:604–611.

Avery, M. L., J. W. Nelson, and M. A. Cone. 1992. Survey of bird damage to blueberries in North America. Proc. East. Wildl. Damage Control Conf. 5:105–110.

Brugger, K. E. 1992. Repellency of sucrose to captive American Robins. J. Wildl. Manage. 56:794–799.

Brugger, K. E., and C. O. Nelms. 1991. Sucrose avoidance by American Robins (*Turdus migratorius*): Implications for control of bird damage in fruit crops. Crop Prot. 10:455–460.

Brugger, K. E., P. Nol., and C. I. Phillips. 1993. Sucrose repellency to European Starlings: Will high-sucrose cultivars deter bird damage in fruit? Ecol. Appl. 3:256–261.

Clark, L., and J. R. Mason. 1993. Interaction between sensory and postingestional repellents in starlings: Methyl anthranilate and sucrose. Ecol. Appl. 3:262–270.

Darnell, R. L., R. Cano-Medrano, K. E. Koch, and M. L. Avery. 1994. Differences in sucrose metabolism relative to accumulation of bird-deterrent sucrose levels in fruits of wild and domestic *Vaccinium* species. Physiol. Plant. 92:336–342.

Denslow, J. S., D. J. Levey, T. C. Moermond, and B. C. Wentworth. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131–134.

Holthuijzen, A. M. A., and C. S. Adkisson. 1984. Passage rate, energetics, and utilization efficiency of the Cedar Waxwing. Wilson Bull. 96:680–684.

Jordano, P. 1984. Seed weight variation and differential avian dispersal in blackberries *Rubus ulmifolius*. Oikos 43:149–153.

Kare, M. R., R. Black, and E. G. Allison. 1957. The sense of taste in the fowl. Poult. Sci. 36:129–138.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. Am. Nat. 129:471–485.

Levey, D. J., and G. E. Duke. 1992. How do frugivores process fruit? Gastrointestinal transit and glucose absorption in Cedar Waxwings (*Bombycilla cedrorum*). Auk 109:722–730.

Levey, D. J., and A. Grajal. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. Am. Nat. 138:171–189.

Levey, D. J., T. C. Moermond, and J. S. Denslow. 1984. Fruit choice in Neotropical birds: The effect of distance between fruits on preference patterns. Ecology 65:844–850.

Mathews, C. K., and K. E. van Holde. 1990. Biochemistry. Benjamin/Cummings Publishing Co., Redwood City, California.

Martínez del Rio, C., W. H. Karasov, and D. J. Levey. 1989. Physiological basis and ecological consequences of sugar preferences in Cedar Waxwings. Auk 106:64–71.

Martínez del Rio, C., and B. R. Stevens. 1989. Physiological constraint on feeding behavior: Intestinal membrane disaccharidases of the starling. Science 243:794–796.

Martínez del Rio, C., R. B. Stevens, D. E. Daneke, and P. T. Andreadis. 1988. Physiological correlates of preference and aversion for sugars in three species of birds. Physiol. Zool. 61:222–229.

MCPHERSON, J. M. 1988. Preferences of Cedar Waxwings in the laboratory for fruit species, colour and size: A comparison with field observations. Anim. Behav. 36:961–969.

MOERMOND, T. C., AND J. S. DENSLOW. 1983. Fruit choice in Neotopical birds: Effects of fruit type and accessibility on selectivity. J. Anim. Ecol. 52: 407–420.

NELMS, C. O., M. L. AVERY, AND D. G. DECKER. 1990. Assessment of bird damage to early-ripening blueberries in Florida. Proc. Vertebr. Pest Conf. 14:302–306.

SALLABANKS, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. Ecology 74: 1326–1336.

SCHULER, W. 1983. Responses to sugars and their behavioural mechanisms in the Starling (*Sturnus vulgaris* L.). Behav. Ecol. Sociobiol. 13:243–251.

SHERBURNE, J. A. 1972. Effects of seasonal changes in the abundance and chemistry of the fleshy fruits of northeastern woody shrubs on patterns of exploitation by frugivorous birds. Ph.D. dissertation, Cornell Univ., Ithaca, New York.

SMITHE, F. B. 1975. Naturalist's color guide. American Museum of Natural History, New York.

SORENSON, A. E. 1983. Taste aversion and frugivore preference. Oecologia (Berlin) 56:117–120.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics, 2nd ed. McGraw-Hill Book Co., New York.

STILES, F. G. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. Condor 78:10–26.

WHITE, D. W., AND E. W. STILES. 1985. The use of refractometry to estimate nutrient rewards in vertebrate-dispersed fruits. Ecology 66:303–307.

WILLSON, M. F., D. A. GRAFF, AND C. J. WHELAN. 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. Condor 92:545–555.