

## FRUIT CHOICES BY CAPTIVE AMERICAN ROBINS<sup>1</sup>

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**Abstract.** Individual variation in fruit choice by captive American Robins (*Turdus migratorius*) was marked, for most of the tested fruit traits (color, nutrient content, seed load), and choices were often contingent on other factors. Robins often favored blue, and sometimes red, artificial fruits over green or yellow ones, although one bird preferred green and rejected blue. Color preference rankings were usually transitive but did not closely correspond with the frequency ranks of fruit colors in nature. Choice tests with naturally occurring polymorphic fruits showed that both color morphs seemed to be palatable and that the robins' preferences did not necessarily reflect the natural frequency of the color morphs. Robins often selected high-lipid and high-glucose fruits when dark in color, but not when the higher nutrient level was a lighter shade of the same color. Slight decreases of accessibility often altered the preference rankings. Robins did not prefer fruits with low seed loads (high pulp/seed ratios). Robins may provide more consistent selection for certain fruit traits, such as color, than several other species previously examined. However, considerable individual variation was evident, and evidence for selection on macronutrient level was mixed.

**Key words:** *Frugivory; American Robin; Turdus migratorius; fleshy fruits; fruit color; fruit characteristics; selective foraging; fruit polymorphism.*

### INTRODUCTION

Phylogenetic or historical factors may determine fruit traits at least to some degree (Herrera 1986, 1992a). However, present-day frugivores may also exert selection pressures on fruit characteristics, although the array of frugivores shifts historically, regionally, and seasonally (e.g., Jordano 1993). Statistical attempts to discern possible selection by dispersal agents on fruit size and shape have yielded differing results (Herrera 1992b, Mazer and Wheelwright 1993). Experimental studies provide one means of detecting the ability of frugivores to exert selection pressure on fruit traits. If frugivore preferences exert strong selection on fruit traits, we should be able to find that fruit choices are quite consistent (for a given set of conditions), both within and among individuals, and not easily altered.

American Robins (*Turdus migratorius*) are seasonally very frugivorous (Martin et al. 1951, Thompson and Willson 1979, Wheelwright 1986, Willson 1986), consuming a wide variety of fruits, ranging from the sweet fruits of *Amelanchier* to the oily fruits of *Cornus stolonifera* (pers. observ.). We examined fruit choices by captive robins in Alaska with respect to an array of fruit

traits (color, lipid and glucose content, and seed load). Three questions were addressed: (1) Do the ranks of color preferences of robins correspond to the ranks of the frequencies of ripe-fruit colors in the field? Evidence that preferences match natural frequencies of fruit colors could indicate that preferences contribute to the maintenance of existing fruit colors, whether such preferences are shaped by experience or are inherent. (2) Do robins forage selectively on fruits in a way that maximizes energy yield per fruit chosen? If so, they are predicted to prefer fruits with higher levels of macronutrients (lipids, glucose) and lower seed loads (higher pulp-seed ratio). (3) For both of the above questions, are the fruit preferences of robins consistent within and among individuals and not easily altered? If so, the case for present-day selection by robins on fruit traits is strengthened.

### METHODS

Robins were captured in mist nets near Juneau, Alaska, in July 1992 and housed individually (but in auditory and visual contact) in cages (2 m × 2 m × 2 m) in an outdoor aviary. They were maintained on a diet of earthworms, fruits (e.g., blueberries, raspberries, cherries, grapes), Science Diet® kitten kibble soaked in fruit juice, and banana-agar mash (Denslow et al. 1987). Six birds were adults (Bird # 2 = female, Birds # 1,

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3, 5–7 = male) and one was a juvenile (# 4). All birds were kept for several days before preference trials began, and all were released at the end of the trials in early September. The robins maintained good body condition in captivity: they usually gained weight during this time, and their furcular fat index was 3 or 4 (on a scale of 0–5) at the time of release.

The same birds were used for all the preference tests. It is possible that the outcome of later tests was influenced by earlier tests. However, all birds have prior histories of food choices, whether in captivity or in the wild; the principal difference is that in captivity the recent history is known. The order of experiments is given, so at least the recent experience of the birds is recorded.

All trials were pairwise, presenting two food types in dishes mounted in front of a perch. For trials in which foods were equally accessible, the test foods were placed in two petri dishes mounted in front of a perch on a pedestal in the center-front of the cage. Each trial consisted of four fruits of type A in one dish and four of type B in the other; the right-left position of the fruits was alternated between trials. Pooled outcomes of four trials/bird comprised each preference test. An observer in a blind recorded the order in which the food types were taken, until half of the offered food was gone, when the trial ended. Repeated, pooled trials with small numbers of fruits were chosen over single trials with larger numbers of fruits because robins generally could not eat more than a few fruits at a time, and the artificial fruits darkened and dried if left too long in the cages. The alternative and perhaps preferred design, in which one fruit of each type is presented per trial, was not used in order to minimize disturbance to the birds. The trials are conservative in that all choices are treated as independent, although when one fruit is taken, fewer of that type remain and thus the chance of the same type being chosen again is diminished. Therefore, any preference that appears in the results occurred despite the continually diminishing number of the favored fruit.

The order in which the experiments were conducted is the order in which they are reported, except that experiments with elderberries were done after the color preference trials (although the results are reported with those for salmon-berry). The order of the pairwise color preference trials was randomly determined, with one constraint: a set of trials with one pair of colors (e.g.,

red vs. yellow) was always followed by a set of trials with the remaining two colors (in this case, blue vs. green). This procedure ensured that all four colors were used before repeating any color in a new combination. To reduce problems associated with repeated use of the same birds for different subsequent experiments, the color cue used was changed at the start of each new experiment.

Most trials used artificial fruits made of banana-agar mash to which commercial food coloring was added. Hot mash was poured into ELISA plates, producing cylindrical pellets of a size easily handled by robins. The banana-agar mash recipe of Denslow et al. (1987), supplemented by three tablespoons of glucose (which seemed to improve palatability to these birds), was used for experiments with color and seed load preferences.

For the color-preference trials with artificial fruits, we used intense shades of red, blue, yellow, and green (Munsell colors approximately 7.5R 3/12, 10B 3/10, 5Y 8/14, 2.5G 4/10 respectively), using commercial food coloring. Pairwise trials with four colors (six pairwise combinations) allowed the determination of transitivity of choices. Transitivity means that choices were internally consistent, a condition necessary for possible directional selection via food preference to occur. If choices are transitive, then A is favored over B, and B is favored over C, and A should be favored over C. Additional experiments used fresh natural fruits of salmonberry (*Rubus spectabilis*), elderberry (*Sambucus racemosa*), and small twisted-stalk (*Streptopus streptopoides*), which are polymorphic for fruit color (red and gold). The fruit morphs do not differ in size but may differ in other traits.

For experiments with lipid and glucose levels, experimental high-nutrient banana-mash fruits were prepared by increasing the amount of lipid (soybean oil) and glucose three times over the basic quantity (relatively low nutrient level). A threefold difference was used to present a marked contrast between high and low nutrient levels. Higher concentrations of lipids changed the texture and structural integrity of the artificial fruits. Natural variation among conspecific fruits is not likely to exceed threefold, but differences among species often vary manyfold. Glucose was used as sweetener, because robins utilize it better than sucrose and tend to avoid sucrose (Karasov and Levey 1990, Brugger 1992, and refs. therein).

Different seed loads were produced by adding one or six seeds of *Rubus spectabilis* to each artificial fruit when the molds were filled; seeds were occasionally visible externally. These seed loads were smaller than the natural range for salmonberry fruits. However, the aim was not to mimic natural fruits; this species of seed was used because it was the largest readily available seed that would still fit inside the artificial fruit at high seed loads. For experiments in which nutrient and seed-load levels were associated with a color cue, the birds were given feeding experience by which they might learn to associate the cue with the fruit type; the experience consisted of exposure to, and opportunity to feed on, fruits exhibiting the experimental cue. The extent of this "training" is indicated in the Results for these experiments; for each day of training, the test foods were available *ad lib.* all day. If the birds were slow to eat the test fruits, other food was removed until the test fruits were eaten.

For all experiments with nutritional value, a single color was used (red for lipid trials, blue for glucose trials, and red again for seed loads), but different intensities (produced by different amounts of food coloring) provided a color cue to nutrient content. By chance (coin-toss), in the initial trials for both lipid level and glucose level, the higher nutrient level was the more intense, darker hue. Darker hue might also signal fruit maturity to birds experienced with natural fruits, most of which darken as they ripen past the young, green stage. Thus, in these experiments, any feeding preferences might indicate either a choice of hue intensity or of nutrient content. Therefore, after the initial series of trials with lipids and glucose, we reversed the color cues so that the fruit type that had been darker was now the lighter hue. The birds were given several days' experience with the new cues and retested. Furthermore, for the seed-load trials, the high-reward (few-seeded) fruits were deliberately made the lighter hue. The difference between dark and light hue was the minimum required for us to distinguish the two fruit types during the trials, allowing for the tendency of the artificial fruits to darken when exposed to air.

The strength of preferences for lipid and glucose levels was examined by reducing accessibility of the fruits favored in the initial trials. Decreased accessibility of a favored food commonly reduces the level of preference for that food (Denslow and Moermond 1982, Moer-

mond and Denslow 1983, Levey et al. 1984). The effect of accessibility on preferences was examined by fastening one food dish 3, 5, or 7 cm below the other in front of a perch inserted into the side wall of the cage.

In addition to the experiments in 1992, two adult females were tested in 1991, using 10 elderberry fruits of each color morph per trial. Preliminary trials on fruit color and composition for these birds are summarized when they supplement the results for 1992. Six juveniles were tested in 1993, with pairwise presentation of one fruit of each color morph of elderberry and twisted stalk, and the first fruit chosen from each pair was recorded.

The conventional level of significance ( $P \leq 0.05$ ) was used (indicated by \*) for  $\chi^2$  tests (see Zar 1984 for heterogeneity tests). In addition, I use a somewhat unconventional level of marginal significance ( $0.05 < P < 0.15$ ) to include a slightly wider spectrum of tendencies to favor one kind of fruit; by this criterion, a ratio of 11:5 is marginally significant by  $\chi^2$  test; marginal significance is indicated by (\*). An alternative approach would have been to use one-tailed  $\chi^2$  tests for cases in which there was an a priori prediction (i.e., a preference for higher nutrient levels). This would make an 11:5 ratio marginally significant ( $P \leq 0.10$ ) by conventional standards. The outcome of these two approaches is similar in detecting marginal significance, but the two-tailed test with a somewhat unconventional criterion allowed the discernment of trends in opposition to the prediction.

## RESULTS

### COLOR PREFERENCES

Presented with equal numbers of red and gold salmonberry fruits in 1992, three birds had no preference, and four preferred the gold morph (three significantly, one marginally). In contrast, six of seven birds preferred the red morph of elderberry, and one had no preference (Table 1). Preferences were significantly heterogeneous for salmonberry but not for elderberry (Table 1). In 1991, one robin preferred red to gold elderberry (39:0 \*), and one had no preference (16:13). The six juveniles in 1993 collectively showed no preference for elderberry (22:20) or twisted-stalk (20:26) color morphs.

Six of seven birds made transitive choices; for these six birds, the average ranks of the four

colors (over all birds) were blue (1.3) > red (2.0) > green (3.2) > yellow (3.5). Five of the six robins preferred blue to the other colors, one preferred red, and all six ranked yellow or green last (Table 2). Significant heterogeneity among birds occurred for choices between blue and yellow, red and green, and green and yellow (Table 2). Preliminary trials in 1991 found that one bird preferred blue, but the other preferred green, and both ranked yellow very low. These results indicate that the robins generally preferred blue, followed by red, and often rejected yellow, but there was considerable individual variation.

#### LIPID PREFERENCES

Series 1 (Cues: dark red = high lipid, light red = low lipid): With equal access, six of seven birds preferred high-lipid fruits (dark red; Table 3). The birds were then tested with increasingly difficult access for the favored fruit. Three birds maintained a "high-lipid" preference even when reaching 7 cm to obtain the favored fruit, two birds lost their preference when required to reach only 3 cm, and one bird had variable responses (Table 3). The remaining bird, which had no preference when access was equal, was tested twice: this bird consistently took high-lipid (dark hue) when it was easy to reach, but had variable responses when it was harder to reach. Significant heterogeneity among birds was present in all choice situations (Table 3). Preliminary trials in 1991 also showed that both birds preferred high-lipid fruits (dark hue).

Series 2 (Color cues reversed: light red = high lipid, dark red = low lipid): When the color cue was reversed, few birds maintained the preferences shown in the first series (with equal access), even after several days of experience with the new cues (Set 1–Set 3, Table 3). Most birds exhibited no significant preferences or occasionally preferred the dark red (now low lipid) fruits. Heterogeneity was observed less often for Series 2 than for Series 1 (Table 3).

#### GLUCOSE PREFERENCES

Series 1 (Cues: dark blue = high glucose, light blue = low glucose): Six of seven birds eventually showed a preference for high glucose (dark blue) over a span of 10 days; one bird was retested and maintained this preference (Table 4). When accessibility of high glucose was progressively reduced for these six birds, one bird lost the preference at 3 cm, one at 5 cm, two at 7 cm, and

TABLE 1. Preferences of captive American Robins for color morphs of salmonberry and elderberry. Experiments done on 22 July 1992 for salmonberry and 5 August 1992 for elderberry. R = red, G = gold fruits.  $\chi^2$  tests for each bird and all birds with each fruit type ( $df = 1$ ); heterogeneity  $\chi^2$  for differences among birds with each fruit type ( $df = 6$ ). Significance levels indicated by asterisks (see text).

Bird	Salmonberry R:G	Elderberry R:G
1	8:8	11:5(*)
2	8:8	15:1*
3	9:7	12:4*
4	1:15*	12:4*
5	5:11(*)	16:0*
6	1:15*	9:7
7	4:12*	14:2*
Total	36:76*	89:23*
Heterogeneity $\chi^2$	16.71*	8.86 ns

two birds had variable responses. No birds maintained a clear preference for high glucose at a 7-cm reach, in contrast to the lipid trials. Individual variation in response to decreased accessibility was pronounced (Table 4).

Series 2 (color cue reversed: light blue = high glucose, dark blue = low glucose): After several days of experience with the reversed color cues, few birds chose high-glucose (light blue) fruits (Table 4). Most birds had no significant preference or sometimes preferred the dark blue fruits (now low glucose). Heterogeneity among birds was more evident in Series 2 than in Series 1. Preliminary trials in 1991 also showed little preference.

#### SEED-LOAD PREFERENCES

Robins showed no general tendency to favor fruits with low seed loads (Table 5). Collectively, they often favored fruits with high seed loads, even after a week of experience with the experimental fruits. Two birds favored fruits with high seed loads (dark hue) fairly consistently, but the others were generally variable or indifferent. Significant individual variation in preferences was evident initially but disappeared as testing continued (Table 5).

#### DISCUSSION

##### COLOR PREFERENCES

There was little evidence of a simple correlation between color preferences of avian frugivores and commonness of fruit colors or presumed familiarity with natural fruit color-morphs. Globally,

TABLE 2. Color preferences of captive American Robins. Data represent the total of four trials/bird. Birds 1–7 were tested on 23 and 24 July, 1992. B = blue, R = red, G = green, Y = Yellow fruits.  $\chi^2$  tests and significance as in TABLE 1.

Bird	B:R	B:G	B:Y	R:G	R:Y	G:Y	Transitivity	Ranks
1	10:6	12:4*	5:11(*)	14:2*	16:0*	11:5(*)	–	
2	1:15*	16:0*	4:12*	16:0*	16:0*	16:0*	+	R > Y > B > G
3	16:0*	15:1*	12:4*	13:3*	12:4*	2:14*	+	B > R > Y > G
4	12:4*	14:2*	16:0*	13:3*	14:2*	14:2*	+	B > R > G > Y
5	13:3*	14:2*	16:0*	11:5(*)	15:1*	15:1*	+	B > R > G > Y
6	13:3*	11:5(*)	13:3*	5:11(*)	15:1*	16:0*	+	B > G > R > Y
7	11:5(*)	14:2*	16:0*	16:0*	16:0*	6:10	+	B > R > G = Y
Total	90:22*	96:16*	82:30*	88:24*	104:8*	80:32		
Heterogeneity $\chi^2$	6.71 ns	4.36 ns	40.36*	21.43*	3.21 ns	44.93*		

most fleshy fruits eaten by birds are red or black (Willson et al. 1989, Willson and Whelan 1990, Wheelwright and Janson 1985). In Southeast Alaska, fleshy fruits of most species are red, but blue and black fruits (e.g., of *Vaccinium*, *Empetrum*) are very abundant (pers. observ.); yellow or gold fruits are less common and no fruits are green when mature. The majority of captive robins ranked blue and red artificial fruits highly, which corresponds to the high frequency of these colors in native fruits, but robins rejected yellow more often than green artificial fruits, which does not correspond to the relative frequency of these hues among ripe fruits in the field.

The experiments with polymorphic fruits also

yielded conflicting results in terms of correlations between preferences and color frequencies in the field. The red morph of elderberry is far more common than the gold morph in southeastern Alaska; I have seen only two gold-fruited plants but thousands of red-fruited plants in four years of field work. Most adult robins preferred the red morph. However, juvenile robins did not prefer red elderberries. In addition, preliminary experiments with varied thrushes (*Ixoreus naevius*) in 1991 (pers. observ.) showed variable results: one consistently preferred red elderberries, one consistently preferred gold, and two shifted from no preference to a preference for gold. In 1993, two juvenile varied thrushes showed no preference

TABLE 3. "Lipid preferences" of captive American Robins. In Series 1, the color cues were dark red for high lipid levels, light red for low lipid levels; equal access experiments were done on 29–30 July, after 1 day of training, 3-cm reach on 30 July, 5-cm reach on 31 July, 7-cm reach on 3 August. In Series 2 the cues were reversed; Set 1 was done on 5 August, after one day of training, Set 2 on 7 August, and Set 3 on 10 August 1992, with training on days between sets.  $\chi^2$  tests (df for heterogeneity tests =  $n$  [birds] – 1) and significance levels as in TABLE 1.

Bird	Series 1				Series 2		
	Equal access Hi:Lo	3 cm reach Hi:Lo	5 cm reach Hi:Lo	7 cm reach Hi:Lo	Equal access		
					Set 1 Hi:Lo	Set 2 Hi:Lo	Set 3 Hi:Lo
1	6:10	16:0*/0:16* <sup>a</sup>	16:0/11:5(*) <sup>a</sup>	16:0*/7:9 <sup>a</sup>	8:8	7:9	9:7
2	16:0*	14:2*	15:1*	15:1*	6:10	10:6	5:11(*)
3	12:4*	11:5(*)	16:0*	14:2*	6:10	7:9	5:11(*)
4	12:4*	5:11(*)	7:9	5:11(*)	7:9	10:6	10:6
5	14:2*	10:6	14:2*	2:14*	8:8	2:14*	8:8
6	15:1*	4:12*	4:12*	0:16*	8:8	2:14*	7:9
7	12:4*	16:0*	16:0*	11:5(*)	4:12*	8:8	11:5(*)
Total	87:25*	60:36*	72:24*	47:49	47:65(*)	46:66(*)	55:57
Heterogeneity $\chi^2$	15.93*	28.50*	33.50*	50.71*	3.36 ns	16.93*	8.21 ns

<sup>a</sup> First ratio presents results when high lipid was in upper dish, easily accessible; second ratio for results when high lipid was in lower dish, harder to reach.

(A. Traveset, pers. comm.). Red-fruited stems of twisted-stalk are much more common than gold-fruited stems, but juvenile robins showed no preference. Red and gold color morphs of salmonberry are both common in southeastern Alaska, although the relative frequency may vary both locally and geographically (J. Zasada, TC. Comet, pers. comm.), but several adult robins preferred the gold morph. Northwestern crows (*Corvus caurinus*) often preferred the red morph, but sometimes favored gold or showed no preference (Willson and Comet 1993).

Although captive adult robins preferred the common red morph of elderberry, both color morphs appeared to be palatable to robins. In the field, gold fruits remained on the bush weeks longer than neighboring red fruits (pers. observ.). These observations could suggest that robins and other frugivores may form a kind of search image for fruits of the more common color, especially with increasing age and experience. Alternatively, adults may have an aversion to any unfamiliar food (neophobia). Either a search image or neophobia would help maintain the high frequency of the common color morph in the elderberry population, but if, for some reason, the rare but apparently palatable gold morph ever became more common, there could be a foraging shift to gold fruits, under either mechanism. The variability of preferences for the salmonberry color morphs for robins (this study) and crows (Willson and Comet 1993) may reflect the naturally high frequency of both color morphs. The extent to which foraging "by expectation" contributes to the maintenance of fruit color polymorphisms remains an interesting question for experimental study. The foraging decisions of frugivores may be important to the evolutionary ecology of fruit color in many species, because many species of fleshy-fruited plants are polymorphic for fruit color (Willson 1986; for southeastern Alaska, at least the three species tested in this study plus *Vaccinium ovalifolium* and *Actaea rubra*).

Captive robins exhibited considerable individual variation in color-preference rankings. However, color choices of robins were somewhat more consistent among birds and more transitive (within bird) than those of northwestern crows (Willson and Comet 1993) or catbirds (*Dumetella carolinensis*) and *Catharus* thrushes (Willson et al. 1990; K. G. Murray, pers. comm.). Captive cedar waxwings (*Bombycilla cedrorum*), foraging in flocks, collectively preferred red and

TABLE 4. "Glucose preferences" of captive American Robins. In Series 1, the color cues were dark blue for high glucose level, light blue for low glucose level; no training prior to 11 August. Dates are given for the first series; the accessibility trials began on 18-20 August 1992, depending on when each bird finished the equal-access trials. In Series 2, the color cues were reversed; trials preceded by five days of training.  $\chi^2$  tests (df for heterogeneity tests =  $n[\text{birds}] - 1$ ) and significance levels as in TABLE 1.

Bird	Series 1										Series 2			
	Equal access										Equal access			
	11 Aug Hi:Lo	12 Aug Hi:Lo	14 Aug Hi:Lo	17 Aug Hi:Lo	18 Aug Hi:Lo	19 Aug Hi:Lo	20 Aug Hi:Lo	3 cm reach Hi:Lo	5 cm reach Hi:Lo	7 cm reach Hi:Lo	25 Aug Hi:Lo	26 Aug Hi:Lo		
1	7:9	10:6	16:0*	—	—	—	—	11:5(*)	7:9	1:15	10:6	2:14*		
2	10:6	7:9	14:2	—	—	—	—	15:1*	12:4*	0:16*	3:13*	0:16*		
3	7:9	10:6	6:10	13:3*	—	—	—	9:7	16:0*	6:10	7:9	10:6		
4	8:8	10:6	3:13*	9:7	14:2*	—	—	6:10	8:8	1:15*	11:5(*)	4:12*		
5	9:7	7:9	5:11(*)	9:7	10:6	9:7	9:7	—	—	—	7:9	8:8		
6	6:10	9:3(*)	—	—	11:5(*)	—	—	15:1*	16:0*	0:16*	5:11(*)	6:10		
7	3:13*	8:8	10:6	9:7	9:7	10:6	11:5(*)	0:16*	3:13*	6:10	2:14*	8:8		
Total	50:62	61:47	54:42	40:24*	44:20*	19:13	30:12	56:40*	62:34*	14:82*	45:67*	38:74*		
Heterogeneity $\chi^2$	7.71 ns	4.69 ns	34:00*	3:00 ns	3.50 ns	0.12 ns	0.50 ns	41:33*	34:33*	10:33(*)	16:93*	19:43*		

TABLE 5. Preferences of American Robins for artificial fruits with different seed loads. Color cues were dark red = high seed load, light red = low seed load. One day of training preceded the first day of trials, and training also occurred on the days between test days.  $\chi^2$  tests and significance levels as in TABLE 1.

Bird	4 Sep Lo:Hi	8 Sep Lo:Hi	10 Sep Lo:Hi
1	3:13*	6:10	5:11(*)
2	1:15*	5:11(*)	4:12*
3	7:9	10:6	6:10
4	7:9	12:4*	6:10
5	4:12*	8:8	8:8
6	12:4*	8:8	8:8
7	6:10	7:9	6:10
Total	40:72*	55:57	41:71*
Heterogeneity $\chi^2$	18.86*	8.71 ns	2.21 ns

rejected green, although the rankings of blue and yellow varied with the experimental set-up (McPherson 1988). It is then plausible to argue that the color preferences of robins (and perhaps waxwings) could provide more directional or stabilizing selection for fruit colors than the other species so far examined.

#### NUTRIENT CHOICES

Most robins favored high-lipid fruits and high-glucose fruits and/or dark-hued fruits; any preference for high nutrient levels was contingent upon hue intensity. A preference for dark hues might reflect a preference for fully matured fruits, which are usually darker than immature fruits. However, robins do not always avoid paler fruits. Wild robins in Illinois often foraged heavily on immature, pink *Amelanchier* fruits, so depleting the crop that no fruits reached the mature, purple hue (pers. observ.). In addition, the majority of outcomes in the second series of lipid trials was not a preference for dark red, as would be expected if the birds were responding simply to hue. Furthermore, the experimental preferences were often lost when accessibility of the favored fruits was reduced. Thus, the preferences were often not very strong, and the strength of the preference varied among individuals. The position of natural fruits on fruit-bearing plants commonly varies at least as much as the experimental positions, and any selectivity for high nutrient levels by wild birds might be contingent on their placement.

When color cues were reversed, preferences seldom shifted to maintain high-nutrient or dark-hue choices, even after several days of experi-

ence. Robins also showed no signs of favoring light-hued fruits that provided higher proportions of pulp (fewer seeds) per fruit, even after several days of training. Instead, most birds showed no preference when high-reward fruits were lighter in hue, suggesting that the birds were responding positively to both hue intensity and nutrient level. An alternative possibility is that they were confused or recalcitrant and never learned the new cues. Only further experiments can distinguish these possibilities. Crows, in contrast, often were capable of switching cues (Willson and Comet 1993).

Stiles (1980) suggested that avian frugivores might prefer high-lipid fruits and found that robins could discriminate between artificial fruits differing by as little as 3% in lipid content (at least at the low end of the range of lipid content) (Stiles 1993). He reported a correlation between the number of fruits of a particular species that were consumed and lipid content of the fruit, as well as a significant preference for higher lipid concentrations in about half of the trials conducted. Field experiments during the migration season in central Illinois, however, showed no preference for high-lipid species of fruit (Whelan and Willson, in press). As emphasized by Martínez del Río and Restrepo (1993) and Whelan and Willson (in press), lipid content of the food is but one factor determining the eventual energy yield to the consumer; digestive utilization of the ingested food, handling/processing time, and nutrient balance are also important variables. Furthermore, several studies have shown that fruit-crop size or other factors are far more important than fruit traits in determining fruit removal (Willson and Whelan 1993). Thus, the potential strength of selection on macronutrient content of fruits remains uncertain.

#### SEED-LOAD CHOICES

The captive robins did not show a preference for high pulp/seed ratios in these experiments. I have suggested that the lack of preference may result from simultaneous, mixed responses to dark hues and high reward levels. However, some other experimental birds have also shown no preference for high pulp/seed ratios. Captive robins in Michigan only sometimes favored fruits that yielded high rates of pulp consumption (Murray et al. 1993). Northwestern crows did not prefer high pulp yield (low seed load) in the aviary or in the field (Willson and Comet 1993). Captive Cedar Waxwings showed no clear tendency to

prefer fruits whose handling characteristics allowed higher pulp consumption (Levey and Grajal 1991), nor did Cedar Waxwings appear to discriminate among fruit species in the field on the basis of pulp/seed ratio (McPherson 1987). These results differ from those of Howe and vande Kerckhove (1980, 1981) for *Virola surinamensis*, in which tropical birds preferentially consumed fruits with high pulp/seed ratios, specifically those for which the high ratio was produced by smaller seeds rather than by larger arils (pulp). Because avian preferences were correlated with small seed size but not with large aril size, Howe and vande Kerckhove suggested that birds might be minimizing the ingestion of indigestible ballast (rather than maximizing the intake per bite). Another factor to be considered is that the avian consumers of *Virola* seeds commonly regurgitate the seed, which averages about 2 cm long, giving the birds immediate feedback about seed size. In contrast, however, captive robins, northwestern crows (Willson and Comet 1993), and waxwings (Levey and Grajal 1991) passed most seeds through the digestive tract, which delays feedback of information about amount of reward per amount of ballast. The faster feedback hypothesized for the *Virola* foragers might permit more selective foraging. Furthermore, regurgitation of seeds rapidly frees space in the digestive tract for the ingestion of additional fruits (Sorensen 1984, Johnson et al. 1985, Levey 1987, Murray et al. 1993) and allows the consumers to increase digestible intake by eating greater numbers of fruits (rather than by choosing those with large arils). Levey and Grajal (1991) showed similar but presumably smaller effects of seed size on passage rates. And finally, only the very largest consumers might be able to regurgitate seeds as large as *Virola* without discomfort, imposing a size limit on the size of the seed ingested, and limiting the seed-handling options of smaller birds.

In sum, robins provide some evidence of potential selection on certain fruit traits. Color preferences appeared to be more transitive and consistent among birds than for other species tested so far, and color choices were also consistent with those of robins tested by Murray et al. (1993). Moreover, lipid/dark hue preferences were less altered by reduced accessibility than were the lipid preferences of crows. However, accessibility did change the preferences of some individual robins and, indeed, a substantial level of individual variation was evident in many of these experiments (Jung 1992, Murray et al. 1993).

Moreover, there was no indication that robin food choices produced selection on seed load per fruit (Sorensen 1981, Murray et al. 1993), and the potential intensity of selection on macronutrient content seems to be contingent, variable, and weak.

The results of experiments with food choices of captive birds obviously depend on many intangible conditions. Captivity itself may alter choice behavior; the maintenance diet or unknown factors in the experimental set-up may also influence choices. The specific nutrient levels and structure, color quality and intensity, and other characteristics of the experimental variables may influence behavior in unknown ways. Mere familiarity is unlikely to explain most choices made by the captive robins, because they had opportunity to feed on and become familiar with the unpreferred morphs during training and testing (cf. Raymond and Allan 1990). However, birds may develop specific associations between the external cues (such as color) and the food value of real fruits that do not pertain to artificial fruits used in many experiments with captives. Results in captivity are commonly assumed to mirror those in the wild, but this may not always be true (e.g., McPherson 1988, Willson and Comet 1993). Choices made by frugivores in field conditions must reflect fruit abundance and spatial distribution, as well as many other factors, and choices are likely to be made hierarchically (Sallabanks 1992, pers. comm.). The ranking of fruit traits in the choice hierarchy may vary among frugivores and it may differ with the species of fleshy fruit or the foraging environment. Nevertheless, studies with captive animals are often the only feasible way to begin to explore food-choice behavior by individual birds in a situation that controls many potentially relevant variables and allows the documentation of individual variation.

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#### LITERATURE CITED

- BRUGGER, K. 1992. Repellency of sucrose to captive American Robins. *J. Wildl. Manage.* 56:794-799.  
 DENSLOW, J. S., AND T. C. MOERMOND. 1982. The effect of accessibility on rates of fruit removal from



- tropical shrubs: an experimental study. *Oecologia* 54:170-176.
- HERRERA, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should, p. 5-18. In T. H. Fleming and A. Estrada [eds.], *Frugivores and seed dispersal*. Junk, Dordrecht, The Netherlands.
- HERRERA, C. M. 1992a. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* 140:421-446.
- HERRERA, C. M. 1992b. Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. *Ecology* 73:1832-1841.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1980. Nutmeg dispersal by tropical birds. *Science* 210:925-927.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1981. Removal of wild nutmeg (*Viola surinamensis*) crops by birds. *Ecology* 62:1093-1106.
- JOHNSON, R. A., M. F. WILLSON, J. N. THOMPSON, AND R. I. BERTIN. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66:819-827.
- KARASOV, W. H., AND D. J. LEVEY. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiol. Zool.* 63:1248-1270.
- JORDANO, P. 1993. Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. *Vegetatio* 107/108:85-104.
- JUNG, R. E. 1992. Individual variation in fruit choice by American Robins (*Turdus migratorius*). *Auk* 109:98-111.
- LEVEY, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129:471-485.
- LEVEY, D. J., T. C. MOERMOND, AND J. S. DENSLOW. 1984. Fruit choice in Neotropical birds: the effects of distance between fruits on preference patterns. *Ecology* 65:844-850.
- LEVEY, D. J., AND A. GRAJAL. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. *Am. Nat.* 138:171-189.
- MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. *American wildlife plants: a guide to wildlife food habits*. Dover, New York.
- MARTÍNEZ DEL RIO, C., AND C. RESTREPO. 1993. Ecological and behavioral consequences of digestion in frugivorous animals. *Vegetatio* 107/108:205-216.
- MAZER, S. J., AND N. T. WHEELWRIGHT. 1993. Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evol. Ecol.* 7:556-575.
- MCIPHERSON, J. M. 1987. A field study of winter fruit preferences of Cedar Waxwings. *Condor* 89:293-306.
- MCIPHERSON, 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.
- MURRAY, K. G., K. WINNETT-MURRAY, E. A. CROMIE, M. MINOR, AND E. MEYERS. 1993. The influence of seed packaging and fruit color on feeding preferences of American Robins. *Vegetatio* 107/108:217-226.
- RAYMOND, D. L., AND J. A. ALLEN. 1990. Wild birds prefer the familiar colour pattern when feeding on similar artificial morphs. *Oikos* 57:175-179.
- SALLABANKS, R. 1992. Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn, *Crataegus monogyna* (Rosaceae). *Oecologia* 91:296-304.
- SORENSEN, A. E. 1981. Interactions between birds and fruit in a temperate woodland. *Oecologia* 50:242-249.
- SORENSEN, A. E. 1984. Nutrition, energy and passage time: experiments with fruit preference in European Blackbirds (*Turdus merula*). *J. Anim. Ecol.* 53:545-557.
- STILES, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated wood plants in the eastern deciduous forest. *Am. Nat.* 116:670-688.
- STILES, E. W. 1993. The influence of pulp lipids on fruit preference by birds. *Vegetatio* 107/108:227-235.
- THOMPSON, J. N., AND M. F. WILLSON. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* 33:973-982.
- WHEELWRIGHT, N. T. 1986. The diet of American Robins: an analysis of U. S. Biological Survey records. *Auk* 103:710-725.
- WHEELWRIGHT, N. T., AND C. H. JANSON. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* 126:777-799.
- WHELAN, C. J., AND M. F. WILLSON. In press. Fruit choice in migrating North American birds: field and aviary experiments. *Oikos*.
- WILLSON, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. *Current Ornithology* 3:223-279.
- WILLSON, M. F., A. K. IRVINE, AND N. G. WALSH. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21:133-147.
- WILLSON, M. F., AND C. J. WHELAN. 1990. The evolution of fruit color in fleshy-fruited plants. *Am. Nat.* 136:790-809.
- WILLSON, M. F., AND C. J. WHELAN. 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. *Ecol. Monog.* 63:151-172.
- WILLSON, M. F., D. A. GRAFF, AND C. J. WHELAN. 1990. Variation in food-color preference of some frugivorous birds. *Condor* 92:545-555.
- WILLSON, M. F., AND T. C. A. COMET. 1993. Food choices by Northwestern Crows: experiments with captive, free-ranging, and hand-raised birds. *Condor* 95:596-615.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2d ed. Prentice-Hall, Englewood Cliffs, NJ.