THE CONDOR
A JOURNAL OF AVIAN BIOLOGY
Volume 92 Number 3 August 1990

The Condor 92:545–555

COLOR PREFERENCES OF FRUGIVOROUS BIRDS IN RELATION TO THE COLORS OF FLESHY FRUITS[1]

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Abstract. Aviary experiments demonstrated that three North American frugivorous migrant bird species often exhibit color preferences, when factors such as taste, nutrition, and accessibility to food sources are equal. Individual birds differed in initial color preferences, transitivity, and temporal stability of color preferences. There was little tendency of these birds to favor red and black, which are the most common colors of fruits of bird-dispersed plants, and a weak tendency to reject yellow. We suggest that avian color preferences may not provide strong selection favoring the evolution of the common fruit colors, and that the frequency distribution of fruit hues is best explained in other ways.

Key words: Color preferences; frugivory; fruit color; Gray Catbird; Swainson's Thrush; Hermit Thrush; Dumetella carolinensis; Catharus ustulatus; C. guttatus.

INTRODUCTION

Fleshy fruits consumed by avian frugivores are often colored red or black, sometimes blue, purple, pink, or white, but rarely orange, yellow, green, or brown (Janson 1983, Willson et al. 1989). Fruit colors are commonly considered to increase the conspicuousness of a ripe fruit crop and/or attract the birds that eat fruits and disperse the enclosed seeds (Darwin 1859, Ridley 1930, van der Pijl 1982). However, there is little documentation of the effects of fruit colors on avian foraging decisions (McPherson 1988) or on variation in color preferences either within or among frugivorous bird species.

An explanation of the frequency distribution of fruit colors must account for the predominance of red and black, the lesser occurrence of blue and white, and the rarity of yellow, green, and brown. A number of hypotheses have been proposed, and several factors may have contributed to this distribution (Willson and Whelan, in press). To begin to assess the importance of different factors that may help account for the observed distribution of fruit colors, we examine the simple hypothesis that the frequency distribution of colors reflects the color preferences of avian frugivores. Under this hypothesis, one would expect that red and black would be preferred most frequently and consistently, followed by blue and white, and then by yellow, green, and brown.

Here we examine the following questions about the attractiveness of different colors, as measured by color preferences of some frugivorous birds of the deciduous forest region of eastern North America: (1) What colors (of food) are preferred (or avoided) by fruit-eating birds? (2) How variable are color preferences among conspecific birds? Do different bird species have similar color preferences? (3) Does a given bird make "transitive" (i.e., internally consistent, see Methods) choices? (4) Are color preferences stable in the face of exposure to other food colors? (5) Does the background against which the fruits are displayed affect color preferences?

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METHODS

SUBJECTS

We used Gray Catbirds (*Dumetella carolinensis*), Swainson's Thrushes (*Catharus ustulatus*), and Hermit Thrushes (*C. guttatus*) for these experiments. The thrushes were entirely passage migrants, but catbirds probably included both migrants and summer residents. The birds were captured locally in mist nets in the fall of 1988 and housed individually in six aviaries (2 × 2 × 2.5 m) at the Shelford Vivarium, University of Illinois. Birds were held less than 3 weeks and were released at the end of the experiment; three birds escaped during the trials. The number of birds tested was constrained by the number of aviaries available, the need to release birds before their local season of migration was over, and the number escaping. Captive birds were fed chiefly on a banana-based maintenance diet designed for fruit-eating birds (Denslow et al. 1987) but augmented with eight teaspoons of glucose (per 2 l), supplemented with mealworms (*Tenebrio molitor*), wax worms (*Galleria mellonella*), and real fruit, of various species and colors, collected locally. All birds were given several days to become accustomed to aviary conditions before testing. Although some of the test birds may have hatched in 1988, all were fully fledged and capable of foraging independently. Two cohorts of catbirds were used: Cohort 1 (birds 1–6), 8–12 September; Cohort 2 (birds 7–12), 28 September–11 October. Swainson's Thrushes (n = 4) were tested on 19–23 September, and Hermit Thrushes (n = 6) on 16 October–2 November. All birds used in these experiments ate well in captivity.

EXPERIMENTAL PROCEDURE

Initial color preferences. Experiments consisted of paired choices of maintenance diet (prepared in 4-mm cubes) treated with commercial food coloring. Colors used were red, blue, yellow, and "black." An approximate indication of the colors achieved is given by comparison to Smithe's (1975) color standards: red #110, blue #68, yellow #18, and black #89. These colors were not intended to mimic those of any particular wild fruits, but they fall within the natural range of fruit colors (to our eyes). Black was produced by a mixture of roughly equal parts of red and blue, producing an extremely dark purple; many naturally black fruits also are, in fact, very dark purple, red, or blue. All of these colors are rendered as perceived by human eyes; we do not know what the birds actually see. Under the initial hypothesis, the expected outcome would be a preference for red and black, followed by blue, and then yellow.

Because we were interested in whether color preferences are transitive (e.g., if red > black, and black > blue, then red > blue, see Moermond and Denslow 1983), we used a pairwise design, in which the direction of preference for each pair of colors was determined independently, rather than a four-way "cafeteria" design. The order of the pairwise comparisons was determined from a random-number table, with the constraint that alternating pairwise comparisons on the same day used all four colors (e.g., red vs. blue, alternating with black vs. yellow). The first comparison alternated with the second, until a predetermined number of replicates (see below) was complete. Likewise, the third comparison alternated with the fourth, and the fifth alternated with the sixth.

Because catbirds reacted quite differently in the aviaries from both thrush species, we used slightly different experimental protocols for the different species. Catbirds adjusted quickly to the aviaries and readily foraged in our presence. In a given foraging trial, two cubes (of two colors) were placed in each of four separate petri dishes (30 mm diameter) arrayed along a wooden perch. Each bird was allowed to feed from this display until four of the eight cubes had been eaten (usually <15 min). For each catbird, there were four replicates of each trial; we did not attempt to analyze any possible patterns of variation among replicates. Because equal numbers of cubes of each color in each comparison were available, we defined no color preference as no statistical difference (determined with the binomial exact test) in the number of cubes of each color taken. Most experiments were conducted between 07:00 and 14:00.

In contrast to the catbirds, neither thrush species would eat in our presence. For these species, therefore, we weighed out a known quantity of dietary cubes in 10-cm petri dishes (each color in a separate dish), which were placed in the middle of the aviary floors. Placement of dishes with different colors of food was alternated to avoid positional bias. We then allowed the birds to feed until roughly half of the total food was eaten (usually <2 hr) and weighed the remainder. The difference was the amount eaten (a small weight loss, <5%, due to evaporation did not affect the analysis). Experiments were conducted between 07:00 and 17:00. There were three replicates of each pairwise comparison, and the data were analyzed by two-way (bird, color) ANOVA (see Sokal and Rohlf 1981, p. 344–348) and t-tests. The t-tests were done separately for each bird and each pairwise color combination (see Appendix 2). Although there was a directional prediction for most pairs of colors (e.g., red > blue), we used a conservative two-tailed test to establish whether there was a significant difference in the amount eaten. The observed direction of color preference was then determined by inspection. This procedure allowed the identification of preferences that were opposite in direction to the prediction.

Stability of color preferences. Because most individual birds of all three species exhibited marked preferences for certain colors, we also examined the temporal stability of these preferences. We attempted to extinguish individual preferences for a certain color by keeping each bird on a maintenance diet of a nonpreferred color. During continuous exposure to the nonpreferred color, the birds might learn that certain characteristics of both colors (e.g., flavor, texture) were identical, and thus decrease their degree of discrimination between the two colors. Here the question concerned the rate at which the birds learned to associate the initially nonpreferred color with food of equal value to that of the preferred color.

Catbirds and Hermit Thrushes were used as subjects. An initial paired choice was conducted as described above for the thrush experiments at the beginning of each day. Subsequently, each bird was given only the maintenance diet treated with the nonpreferred color (often supplemented with various real fruits, mealworms, and waxworms) until the next trial. This procedure was repeated for 6 days. Red and yellow were used in these experiments, because most birds showed strong preferences for one of these colors. Instability was indicated by a change in color preference.

Effect of background. For certain pairwise comparisons, we examined the effect of background on color choice by catbirds, because of the possibility that color preferences might differ with the background against which the color is displayed. Many fruits are naturally displayed against a background of green foliage on the parent plant. We placed each pair of dietary cubes on a spray of green artificial foliage attached to the perch. A bird on the perch could reach any of the pairs of cubes with two or three hops. Results of these trials were compared with those described earlier, in which the cubes were presented in petri dishes. Trials that used different backgrounds were alternated until four replicates were completed. A significant shift of preference was indicated by direct comparison of the preferences exhibited on the two different backgrounds, using χ^2 ($P < 0.05$).

RESULTS

INITIAL COLOR PREFERENCES

Catbirds. The evidence of a general preference for red and black is not strong (Table 1). Of all 62 trials, 40 (65%) indicated no significant preference between paired colors. Of 46 trials involving red or black with some other color (i.e., blue or yellow), only 16 showed a significant preference for red or black. Twenty-five trials showed no preference for red or black over the other color, and five trials indicated a preference for the other color. Thus, 65% (30/46) of the trials failed to indicate a preference for red or black. Preferences for blue vs. yellow were also not marked: Only one of five birds preferred blue (Table 1). Although none of the catbirds discriminated between red and black, red was favored over blue and yellow more often than black: Four of 11 birds preferred red to blue, and nine of 12 birds preferred red to yellow, but only three of 11 birds preferred black to yellow (but see Appendix 1), and no birds preferred black to blue.

However, yellow was *rejected* more often than the other colors (13 of 28 trials vs. 4 of 28 for blue, 1 of 34 for red, 4 of 34 for black; all $\chi^2 > 3.84$, $P < 0.05$). Also recall that most birds rejected yellow when paired with red. Thus, the results suggest some tendency to reject yellow, but little tendency to discriminate among the other colors.

It may be argued that, if many birds have a weak, statistically insignificant, preference for a color, the collective effect nevertheless could be biologically significant. This possibility was assessed in two ways. (1) For each pairwise comparison, data for all birds were pooled and a single χ^2 performed on the totals. Red was preferred over all other colors except black, black

TABLE 1. Summary of color preferences of Gray Catbirds (details in Appendix 1). Statistical significance as follows: * = $P < 0.05$, (*) = $0.05 < P < 0.10$. Entries in the table are the number of birds that made the indicated choice. For each pair of colors, the first one is labelled 1, the second, 2, and these numerical labels are used in the left-hand column (for example, the data for 1 > 2 indicate that no birds preferred black to blue, two birds preferred black to yellow, three birds preferred red to blue, etc.). For black vs. yellow, see detailed explanation in Appendix 1.

	Color combinations					
	Black vs. blue (1 vs. 2)	Black vs. yellow (1 vs. 2)	Black vs. red (1 vs. 2)	Red vs. blue (1 vs. 2)	Red vs. yellow (1 vs. 2)	Blue vs. yellow (1 vs. 2)
Cohort 1						
No. of birds with the following preferences:						
1 > 2	0	2	0	3	3	—
1 = 2	6	3	6	2	3	—
2 > 1	0	1	0	1	0	—
χ^2 test of heterogeneity:		*		*		
Cohort 2						
No. of birds with the following preferences:						
1 > 2	0	1	0	1	6	1
1 = 2	3	4	5	4	0	4
2 > 1	3	0	0	0	0	0
χ^2 test of heterogeneity:	(*)	*		(*)		*

was preferred only over yellow, and blue was preferred to both yellow and black. This procedure encounters possible risks of pseudoreplication (Hurlbert 1984) and, although a preference for red is indicated, black was not totally favored. Thus, even by this possibly questionable analysis, the hypothesis of a red/black preference is not wholly supported for catbirds. (2) For all birds that showed some tendency to prefer one color (i.e., outcome not equal for both colors), the frequency of preference for one color of each pair was totalled and tested by a sign test. Eight of 11 birds tended to favor red over blue (not a significant difference), but all 11 birds showing a tendency to favor one color over another favored red over yellow ($P < 0.01$). Only two of 10 birds tended to prefer black to blue and six of 10 birds tended to prefer black to yellow. In neither case is the observed frequency of tendency significantly different from a null hypothesis of equal tendency to favor each color.

The data are perhaps characterized as much by their variation as by their congruence. χ^2 tests of heterogeneity showed that birds of the first cohort differed significantly with respect to choices between red and blue, and between black and yellow. Birds of the second cohort differed significantly with respect to blue vs. yellow, black vs. yellow, and, marginally, red vs. blue, and black vs. blue. Although a preference for red over yellow was common, one bird (5) showed no sign at all of such a preference (Appendix 1). Bird 5 was also unusual in showing a strong preference for yellow over black, and blue over red.

Intransitivity of color preferences occurred for nine of the 12 catbirds, in at least some of the color choices. Birds 6 and 12 made transitive choices, insofar as any preferences were exhibited, and the data for Bird 7 were too incomplete to assess transitivity.

Thrushes. Both species of thrush exhibited some color preferences in the majority of trials (in contrast to catbirds). However, red and black were preferred over the other colors about as often as the other colors were preferred to red and black (Table 2). In six of 14 trials involving red or black vs. the other colors, Swainson's Thrushes preferred red or black (and in six trials they preferred the other colors), and in 11 of 24 trials, Hermit Thrushes preferred red and black (and in eight they preferred the other colors). Blue was only sometimes preferred to yellow (three of four Swainson's Thrushes, one of six Hermit Thrushes).

Swainson's Thrushes had a marginally significant tendency to reject yellow more often than two of the other colors (seven of 11 trials vs. three of 12 for blue and red; $\chi^2 = 3.4$, $0.05 < P < 0.10$). Hermit Thrushes, however, rejected yellow, black, and blue about equally (six to eight

TABLE 2. Summary of color preferences of Swainson's and Hermit thrushes (details in Appendix 2). Individual variation was significant for all color combinations. Entries in the table are the number of birds that made the indicated choice. For each pair of colors, the first one is labelled 1, the second, 2, and these numerical labels are used in the left-hand column (see legend for Table 1).

	Color combinations					
	Black vs. blue (1 vs. 2)	Black vs. yellow (1 vs. 2)	Black vs. red (1 vs. 2)	Red vs. blue (1 vs. 2)	Red vs. yellow (1 vs. 2)	Blue vs. yellow (1 vs. 2)
Swainson's Thrushes						
No. of birds with the following preferences:						
$1 > 2$	1	2	1	1	2	3
$1 = 2$	0	0	2	2	0	0
$2 > 1$	3	1	1	0	2	1
Hermit Thrushes						
No. of birds with the following preferences:						
$1 > 2$	1	2	1	4	4	1
$1 = 2$	3	0	3	1	1	2
$2 > 1$	2	4	2	1	1	3

of 18 trials) and rejected red marginally less often than black or blue (three of 18 trials, $\chi^2 = 3.3$, $0.05 < P < 0.10$). Thus, thrushes showed less tendency to reject yellow than the catbirds.

If we pool the data for all conspecific thrushes, we encounter not only the potential for pseudoreplication but also unequal weightings for each bird, reflecting the different total amounts eaten. Ignoring such difficulties for the moment, no clear preferences for red and black emerge. Swainson's Thrushes collectively ate more red than other colors, but black was equivalent to blue and somewhat less than yellow. Hermit Thrushes collectively ate more yellow than red and more blue than black. (The sample for both species of thrush is too small to allow much information to be extracted from a sign test like that done for the catbird data.) Thus, for thrushes as well as for catbirds, the hypothesis of a general preference for red/black hues is not well supported.

All interactions between bird and color combination were significant (ANOVA, $P < 0.05$) for both species of thrush, again emphasizing the prevalence of individual variation in color preferences. Two Swainson's Thrushes and two Hermit Thrushes made transitive choices and one Swainson's Thrush and four Hermit Thrushes exhibited some intransitivity (one Swainson's Thrush had incomplete data).

STABILITY OF COLOR PREFERENCES

Both catbirds and Hermit Thrushes varied markedly in the stability of their color preferences (Table 3). Two catbirds maintained a consistent preference for red. Bird 11 wavered in its preferences for red only on the last day. One catbird (Bird 9) switched briefly to yellow and then back to red for the duration of the trials. Bird 12 initially preferred red, vacillated for a couple of days, and returned to a preference for red.

Hermit Thrushes were somewhat more variable than the catbirds. The preference of Bird 2 for red was not extinguished during the course of the 6-day trial. Bird 6 showed a relaxation of red-preference only on the 6th day. Bird 5 switched from red to yellow on the 2nd day and subsequently maintained a preference for yellow. Both Bird 3 and especially Bird 4 switched preferences more than once during the 6-day trials.

EFFECT OF BACKGROUND

Background had little influence on color preferences of catbirds (Table 4), at least for the color combinations used in these experiments. In only three paired comparisons was there a significant preference, and the background on which the preference was exhibited differed among birds. Two birds showed a significant shift of preference, but in both cases the shift was from an insignificant tendency to choose one color (red or black) to a significant preference for the same color.

DISCUSSION

These frugivorous birds often exhibited marked food-color preferences, when other factors were held constant, and these preferences appeared to be largely independent of the background (see also Pank 1976). All three species of frugivores exhibited considerable individual variation in

TABLE 3. Stability of red-yellow color preferences of Gray Catbirds and Hermit Thrushes. Entries in the table are the names of the preferred color (R = red, Y = yellow) on each day of the trial, as determined by a choice test. Catbirds were tested twice on some days (a, b). Following each choice test each bird was fed on the maintenance diet of its nonpreferred color, as determined by that choice test. Switches are underlined.

<table>
<tr><th></th><th colspan="10">Day</th></tr>
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<tr><td>Gray Catbirds</td><td></td><td>a</td><td>b</td><td>a</td><td>b</td><td></td><td>a</td><td>b</td><td>a</td><td>b</td></tr>
<tr><td>8</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td></tr>
<tr><td>9†</td><td>Y</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td></tr>
<tr><td>10</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td></tr>
<tr><td>11</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R & Y</td></tr>
<tr><td>12</td><td>R</td><td>R</td><td>R & Y</td><td>R</td><td>R & Y</td><td>R</td><td>R</td><td>R</td><td>R</td><td>R</td></tr>
<tr><td>Hermit Thrushes</td><td></td><td colspan="2"></td><td colspan="2"></td><td></td><td colspan="2"></td><td colspan="2"></td></tr>
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<tr><td>3</td><td>Y</td><td colspan="2">Y</td><td colspan="2">R</td><td>R</td><td colspan="2">Y</td><td colspan="2">Y</td></tr>
<tr><td>4‡</td><td>Y</td><td colspan="2">R</td><td colspan="2">Y</td><td>Y</td><td colspan="2">R</td><td colspan="2">R</td></tr>
<tr><td>5</td><td>R</td><td colspan="2">Y</td><td colspan="2">Y</td><td>Y</td><td colspan="2">Y</td><td colspan="2">Y</td></tr>
<tr><td>6</td><td>R</td><td colspan="2">R</td><td colspan="2">R</td><td>R</td><td colspan="2">R</td><td colspan="2">R & Y</td></tr>
</table>

† Bird 9 preferred R in earlier choice tests (Appendix 1) and switched at the beginning of these trials.
‡ Bird 4 preferred R in earlier choice tests (see Appendix 2) and switched at the beginning of these trials.

color preference. The variability observed among birds is probably not an artifact of using artificial fruits in the feeding trials. Captive birds also showed marked variation among individuals in preference trials using real fruits (unpubl. observ. of MFW and CJW, and R. Jung). Preferences of some individuals were firmly retained for several days, even when food flavor, consistency, and nutritional quality were identical (see also Winkel 1969), but other individuals had more labile preferences (see also references in Wheelwright and Janson 1985). The experimental frugivores showed little evidence of a general preference for red or black (or indeed, for any other color); but catbirds and possibly Swainson's Thrushes tended to reject yellow more often than other colors. Transitivity of color preference was low, in contrast to a high transitivity of preferences for fruit types (Moermond and Denslow 1983).

Other studies of avian fruit-color preferences are few, and mostly come from cultivated fruits. European Starlings (*Sturnis vulgaris*) in Czechoslovakia preferred red to white cherries (*Prunus* sp.) and blue to white grapes (*Vitis* sp.) (Feare 1984). Eurasian Blackbirds (*Turdus merula*) in Bavaria ate both red (ripe) and yellowish (unripe) cherries, despite the difference in taste and consistency, but favored red over white currants (*Ribes* sp.) (Diesselhorst 1972). The taste of the currants may differ (White 1789 *in* Snow and Snow 1988) and other factors may also differ between the cultivars. American Robins (*Turdus migratorius*) foraging in Ontario vineyards favored a black grape variety over a red one of similar sweetness and a larger but less sweet blue one, although the varieties differed somewhat in how much the foliage concealed the fruit (Brown 1974), and possibly in other factors. Robins and starlings in another vineyard tended to forage most extensively on blue rather than white or red grapes (Brown 1974). Frugivorous birds in Ontario also preferred black to pink or yellow sweet-cherry cultivars, but the pink variety was reported to ripen slightly later than the black ones (Brown 1974). Polymorphic fruits (red, yellow, white) of *Rhagodia parabolica* in Australia were eaten nearly equally by avian foragers (Willson and O'Dowd 1989).

Individually caged robins given a three-way choice between red sour cherries (14% sugar, lower pH) and black (14%) and yellow (18%) sweet cherries exhibited much variation among birds (Brown 1974): some preferred black to red, while others favored red. All birds initially rejected yellow cherries, and most eventually accepted them (after 2–6 days), in some cases even favoring them. The robins differed markedly in how fast the yellow cherries were accepted. Small, captive flocks of starlings often preferred black or red cherries initially, but some flocks quickly (<2 hr) accepted yellow cherries (Brown 1974, Stevens and DeBont 1980).

McPherson (1988) showed that two captive flocks (tested separately but data pooled) of Cedar Waxwings (*Bombycilla cedrorum*) collectively ate more red than yellow dietary mash and ate little blue or green. A second trial (about 1 week later) was done with the same two flocks but with greater access to food for all flock members; in this case the birds collectively favored red and blue and, to a somewhat lesser extent, yellow, and again ate relatively little green. This study was not designed to examine individual preferences, and the most notable results are that the favored colors shifted somewhat between trials (although red was included in the top rank) but that green was consistently rejected.

Many of the field observations of "color preferences" reported above could be confounded by other variables, such as crop size, nutritional value, palatability, and ripening times. Nevertheless, they indicate that foraging choices can be variable with respect to fruit color. The experiments with captive birds document both the variability of color choices and the ability to learn to eat food that is initially not favored. In addition, flower-foraging birds readily learn to visit flowers of many colors (references in Willson and Whelan, in press). Although foraging experience no doubt influences food-color choices, the natural experience of frugivores with the common red and black native fruits does not seem to produce an overwhelming preference for fruit of these colors. Even if young birds have any innate preference for these colors, by the time they are fully grown they often seem to have acquired preferences for colors other than red or black.

A remaining possibility is that experiments using some other shades of red, blue, and yellow in artificial fruits might yield different results, especially if a certain shade matched that of some particularly favored natural fruit. However, the extensive variation among individuals in preferences for natural fruits observed in both aviary and field (pers. observ.) suggests that the use of other shades of artificial fruits would also produce results demonstrating variable preferences.

Variation among individuals in many aspects of foraging has been reported (e.g., Ficken and Kare 1961, Joern 1988, Ritchie 1988, Rowley et al. 1989, other references below), so that variation in color preferences may not be surprising. Individual variation in avian color preferences in other contexts is known (e.g., Kear 1966), as is variation in strengths of preference for different fruit types (Levey et al. 1984). Visual sensitivity may vary among individuals (e.g., Jacobs 1977, for the squirrel monkey, *Saimiri sciureus*). Selection for lines of different color preferences (Kovach et al. 1976, Kovach 1980) indicates a genetic basis for at least some of these kinds of variation. However, color preferences also may depend, in part, on the diet of the individual, specifically the inclusion of carotenoids, which are important in color vision (Kovach et al. 1976). Furthermore, some variation may arise as offspring follow their parents and learn to forage (Werner and Sherry 1987, Peacock and Jenkins 1988). It seems reasonable to expect more variation among young birds that are learning to forage than among older, more experienced birds.

TABLE 4. Color preferences of Gray Catbirds when food was presented on different backgrounds. Significant preferences are marked *; significant shifts of preferences are marked S.

Catbird	Number eaten In dishes	 On leaves
	Black : Blue	Black : Blue
1	8:8	7:9
2	7:9	8:8
3	7:9	6:10
4	8:8	9:7
5	6:10	8:8
6	11:5	8:8
	Black : Yellow	Black : Yellow
8	5:11	9:7
9	9:7	14:2* S
10	6:10	9:7
11	7:9	9:7
12	16:0*	10:6 S
	Red : Black	Red : Black
8	10:6	12:4*
9	8:8	8:8
10	9:7	8:8
11	8:8	9:7
12	6:10	7:9

A major finding of our study is that color preferences of many individuals were at least partly intransitive. In some individuals, preferences for some color combinations were transitive, while preferences for other color combinations were not. Transitivity of food preferences is one criterion for "rational" decision making (Moermond and Denslow 1983) and has been invoked as support for foraging preferences being based on some kind of cost/benefit analysis (e.g., Moermond and Denslow 1983, Levey et al. 1984, Whelan 1989). Furthermore, many studies of individual differences in foraging behavior explain those differences in terms of nutritional gain (e.g., Partridge 1976, Werner and Sherry 1987, Harder 1988). The observed lack of transitivity of color preferences for food items differing only in color, in our study, may indicate that color preferences are not based on considerations of energy or nutrient utilization. Thus, the basis for color preferences may be fundamentally different from the basis for many other foraging decisions.

Indeed, color is not necessarily a reliable indicator of nutritional value of mature fruits. Fruit colors are not generally correlated with other aspects of fruit composition in mature fruits, either among species (Willson and Thompson 1982, Wheelwright and Janson 1985) or within species (Willson and O'Dowd 1989). Fruit colors indicate the degree of maturity in a variety of species, and birds may use color as a cue to the choosing of more mature fruits (e.g., Moermond et al. 1986; other references in Willson and Whelan, in press). Nevertheless, the development of mature fruit color in cultivated cranberries, grapes, and some other fruits is related to many environmental factors, including temperature, light, nitrogen, precipitation, CO_2, and available sugars (e.g., Hall and Stark 1972, Kliewer and Weaver 1971, Kliewer and Schultz 1973, Kliewer 1977, Goldschmidt 1980). In addition, preferences for hue may be affected by other visible traits such as brightness (e.g., Kear 1966, Delius and Thompson 1970), but brightness is not necessarily correlated with fruit ripeness (Sherburne 1972). All of these considerations introduce variation in the utility of color as a signal on which preferences could be based (see also Willson and Whelan, in press).

IMPLICATIONS FOR THE EVOLUTION OF FRUIT COLORS

The apparent lack of strong and consistent fruit-color preferences may contribute to the existing range of fruit colors, but color preferences seem unlikely to be a strong factor maintaining the observed frequencies of fruit colors in the wild. If the earliest frugivores, back in Paleozoic and Mesozoic times, had color preferences as variable and labile as those of today seem to be, even the beginning of predominance of red and black as fruit colors is difficult to attribute to color preferences of frugivores. If the tendency to reject yellow and green (McPherson 1988) receives reinforcement from additional studies of other species, it could help account for the rarity of yellow and green bird-fruits.

It remains possible that fruit-color preferences are contingent upon a variety of associated traits and conditions (e.g., red could be preferred for certain fruit shapes or sizes, or in certain habitats, or by certain birds), such that they are specific to particular circumstances. Such contingency of color responses is known in insects, depending on activity (e.g., courtship vs. feeding, Swihart and Gordon 1971) or shape and size of the object (e.g., Hill and Hooper 1984; which may then be related to activity, Prokopy 1968), although intensity, contrast, and learning may also be important (Prokopy 1968, Prokopy et al. 1982). Contingency of color responses no doubt occurs in vertebrates as well—a relevant instance concerns the fact that red and black can be warning colors for arthropods that are avian prey, but they may be advertising colors in some positive sense for fruits.

An alternative hypothesis is that fruit colors are a form of long-distance advertisement for avian seed-dispersers (e.g., Kerner 1895, Ridley 1930). This hypothesis has not been tested directly, so far as we can determine, and circumstantial evidence provided mixed support (Willson and Whelan, in press). Many additional ecological factors may have influenced the evolution of fruit colors, including costs (both direct and indirect) of pigment production and the possible utility of pigments in defense of the fruit against herbivores and pathogens (Wheelwright and Janson 1985; Willson and Whelan, in press). Any comprehensive theory of fruit-color evolution must encompass a spectrum of selection pressures.

ACKNOWLEDGMENTS

We thank T. Audo and J. Turkot for help in aviary maintenance, K. Halupka and D. Niven for mist-netting, and R. T. Holmes, L. Hogan-Warburg, and D. J. Levey for constructive criticism of the manuscript. This work was funded by a grant from the Whitehall Foundation to MFW.

LITERATURE CITED

BROWN, R.G.B. 1974. The bird damage problem in southern Ontario. Can. Wildl. Serv. Rep. Ser. 27: 1–56.

DARWIN, C. 1859. The origin of species. Murray, London.

DELIUS, J. D., AND G. THOMPSON. 1970. Brightness dependence of colour preferences in herring gull chicks. Z. Tierpsychol. 27:842–849.

DENSLOW, J. S., D. J. LEVEY, T. C. MOERMOND, AND B. C. WENTWORTH. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131–135.

DIESSELHORST, G. 1972. Beeren und Farbenwahl durch Vögel. J. Ornithol. 113:448–449.

FEARE, CHRISTOPHER. 1984. The starling. Oxford, New York.

FICKEN, M. S., AND M. R. KARE. 1961. Individual variation in the ability to taste. Poultry Sci. 40: 1402.

GOLDSCHMIDT, E. E. 1980. Pigment changes associated with fruit maturation and their control, pp. 207-217. *In* K. V. Thimann [ed.], Senescence in plants. CRC Press, Boca Raton, FL.

HALL, I. V., AND R. STARK. 1972. Anthocyanin production in cranberry leaves and fruit, related to cool temperatures at a low light intensity. Hort. Res. 12:183–186.

HARDER, L. D. 1988. Choice of individual flowers by bumble bees: interaction of morphology, time, and energy. Behaviour 104:60–77.

HILL, A. R., AND G.H.S. HOOPER. 1984. Attractiveness of various colours to Australian tephritid fruit flies in the field. Entomol. Exp. Appl. 35:119–128.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

JACOBS, G. H. 1977. Visual sensitivity: Significant within-species variations in a nonhuman primate. Science 197:499–500.

JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. Science 219:187–189.

JOERN, A. 1988. Foraging behavior and switching by the grasshopper sparrow *Ammodramus savannarum* searching for multiple prey in a heterogeneous environment. Am. Midl. Nat. 119:225–234.

KEAR, J. 1966. The pecking response of young coots *Fulica atra* and moorhens *Gallinula chloropus*. Ibis 108:118–122.

KERNER, A. 1895. The natural history of plants. (English translation by F. W. Oliver.) 2 vols. Holt, New York.

KLIEWER, W. M. 1977. Influence of temperature, solar radiation and nitrogen on coloration and composition of emperor grapes. Am. J. Enol. Vitic. 28: 96–103.

KLIEWER, W. M., AND H. B. SCHULTZ. 1973. Effect of sprinkler cooling of grapevines on fruit growth and composition. Am. J. Enol. Vitic. 24:17–26.

KLIEWER, W. M., AND R. J. WEAVER. 1971. Effect of crop level and leaf area on growth, composition, and coloration of "Tokay" grapes. Am. J. Enol. Vitic. 22:172–177.

KOVACH, J. K. 1980. Mendelian units of inheritance control color preferences in quail chicks (*Coturnix coturnix japonica*). Science 207:549–551.

KOVACH, J. K., G. WILSON, AND T. O'CONNOR. 1976. On the retinal mediation of genetic influences in color preferences of Japanese quail. J. Comp. Physiol. Psychol. 90:1144–1151.

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.

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 neotropical birds: effects of fruit types and accessibility on selectivity. J. Anim. Ecol. 52: 407–420.

MOERMOND, T. C., J. S. DENSLOW, D. J. LEVEY, AND E. SANTANA C. 1986. The influence of morphology on fruit choice in neotropical birds, p. 137–146. *In* A. Estrada and T. H. Fleming [eds.], Frugivores and seed dispersal. Junk, Dordrecht.

PANK, L. F. 1976. Effects of seed and background colors on seed acceptance by birds. J. Wildl. Manage. 40:769–774.

PARTRIDGE, L. 1976. Individual differences in feeding efficiencies and feeding preferences of captive great tits. Anim. Behav. 24:230–240.

PEACOCK, M. M., AND S. H. JENKINS. 1988. Development of food preferences: social learning by Belding's ground squirrels *Spermophilus beldingi*. Behav. Ecol. Sociobiol. 22:393–399.

PROKOPY, R. J. 1968. Visual responses of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae): orchard studies. Entomol. Exp. Appl. 11:403–422.

PROKOPY, R. J., A. L. AVERILL, S. S. COOLEY, AND C. A. ROITBERG. 1982. Associative learning in egg-laying site selection by apple maggot flies. Science 218:76–77.

RIDLEY, H. N. 1930. The dispersal of plants throughout the world. Reeve, Ashford, United Kingdom.

RITCHIE, M. E. 1988. Individual variation in the ability of Columbian ground squirrels to select an optimal diet. Evol. Ecol. 2:232–252.

ROWLEY, I., E. RUSSELL, AND M. PALMER. 1989. The food preferences of cockatoos: an aviary experiment. Aust. Wildl. Res. 16:19–32.

SHERBURNE, J. 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. diss., Cornell Univ., Ithaca, NY.

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

SNOW, B., AND D. SNOW. 1988. Birds and berries. Poyser, Calton, United Kingdom.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Co., San Francisco.

STEVENS, J., AND A. F. DEBONT. 1980. Choice by starlings (*Sturnus v. vulgaris* L.) among different cherry cultivars. Agricultura (Heverlee) 28:421–436.

SWIHART, S. L., AND W. C. GORDON. 1971. Red photoreceptor in butterflies. Nature 231:126–127.

VAN DER PIJL, L. 1982. The principles of dispersal in higher plants. 3rd ed. Springer-Verlag, Berlin.

WERNER, T. K., AND T. W. SHERRY. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin Finch" of Cocos Island, Costa Rica. PNAS 84:5506–5510.

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. 1989. Avian foliage structure preferences for foraging and the effect of prey biomass. Anim. Behav. 38:839–846.

Willson, M. F., and D. J. O'Dowd. 1989. Fruit color polymorphism in a bird-dispersed shrub (*Rhagodia parabolica*) in Australia. Evol. Ecol. 2:40–50.

Willson, M. F., and J. N. Thompson. 1982. Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are "green." Can. J. Bot. 60:701–713.

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. In press. The evolution of fruit color in fleshy-fruited plants. Am. Nat.

Winkel, W. 1969. Experimentelle Untersuchen an Zuckervögeln (Coerebidae) in Funktionkreis der Nahrungssuche: Über die Bedeutung von Farben, Formen und Zuckerkonzentrationen. Z. Tierpsychol. 26:573–628.

APPENDIX 1. Numbers of dietary cubes of different colors eaten by Gray Catbirds. Statistically significant preferences are marked *. For Bird 2†, the outcome of the choice between black and yellow could have been 12:4; because of this uncertainty, the summary in Table 1 could be that three birds preferred black and two showed no preference. In the rows for each cohort, between-individual heterogeneity is indicated by ** when $P < 0.05$ and as (**) when $0.05 < P < 0.10$.

	Color combination											
	Black	Blue	Black	Yellow	Black	Red	Red	Blue	Red	Yellow	Blue	Yellow
Bird												
Cohort 1			**				**					
1	8	8	8	8	6	10	12	4*	14	2*	—	—
2	7	9	11	5†	10	6	11	5	14	2*	—	—
3	7	9	11	5	9	7	12	4*	10	6	—	—
4	8	8	14	2*	5	11	12	4*	11	5	—	—
5	6	10	1	15*	9	7	3	13*	8	8	—	—
6	11	5	14	2*	7	9	11	5	13	3*	—	—
Cohort 2	(**)		**				(**)				**	
7	4	12*	—	—	—	—	—	—	16	0*	—	—
8	2	14*	5	11	6	10	13	3*	13	3*	6	10
9	3	13*	9	7	8	8	5	11	13	3*	16	0*
10	5	11	6	10	7	9	10	6	16	0*	11	5
11	10	6	7	9	8	8	7	9	16	0*	11	5
12	5	11	16	0*	10	6	9	7	16	0*	11	5

APPENDIX 2. Average amount of food (g) of different colors eaten by Swainson's and Hermit thrushes. All interactions between bird and color combination are statistically significant (ANOVA, $P < 0.05$). All pairwise choices are significantly different except as indicated. Up to ca. 1 g could have been lost by evaporation. Variation among individuals was statistically significant for both species, for all color combinations.

	Color combination											
	Black	Blue	Black	Yellow	Black	Red	Red	Blue	Red	Yellow	Blue	Yellow
Swainson's Thrush												
2	0.90	5.95	6.52	0.53	0.42	5.55	1.68[c]	6.03	6.66	0.72	8.12	0.60
3	8.91	0.95	6.08	0.35	3.57	1.58 ns	4.20	1.42 ns	7.31	0.60	7.32	0.57
5	0.95	8.44	0.90	9.00	10.28	1.12	7.88	1.17	0.62	10.75	1.63	9.12
6	0.25	10.08	—	—	6.25	1.90 ns	—	—	0.60	10.90	9.83	0.62
Hermit Thrush												
1	0.80	2.40	0.47	5.47	0.40	6.10	7.17	0.40	5.67	0.33	2.40	6.63
2	1.70	3.57 ns	0.50	7.03	0.37	7.43	8.97	0.67	6.33	1.27	0.57	5.20
3	0.30	5.57	0.97	4.77	0.27	4.43	5.37	0.67	0.27	5.80	2.73	2.73 ns
4	3.90	4.23 ns	6.97	0.23	2.83	3.77 ns	7.37	0.67	7.43	0.27	3.83	0.33
5	7.20	0.63	0.70	6.10	3.17	0.93	5.93	2.20 ns[a]	4.43[b]	1.80	0.87	5.77
6	5.23	3.13 ns[a]	5.67	1.07	5.80	3.03 ns	1.60	7.97	5.20 ns	3.77	3.50	2.67 ns

[a] Not significantly different by t-test, but results were consistent in direction in all three trials.

[b] Marginally significant ($0.05 < P < 0.10$), and results were consistent in direction in all three trials. Counted as significant for Table 2.

[c] Marginally significant ($0.05 < P < 0.10$).