

## INDIVIDUAL VARIATION IN FRUIT CHOICE BY AMERICAN ROBINS (*TURDUS MIGRATORIUS*)

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**ABSTRACT.**—I tested American Robins (*Turdus migratorius*) for individual differences in fruit consumption and preference when offered six trials of a three-way choice of white mulberry (red variety; *Morus alba* L.), Bella honeysuckle (*Lonicera × bella*), and red-osier dogwood (*Cornus stolonifera* Michx.) fruits. Fruit choice was examined secondarily in relation to indices of fruit quality (fruit mass, percent water, refractive index, trial date, source plant) and in relation to age, sex, and individual morphometric variation of the birds. Pooling all trials and all birds, mulberry was eaten significantly more than either honeysuckle or dogwood. Although adults differed from juveniles in body mass at capture and in relative bill dimensions, fruit choice did not vary in relation to age or sex. Also, juveniles were not more variable than adults in fruit choice. However, individual birds differed significantly in fruit choice (15 preferred mulberry, 2 preferred dogwood, 0 preferred honeysuckle), and 15 individuals were consistent in fruit choice from trial-to-trial. Indices of fruit quality changed over the course of the study. For each of the three fruit species, some variables were significantly different among individual plants, over time, or both. Some fruit-quality variables explained small but significant amounts of variation in fruit consumption (numbers of fruits eaten) and preference (number of fruit A eaten / [(number of fruit B eaten) + (number of fruit C eaten)]). Robins preferred fruits from mulberry trees that had fruits of relatively lower mass and higher refractive index. After I controlled for effects of fruit quality, trial date, and source plant in multiple regression analyses, residual consumption and preference scores still differed significantly among individuals. Residuals for mulberry and dogwood were negatively correlated, which implies a trade-off in consumption of these two fruits. Individual differences in body mass, but not in bill or wing dimensions, explained significant amounts of the variation in residual mulberry consumption and in mulberry and dogwood preference. Heavier robins tended to prefer and eat more mulberries, the largest fruit, whereas lighter robins preferred dogwood fruits, which were the smallest. Dietary diversity correlated positively with wing length. Received 26 December 1990, accepted 8 June 1991.

INDIVIDUAL differences are important to document, for it is variation among individuals on which natural selection acts. Individual differences in foraging behavior and food choice have been noted in a wide range of animal taxa, including invertebrates (Heinrich 1976, Rissing 1981, West 1986), fish (Bryan and Larkin 1972, Ringler 1983, 1985), reptiles (Arnold 1981), and mammals (Ritchie 1988). Variation in food choice by individual birds has been reported, but only occasionally quantified (Inman et al. 1987, Pirotti and Annett 1987, Price 1987, Werner and Sherry 1987, Joern 1988, Rowley et al. 1989, Grundel 1990). Differences in fruit choice by individual birds also have been shown, but most studies suffer from small sample sizes, which preclude strong statistical inference (Heppner 1965, Brown 1974, Moermond and Denslow 1983, Levey et al. 1984, Borowicz 1988, Levey

and Karasov 1989, Willson et al. 1990, Levey and Grajal 1991).

Apparently, no investigators have tested whether individual morphometric variation in birds is associated with differences in fruit choice, or examined in detail how variation in fruit quality may influence fruit choice by individual birds. Interspecific differences in fruit choice correlate with morphological differences among species, particularly bill dimensions (Herrera and Jordano 1981, Moermond and Denslow 1985, Wheelwright 1985, Moermond et al. 1986, Jordano 1987). Individual differences in selection and in handling time of both invertebrate prey and seeds have also been related to morphometric variation (Herrera 1978, Grant 1981, Paszkowski and Moermond 1984, Gosler 1987, Price 1987). Differences in fruit choice among bird species have been related to fruit

abundance and to characteristics of fruits, such as accessibility, color, and seed size (Denslow and Moermond 1982, Moermond and Denslow 1983, Sorensen 1984, Johnson et al. 1985, Wheelwright 1985, Levey 1987a, b, McPherson 1987, 1988, Moermond et al. 1987, Willson et al. 1990, Levey and Grajal 1991). Species and intraspecific differences in taste (Sorensen 1983, Levey 1987b), digestive capacities (Sorensen 1984, Johnson et al. 1985, Martínez del Rio et al. 1989, Levey and Karasov 1989), and visual acuity and color vision (Kear 1964, Willson et al. 1990) also may be related to fruit choice.

In this study, I quantified individual differences in fruit choice by American Robins (*Turdus migratorius*), and examined whether these differences were related to variation in fruit quality (mass, percent water, refractive index, trial date, source plant) or to characteristics of individual birds (age, sex, morphology). Dietary diversity was also tested in relation to morphometrics. I repeatedly observed individuals to allow explicit tests for individual differences.

I studied the American Robin because it is abundant, it is relatively easy to maintain in captivity, and it is one of nine species in eastern North America whose diet is made up of a substantial portion of fruit (Martin et al. 1951, Willson 1986). Robins in the eastern and midwestern United States consume at least 65 wild and 10 cultivated fruit species (Beal 1915, Brown 1974) from 50 genera (Wheelwright 1986). Between June and August, when this study was conducted, fruits may constitute 56–79% of the diet of robins (Forbes 1880, Hamilton 1940). Fruits alone do not meet the energy and nutrient requirements of robins (Levey and Karasov 1989); robins also eat fish (Bayer 1980), snakes (Richmond 1975), small mammals (Powers 1973), and many invertebrates, including molluscs (Hamilton 1940).

I offered robins a three-way choice of white mulberry, Bella honeysuckle, and red-osier dogwood fruits. These fruits represent three of the most abundant summer fruits in Madison, Wisconsin. Seed dispersal in Bella honeysuckle is primarily by birds (Kreftin and Roe 1949, Hauser 1966), and dogwood and mulberry species are among the 10 most common fruits in stomach contents of robins (Wheelwright 1986). White mulberry and Bella honeysuckle were introduced to the United States before 1770 and 1878, respectively (Barnes 1972, Petrides 1986).

## METHODS

Birds were captured using mist nets (12-m, 4-shelf, 36-mm mesh) in Madison, Wisconsin, and transported immediately to aviary cages. From 26 June to 8 August, 1990, we captured 35 American Robins (19 juveniles, 7 adult females, 9 adult males). Sex of adults was determined by plumage and the presence of a brood patch, whereas sex of juveniles cannot be determined by plumage (Gochfeld and Burger 1984); laparotomies were not performed. Robins were housed individually in nine outdoor aviaries (2.40 × 2.03 × 1.75 m). Occupants were isolated visually from their neighbors by hanging cloth on the adjoining sides of cages. This prevented observational learning, known to influence food choice in some birds (Mason and Reidinger 1981). Except during fruit-choice trials, robins were given water *ad libitum* and maintained on red marsh worms (*Lumbricus rubellus*), medium-sized mealworms (*Tenebrio molitor*), a hamburger-carrot-egg-eggshell diet (modified Lanyon recipe; S. Wendel, pers. comm.), and a banana-and-soy-protein fruit diet (Denslow et al. 1987). Individual differences were noted in food consumption, but they were not quantified. Birds were fed approximately equal amounts of all food items daily at 0800, 1300, and 1800 (if not on trial) or 1900 (if on trial).

Morphometric data were recorded upon capture ( $n = 35$  birds) and, for a subset of individuals ( $n = 24$ ), upon release. I used a 100-g Pesola scale for mass (to 0.1 g), a Rose wing measure (to 0.1 cm) for wing chord, and Tajima dial calipers (to 0.1 mm) for bill measurements. For analyses, mass at release, rather than at capture, was used for two birds, because of missing data and egg reabsorption. Wing measurements at release were less reliable than other morphometric data, because many birds had frayed wings from flying against the cage. The tarsal length was measured from the notch on the back of the intertarsal joint to the lower edge of the last complete scale before the toes begin. Bill length was measured as exposed culmen, and bill width and depth were measured at the anterior edge of the nostril perpendicular to the commissure. The middle toe-hallux was measured on the flattened foot from the tip of the middle toe to the tip of the hallux (excluding claws).

Each bird experienced six fruit-choice trials over a 10-day period. Birds were given two days to become accustomed to aviary conditions before testing, and trials were conducted on days 3 and 4, 6 and 7, and 9 and 10 of captivity from 1800 to 1900. This time was chosen because robin stomach contents are reported to contain a higher proportion of fruits in the afternoon than in the morning (Wheelwright 1986). For the trials, 15 fruits of each of three species—white mulberry (red variety), *Morus alba* L.; Bella honeysuckle, *Lonicera × bella*, (a hybrid of *L. tatarica* and *L. morrowi*, Barnes 1972), and red-osier dogwood, *Cornus stolonifera* Michx.—were placed haphazardly within

a 150 × 20 mm Pyrex petri dish. Maintenance food was removed when trial dishes were presented.

The trial length and number of fruits presented were chosen to minimize the possibility that any individual would consume all fruits of a given species. Preliminary experiments showed that fruits dried or stuck to the petri dish within an hour. I therefore misted 0.5 to 1.0 g of water onto the dish before adding fruits. This practice prevented the use of mass of fruit consumed as a variable in the analysis of individual differences.

Because only nine cages were available, birds were in captivity at different times (Appendix 1) and potentially did not experience the same quality of fruits. To assess fruit quality, I collected data each day on fruit mass, percent water, and refractive index. Mean mass was determined for each fruit species in each trial dish by dividing the total fruit mass by the number of fruits offered ( $n = 15$ ). Percent water was determined by drying five weighed fruits for 48 h (sufficient to yield constant mass) at 55°C. Refractometer readings were made on five additional fruits of each species (using an Otago Co., Japan, ATC 1 Brix 0–32% refractometer). Whole fruits were crushed onto the refractometer prism surface to express juice. Although refractive index has been equated with percent soluble sugar (Denslow 1987), White and Stiles (1985) showed that refractive index best correlates with the percent total lipid-free solute concentration of a fruit. Mulberry fruits have a greater crude protein content (11.6%) than either honeysuckle (8.0%) or dogwood (6.9%) on a dried-fruit basis (Wainio and Forbes 1941, King and McClure 1944, Bonner 1974). Dogwood fruits have a higher fat content (12.0%) than mulberry (3.8%) or dogwood (3.9%).

The ripest fruits available and within reach (a 2.4-m ladder was used to collect mulberry fruits) were chosen for trials. Fruits were collected 1–2 h before trials. Four mulberry trees, three honeysuckle, and four dogwood bushes in the Madison area were used. Depletion of accessible ripe fruits prevented use of a single shrub or tree of each species. Ripeness was determined in the field by color comparisons with color swatches in Smithe (1975). White mulberry fruits were jet black (Color 89) throughout the study. Bella honeysuckle fruits were initially intermediate between geranium (12), spectrum red (11), and carmine (8), and shifted to carmine by 7 July. Red-osier dogwood was primarily pearl gray (81), yet appeared smoke gray (44) or tinted with green (i.e. not fully ripe) for trials in June and early July.

*Statistical analyses.*—I used the “forage ratio” (Jacobs 1974) or “Index 4” of Cock (1978) to calculate fruit preference (based on numbers of fruit eaten) for each fruit species:

$$\text{Fruit preference} = (\text{fruit A} + 1) \div [(\text{fruit B} + 1) + (\text{fruit C} + 1)].$$

The one was added for each fruit to avoid division

by zero. Thus, a fruit preference of 0.5 indicates no preference for the species in the numerator (including cases in which no fruits of any species were eaten). Values greater than 0.5 indicate positive preference and values less than 0.5 indicate negative preference relative to other fruits. This index can be applied, because no bird ever ate all 15 fruits of one species in a single trial (Appendix 2).

My study was not designed specifically to quantify differences in fruit quality among individual plants. Nevertheless, variation in fruit quality or among individual plants was unavoidable over the course of the experiment. Because this has the potential to influence fruit choice, fruit quality was assessed. Tests for variation in fruit quality were complicated by the fact that individual plants generally were used sequentially over the trials. I used one-way analyses of covariance (ANCOVAs) to test simultaneously for effects of date (as the covariate) and source plants (as factors) on fruit quality.

I used stepwise multiple-regression analyses to test whether fruit choice was related to fruit-quality measures. The independent variable (number of fruit eaten or preference for each fruit species) was regressed on variables indicating fruit quality, trial date, and (trial date)<sup>2</sup>, as well as fruit source and age/sex cohorts (coded as dummy variables; Kleinbaum and Kupper 1978). To reduce multicollinearity, the covariate (trial date)<sup>2</sup> was created by standardizing and then squaring trial date. Based on analysis of residuals, fruit-consumption residuals were log-transformed, whereas log, square root, and inverse transformations were used for the mulberry, honeysuckle, and dogwood preference ratios, respectively. Variables significant at the  $P < 0.05$  level were retained, and residuals were computed. In these analyses, all 210 trials (35 birds × 6 trials/bird) were treated as independent data points.

To test for effects of age or sex, individual bird, replicated trial, and the interaction of bird and trial, I performed two-way nested analyses of variance (ANOVA) on the preference residuals, which were approximately normally distributed (skewness < 0.001; kurtosis range = 0.060–2.383) and homoscedastic (Cochran’s  $Q$  and Bartlett’s Box  $F$  tests). The two-way nested ANOVAs used in the analysis are the equivalent of repeated-measures ANOVAs, because I combined trials 1 and 2, 3 and 4, and 5 and 6 as three repeated measures of the same individual (see Sokal and Rohlf 1981:344, substituting two numbers per cell for the one number per cell in their example). I used one-way Kruskal-Wallis ANOVAs to compare age and sex groups for residual numbers of fruit eaten and preference indices. One-way ANOVAs and ANCOVAs were used to compare morphometrics of males and females, and of adults and juveniles.

Residuals from the fruit consumption and preference multiple-regression analyses ( $n = 210$ ) were summed by bird (6 residuals for each bird) to yield 35 values. I tested these composite values for corre-



Fig. 1. Total number of mulberry fruits eaten versus total number of dogwood fruits eaten in six trials by 35 American Robins.

lations with the morphometric data by bivariate-correlation and multiple-regression analyses. The middle-toe-to-hallux measurement was excluded because of missing data, but the bill index, computed as bill depth/bill length (Gosler 1987), was tested. Adult vs. juvenile, and male vs. female, were treated as dummy variables in the multiple regression as a final test for age and sex differences. I performed multiple-regression analysis to relate dietary diversity (Morton and Davies 1983) to morphometric variables.

All statistical analyses were performed using the Statistical Package for the Social Sciences (SPSS/PC+, version 3.1; Norusis 1988). Significance was set at the 0.05 level in all cases.

RESULTS

The total numbers of the three fruit species eaten by the 35 robins differed significantly ( $\chi^2 = 256.47$ ,  $df = 2$ ,  $P < 0.001$ ). Birds ate 318 mulberries as compared with 150 dogwood fruits and only 28 honeysuckle fruits (Appendix 1). Friedman two-way ANOVA comparing the total numbers eaten across all 35 birds confirmed this result ( $\chi^2 = 26.3$ ,  $df = 2$ ,  $P < 0.0001$ ).

*Analysis of raw data for individual differences in fruit choice.*—The numbers of fruits consumed in single 1-h trials ranged from 0 to 8 for mulberry, 0 to 4 for honeysuckle, and 0 to 13 for dogwood for all birds. The greatest number of fruits consumed in a single trial was 15 (2 mulberry + 13 dogwood). In 38.6% of the trials, no fruits were eaten (Appendix 2). Summing over all trials, the total number of fruits eaten ranged from 0 to 63 for individual robins (Appendix 1). Of 13 birds that ate more than 15 fruits total (allowing expected frequencies greater than five per cell in chi-square tests; Siegel 1956), 11 showed significant differences in the numbers of the three fruit species eaten. Of these birds, eight ate mostly mulberry and two ate mostly

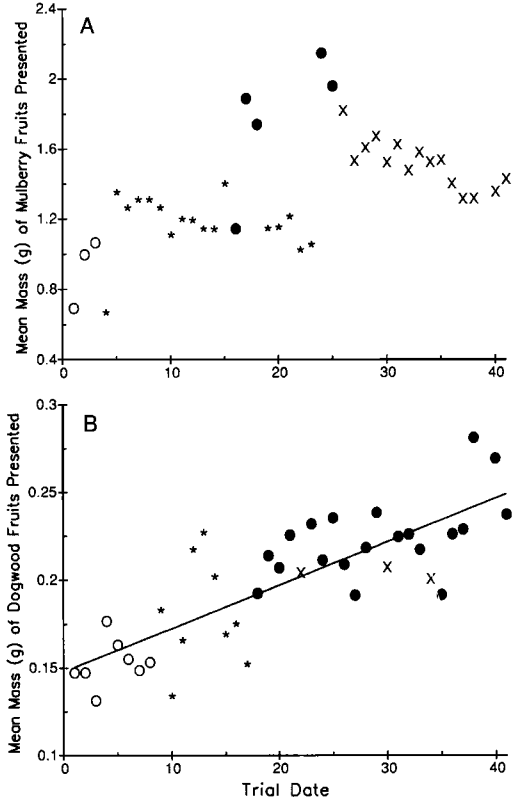


Fig. 2. Mean mass of (A) mulberry and (B) dogwood fruits given to American Robins over 40 trial days. Trial date 1 was 29 June 1990. Each point represents mean value for 1-9 dishes of 15 fruits each. Symbols represent individual plants:  $\circ$  = plant 1, \* = plant 2,  $\bullet$  = plant 3,  $\times$  = plant 4.

dogwood; only one bird ate significantly fewer honeysuckle than mulberry and dogwood fruits.

For birds that ate 6 to 15 fruits, I used binomial tests to compare the numbers of the fruit eaten most frequently against the sum of the two fruits eaten the least. Of these 10 birds, 7 ate significantly more mulberry than the other two fruits combined. In summary, 15 birds ate mostly mulberry, 2 birds ate mostly dogwood, and no birds ate mostly honeysuckle. Typically, individuals that consumed the most dogwood fruits ate few mulberries, and vice versa (Fig. 1).

To determine consistency of fruit choice from trial-to-trial, I compared—using cumulative binomial probabilities (Wonnacott and Wonnacott 1985:table IIIc)—the numbers of trials in which birds ate more of one fruit than the other fruits. Thirteen of the 15 birds that preferred

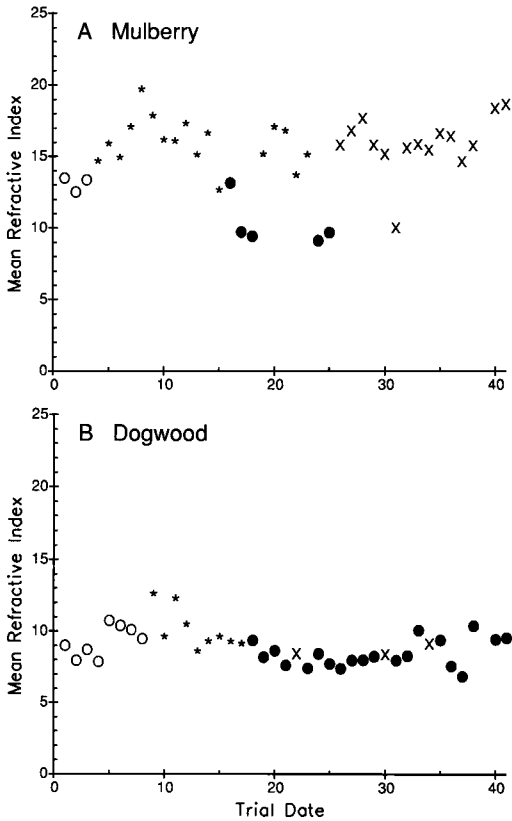


Fig. 3. Mean refractive index of (A) mulberry and (B) dogwood fruits given to American Robins over 40 trial days. Each point represents mean of five individual fruits. Symbols represent individual plants: ○ = plant 1, \* = plant 2, ● = plant 3, × = plant 4.

mulberry and both that preferred dogwood were significantly consistent in their choice across trials. Eleven birds consistently ate no fruits, and nine were inconsistent in fruit choice across trials (Appendix 2).

*Analysis of raw data for age/sex differences in fruit choice.*—Some individual differences in fruit choice could be the result of differences between juveniles and adults or between adult males and females. However, neither fruit consumption nor preference (summed across all six trials) differed between age or sex groups (Kruskal-Wallis one-way ANOVAs). To test whether juveniles might be more variable in fruit choice than adults (Wheelwright 1986, Willson et al. 1990), I also compared age groups in terms of: (1) the standard deviation of the number of fruit species eaten per trial by each individual; and (2) the maximum number of fruit species eaten

TABLE 1. Indices of fruit quality of fruits used in choice trials.<sup>a</sup> Values represent means  $\pm$  SD of 40 trial days (range in parentheses).

Fruit mass (g)	Percent water	Refractive index
<b>Mulberry</b>		
1.35 $\pm$ 0.311 (0.66–2.14)	80.89 $\pm$ 2.634 (76.30–87.10)	15.01 $\pm$ 2.601 (9.12–19.66)
<b>Honeysuckle</b>		
0.87 $\pm$ 0.093 (0.68–1.13)	80.00 $\pm$ 1.847 (76.90–83.70)	15.99 $\pm$ 1.801 (11.24–19.14)
<b>Dogwood</b>		
0.20 $\pm$ 0.036 (0.13–0.28)	75.40 $\pm$ 2.236 (70.70–79.80)	9.01 $\pm$ 1.241 (6.88–12.60)

<sup>a</sup> In all cases  $n = 40$ , each of which represents means of one to nine values for fruit mass, and means of five values for percent water and refractive index.

in any or all of the trials (Kruskal-Wallis one-way ANOVAs). Both tests were not significant, and I conclude that juveniles were not more variable than adults in fruit choice.

*Fruit-quality variation.*—The mean mass, percent water, and refractive index of the three fruit species varied (Table 1). Fruit quality by trial date showed complicated trends over time and within individual source plants (Figs. 2 and 3). The ANCOVA of mean mass of fruits given in trials were significantly different among source plants for both mulberry ( $F = 12.32$ ,  $df = 3$  and 35,  $P < 0.001$ ; for date,  $F = 3.86$ ,  $df = 1$  and 35,  $P = 0.538$ ; Fig. 2A) and honeysuckle ( $F = 4.82$ ,  $df = 2$  and 36,  $P = 0.014$ ; for date,  $F = 1.00$ ,  $df = 1$  and 36,  $P = 0.323$ ; not shown). For dogwood, ANCOVA indicated that mean fruit mass increased significantly with date ( $F = 5.53$ ,  $df = 1$  and 35,  $P = 0.024$ ), but did not vary significantly among plants ( $F = 1.75$ ,  $df = 3$  and 35,  $P = 0.175$ ; Fig. 2B). The percent water of mulberry ( $F = 4.56$ ,  $df = 3$  and 35,  $P = 0.008$ ; for date,  $F = 0.080$ ,  $df = 1$  and 35,  $P = 0.786$ ) and honeysuckle fruits ( $F = 4.28$ ,  $df = 2$  and 36,  $P = 0.022$ ; for date,  $F = 1.86$ ,  $df = 1$  and 36,  $P = 0.181$ ) differed among plants. Finally, the mean refractive index of fruits from individual mulberry ( $F = 15.73$ ,  $df = 3$  and 35,  $P < 0.001$ ; for date,  $F = 0.125$ ,  $df = 1$  and 35,  $P = 0.725$ ; Fig. 3A) and dogwood ( $F = 3.68$ ,  $df = 3$  and 35,  $P = 0.021$ ; for date,  $F = 1.08$ ,  $df = 1$  and 35,  $P = 0.305$ ; Fig. 3B) plants differed significantly. For honeysuckle, the refractive index increased significantly with trial date ( $F = 5.50$ ,  $df = 1$  and 36,  $P = 0.025$ ), but did not differ among plants ( $F = 0.76$ ,  $df = 2$  and 36,  $P = 0.474$ ; not shown).

TABLE 2. Fruit-preference residuals in relation to replicated trial ( $n = 3$ ), bird ( $n = 35$ ) within age/sex group ( $n = 3$ ), and bird by trial interaction (two-way nested ANOVAs). Mulberry-preference residuals were log-transformed, honeysuckle-preference residuals were square-root transformed, and inverse of dogwood-preference residuals were used to improve normality.

Source of variation	Sum of squares	df	Mean square	F	P
<b>Mulberry-preference residuals</b>					
Within cells	3.49	105	0.03		
Trial	0.19	2	0.09	2.86	0.062
Age/sex	0.03	2	0.02	0.49	0.614
Bird by trial	4.97	68	0.07	2.20	<0.001
Bird within age/sex	15.27	33	0.46	13.94	<0.001
<b>Honeysuckle-preference residuals</b>					
Within cells	1.06	105	0.01		
Trial	0.00	2	0.00	0.08	0.927
Age/sex	0.03	2	0.02	1.56	0.216
Bird by trial	1.37	68	0.02	1.99	0.001
Bird within age/sex	2.55	33	0.08	7.62	<0.001
<b>Dogwood-preference residuals</b>					
Within cells	163.43	105	1.56		
Trial	34.38	2	17.19	11.05	<0.001
Age/sex	3.53	2	1.77	1.13	0.325
Bird by trial	245.86	68	3.62	2.32	<0.001
Bird within age/sex	458.35	33	13.89	8.92	<0.001

*Effects of variation in fruit quality on fruit choice.*—Stepwise multiple regression of fruit consumption data revealed that mean mulberry mass explained 6.9% of the variation in the number of mulberry fruits eaten ( $F = 15.40$ ,  $df = 1$  and  $208$ ,  $P = 0.0001$ ); fewer fruits were eaten when mulberries were larger. Trial date explained 3.8% of the variation in the number of honeysuckle fruits eaten ( $F = 8.09$ ,  $df = 1$  and  $208$ ,  $P = 0.0049$ ); no honeysuckle fruits were eaten after 19 July. (Trial date)<sup>2</sup> explained 3.3% of the variation in dogwood consumption ( $F = 7.08$ ,  $df = 1$  and  $208$ ,  $P = 0.0084$ ), with more dogwood eaten during trials from mid-July to late July.

Regression analyses for fruit-preference data yielded slightly different results than for fruit-consumption data. Mulberry preference was related significantly to (trial date)<sup>2</sup> ( $r^2 = 7.1\%$ ,  $F = 15.80$ ,  $df = 1$  and  $208$ ,  $P = 0.0001$ ) and positively to mulberry refractive index ( $r^2 = 2.3\%$ ,  $F = 10.74$ ,  $df = 1$  and  $208$ ,  $P < 0.0001$ ). Honeysuckle percent water (positive slope,  $r^2 = 2.2\%$ ,  $F = 4.65$ ,  $df = 1$  and  $208$ ,  $P = 0.0322$ ) and mean mulberry mass (positive slope,  $r^2 = 2.2\%$ ,  $F = 4.66$ ,  $df = 2$  and  $207$ ,  $P = 0.0105$ ) explained a small amount of the variation in honeysuckle preference. (Trial date)<sup>2</sup> explained 4.5% of the variance for dogwood preference ( $F = 9.82$ ,  $df = 1$  and  $208$ ,  $P = 0.002$ ). Source plant and bird

age/sex were never significant predictors of fruit-choice indices.

Fisher exact tests were used to examine whether birds preferred fruits from certain conspecific plants over others. Source plants were tested in pairwise comparisons of the number of trials when a source plant's fruits were preferred (number eaten greater than that of the other two fruit species) versus not preferred. The only significant differences were between mulberry trees 2 and 4 in comparison with tree 3, due to the low preference by robins for the high-mass and low-refractive-index fruits from tree 3 (Figs. 2A and 3A).

*Analysis of residuals for individual and age/sex differences in fruit choice.*—I used nested two-way ANOVAs to analyze the residuals from the previous multiple regressions. Individual birds were nested within age and sex categories (adult male, adult female, juvenile) by repeated-measures trials ( $n = 3$ ). Individual birds within age/sex groups, and bird  $\times$  trial interactions, were significant for all fruits (Table 2). The bird  $\times$  trial interaction indicated that individuals showed nonparallel changes in preference across trials. Trial was significant only for dogwood. Bird age/sex was not significant for any of the fruit-preference residuals. Thus, although indices of fruit quality and/or trial date

TABLE 3. Pearson product-moment correlation coefficients (above) and two-tailed significance (below) between residual fruit preference statistics and selected morphometric variables, as well as among morphometric variables.

	Mass (capture)	Wing chord	Tarsus length	Bill		
				length	depth	width
Mulberry consumption	0.448 0.007	0.050 0.774	0.258 0.134	0.197 0.257	0.094 0.591	-0.013 0.941
Honeysuckle consumption	0.189 0.276	0.192 0.270	0.324 0.058	0.087 0.620	-0.109 0.532	0.052 0.765
Dogwood consumption	-0.154 0.377	0.095 0.589	0.094 0.590	-0.081 0.643	-0.390 0.021	-0.060 0.731
Mulberry preference	0.388 0.021	-0.031 0.858	0.103 0.557	0.171 0.325	0.344 0.043	-0.031 0.860
Honeysuckle preference	-0.086 0.624	0.039 0.826	-0.091 0.605	-0.066 0.707	0.057 0.745	0.101 0.563
Dogwood preference	-0.433 0.009	-0.004 0.980	-0.236 0.173	-0.258 0.135	-0.347 0.041	-0.027 0.880
Mass (capture)		0.294 0.086	0.243 0.159	0.353 0.037	0.239 0.166	0.350 0.039
Wing chord			0.307 0.073	0.221 0.202	0.084 0.632	0.124 0.479
Tarsus length				0.215 0.215	0.216 0.213	0.010 0.955
Bill length					0.496 0.002	0.376 0.026
Bill depth						0.394 0.019

explained small but significant amounts of the variance in fruit choice, individual differences in fruit choice were still highly significant even after I controlled for these effects.

*Fruit choice in relation to morphometric variation.*—All measurements taken at capture and release were significantly repeatable ( $r = 0.488$  to  $0.948$ ). Over the 10-day period, juveniles gained significantly more mass than did adults (Kruskal-Wallis one-way ANOVA,  $X^2 = 5.83$ ,  $n = 34$ ,  $P = 0.0158$ ). Adults and juveniles differed significantly in wing chord (one-way ANOVA,  $P = 0.028$ ), bill length ( $P = 0.006$ ), bill width ( $P = 0.007$ ), bill depth ( $P = 0.004$ ), and mass at capture ( $P = 0.030$ ), but not for tarsus length, middle toe-hallux, or mass at release. After accounting for mass differences, adults had larger bills than did juveniles, but not larger wings (ANCOVA). None of the ANOVAs comparing adult male and female morphometric characters were significant. Morphometric variables were positively (though not all significantly) correlated with each other (Table 3), but not so strongly as to preclude valid multiple regression analyses due to multicollinearity (no pair-

wise correlations exceed  $r = 0.70$ ; Slinker and Glantz 1985).

Mulberry fruit-consumption residuals were significantly predicted by bird mass (Table 3). Dogwood-consumption residuals were significantly related only to bill depth. However, the result was unreliable, because the regression was significant due to the effect of only one robin, which had the smallest bill depth and ate the greatest number of dogwood fruits. None of the fruit-consumption residuals were significantly intercorrelated (mulberry and honeysuckle,  $r = 0.277$ ,  $P = 0.108$ ; mulberry and dogwood,  $r = -0.087$ ,  $P = 0.619$ ; honeysuckle and dogwood,  $r = -0.001$ ,  $P = 0.998$ ).

For preference residuals, mulberry and dogwood preference were significantly related only to bird mass (Fig. 4, Table 3). Mulberry- and dogwood-preference residuals were significantly correlated ( $r = -0.862$ ,  $n = 35$ ,  $P < 0.001$ ; see also Fig. 1). Principal-components analyses yielded similar results and are not reported. I repeated the multiple-regression analyses with age and sex groups treated as dummy variables, but neither age nor sex was significant in ex-

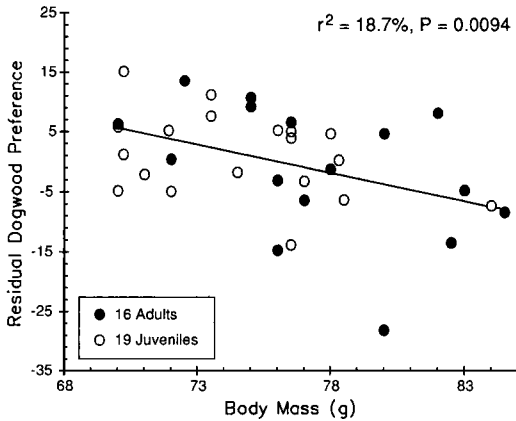


Fig. 4. Residual fruit preference of dogwood versus body mass.

plaining fruit consumption or preference residuals.

A multiple regression was used to examine whether dietary diversity ( $1/\sum p_i^2$ , where  $p_i$  refers to the proportion in the diet of the  $i^{\text{th}}$  fruit species eaten over 6 trials; Morton and Davies 1983) was related to morphometric variables or age (adult vs. juvenile). Dietary diversity related significantly only to wing chord ( $r^2 = 12.8\%$ ,  $F = 4.823$ ,  $df = 1$  and  $33$ ,  $P = 0.0352$ ; Fig. 5).

#### DISCUSSION

*Individual differences.*—As a group, robins preferred mulberry and avoided honeysuckle fruits, but I found consistent individual differences in fruit choice. These differences were not due to age or sex, and cannot be explained solely by differences in fruit quality. Only variation in bird mass (independent of age) had some predictive value for fruit choice.

The individual variation present in juveniles suggests that differences in fruit choice are innate or learned before, during, or soon after fledging (cf. Rabinowitch 1969). Young robins do not become completely independent until approximately two weeks after fledging, at which time they are fed by parents but are learning to forage on their own (Young 1955). After independence, juveniles often form foraging flocks (Hirth et al. 1969). Presumably by observing parents and other conspecifics—or through trial and error, as has been suggested for the Cocos Finch (*Pinaroloxias inornata*; Werner and Sherry 1987)—young birds may develop individual fruit preferences. An interest-

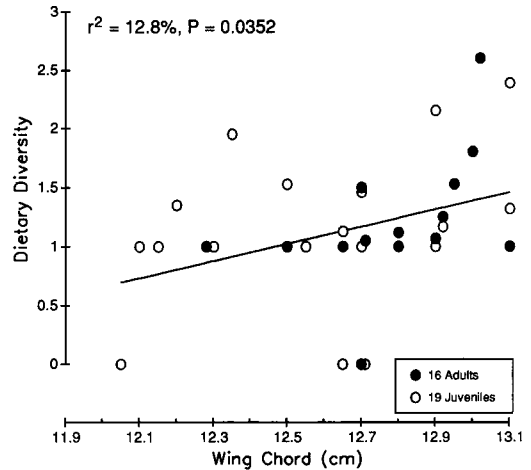


Fig. 5. Dietary diversity in relation to wing chord.

ing area for future research would be to determine the relative magnitudes of environmental (e.g. via learning) and genetic (cf. Arnold 1981) influences on the origin and development of individual differences in fruit choice by birds.

Although adult and juvenile robins differed in body mass and in bill dimensions (even after accounting for mass differences), I found no age differences in fruit choice. Wheelwright (1986) showed that stomachs of wild-caught juvenile robins contained a higher proportion of fruits than did stomachs of adults. Age-specific differences in foraging ability may be responsible for this difference, as fruits are an easier prey than invertebrates for juveniles (Gochfeld and Burger 1984). In my work, juveniles did not consume more fruit species or show greater variability in fruit choice than adults, which counters the intuitive idea that juveniles should be more variable in fruit choice (Wheelwright 1986, Willson et al. 1990). In agreement with my results, Wheelwright (1986) found, based on stomach content data, that adult male and female robins have similar diets throughout the year.

Feeding specializations over an entire year have been noted in individual Cocos Finches in the wild (Werner and Sherry 1987). In comparison, it is not known whether an individual robin's fruit preference is stable over the summer, much less from year-to-year. Previous studies have reported that captive groups of robins show temporal changes in fruit preference (Jones and Wheelwright 1987, Wheel-



wright 1988). In my study, trial date, which may reflect temporal changes in fruit quality, fruit preference, or both had a small but significant effect on fruit choice.

*Fruit quality and potential influences on fruit choice.*—Although this study was not designed to determine why robins preferred a particular fruit species, fruit characteristics (as well as date) explained a small amount of variation in fruit choice. Fewer mulberries were eaten and honeysuckle fruits tended to be preferred when mulberries were large. Honeysuckle fruits were preferred when their percent water was high, and mulberry was preferred when mulberry refractive index was high. Birds can detect variation in fruit sugar and may select sweeter fruits (Levey 1987b). Mulberries have the greatest crude protein content, whereas dogwood fruits have the highest fat content relative to the other fruits, and differences in nutritional value may influence a bird's fruit choice. I also suggest that birds may preferentially forage from certain source plants with superior fruit qualities (cf. Grieg-Smith and Willson 1985). As noted previously, temporal variation in fruit choice may be due to temporal variation in fruit quality or color, or might be due to intrinsic seasonal changes in preference by birds.

Color, secondary compounds, and seed size may have affected fruit choice in my experiments. Black is the most common color of fruits of bird-dispersed plants, and when a black fruit such as mulberry is presented with a red fruit (honeysuckle), black may signify ripeness and red may indicate unripeness (Wheelwright and Janson 1985, Willson and Thompson 1982). Birds avoid wild and artificial fruits that contain secondary compounds (Herrera 1982, Sorensen 1983). Fruits in the genus *Cornus* contain aucubin (Sherburne 1972), and *L. tatarica* (one parent of *L. ×bella*) fruits contain saponin, a glycoside, known to cause death in robins (Bergtold 1930). The multiple, small seeds of mulberries usually pass through the gut of a bird (Beal 1915), whereas the larger dogwood stones (containing 0–2 seeds) are primarily regurgitated (Borowicz 1988). Honeysuckle seeds (5–7 per berry) may be either regurgitated or defecated. Whether these differences affected fruit choice in the present trials is unknown (cf. Sorensen 1984, Johnson et al. 1985, Levey and Grajal 1991).

*Morphometrics and fruit choice.*—I found that individual variation in body mass (but not in wing, tarsus, or bill dimensions) correlated with

differences in fruit consumption and preference. Heavier robins tended to eat more and prefer the larger mulberry fruits. Smaller birds preferred the smaller dogwood fruits. Smaller robins may have higher metabolic rates and energy requirements relative to body mass than do larger individuals, and may prefer lipid-rich fruits, such as dogwood. This is consistent with Herrera's (1985) observation that the proportion of lipid-rich fruits in the diet of avian frugivores decreases with increasing body weight. One possible reason for a lack of correlation between bill dimensions and fruit choice might be a low repeatability of morphometric measurements. However, repeatabilities in my study were all significant and compare favorably with those reported by other workers (Smith and Zach 1979, Boag 1983, Price and Grant 1984, Gosler 1987).

Interspecific comparisons show that differences in locomotor morphology (e.g. wing loading, leg structure) may correlate with fruit choice (Moermond and Denslow 1985, Moermond et al. 1987). I found that dietary diversity was significantly related to wing chord. Perhaps individuals with longer wings (and so possibly lower wing loading) were better able, when in the wild, to exploit more fruit species (fruits are taken by robins both in flight and when perched; Paszkowski 1982).

Several authors have correlated morphometric variation with individual differences in food choice in birds. For example, individual differences in size account for some feeding variation in *Geospiza fortis* (Grant 1981, Price 1987). Correlations between bill dimensions and diets within species have been reported (e.g. Herrera 1978, Paszkowski and Moermond 1984, Gosler 1987). Wiens and Rotenberry (1980:287), on the other hand, found little correlation between morphology and diet within species and believe that "close associations between morphology and ecology are obscured by the substantial variability in both," although James and McCulloch (1985) have expressed concern over the statistical analyses employed. Morphometric differences did not explain variation in individual food choices in the Cocos Finch (Werner and Sherry 1987).

*Implications for plant–bird coevolution.*—Dietary specialization of individual birds under natural conditions may be due to both extrinsic (e.g. environmental) and intrinsic factors. I believe that some of the variation (e.g. Werner and

Sherry 1987) may reflect inherent differences among individuals, differences that are quantifiable under controlled laboratory conditions. Future studies should address the consistency with which individual preferences are expressed under natural conditions, such as when individuals are in flocks or are faced with numerous food choices at different times of the year. Moreover, what has yet to be demonstrated in any study is that differences in fruit preference translate into differential fitness (i.e. that selection acts on preferences) or that preferences have a heritable basis (but see Arnold 1981). Regardless of its selective consequences or genetic bases, consistent individual variation in fruit choice by seed dispersers, such as robins, may influence plant community dynamics. For example, seeds of preferred fruit species may be proportionately overrepresented in an individual bird's territory, with the consequence that preferred plants may come to dominate areas in which individual dispersers with distinct preferences reside (cf. Herrera 1985).

Recently, M. F. Willson and C. J. Whelan (unpubl. manuscript) compared individual *Cornus drummondii* shrubs to study potential relationships between certain fruit (e.g. lipid and protein content) and plant (e.g. crop size) traits, on the one hand, and fruit removal rates, dispersal efficiency, and seed dispersal success, on the other. They found great variation in space and time in these relationships, and suggest that environmental variation and aspects of avian behavior, such as flocking and social organization, may influence fruit removal more than do characteristics of individual fruiting plants. Similarly, even in my controlled laboratory experiment, although variation in fruit quality explained significant amounts of the variance in fruit choice, the absolute amount of variation explained (i.e. the multiple  $r^2$  in regressions) was quite small (always <10%). Such results are consistent with the idea that coevolution between frugivores and fruiting plants is generally "diffuse" (Wheelwright and Orians 1982), as compared with coevolution between pollinators and plants. Variability in the determinants of fruit choice and in the site of seed deposition, as well as the influence of postdispersal agents and environmental factors, may allow only weak natural selection due to interactions between frugivorous birds and fruiting plants (M. F. Willson and C. J. Whelan, unpubl. manuscript).

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## LITERATURE CITED

- ARNOLD, S. J. 1981. Behavioral variation in natural populations. II. The inheritance of a feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans*. *Evolution* 35:510-515.
- BARNES, W. J. 1972. The autecology of the *Lonicera × bella* complex. Ph.D. dissertation, Univ. Wisconsin, Madison.
- BAYER, R. D. 1980. Novel use of an unusual food: American Robins (*Turdus migratorius*) eating parts of fish. *J. Field Ornithol.* 51:74-75.
- BEAL, F. E. L. 1915. Food of the robins and bluebirds of the United States. U.S. Dep. Agric. Tech. Bull. 171:1-31.
- BERGTOLD, W. H. 1930. Intoxicated robins. *Auk* 47: 571.
- BOAG, P. T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galapagos. *Evolution* 37: 877-894.
- BONNER, F. T. 1974. Chemical components of some southern fruits and seeds. U.S. Dep. Agric. For. Serv. Res. Note SO-13:1-3. South. For. Exp. Stn., New Orleans.
- BOROWICZ, V. A. 1988. Fruit consumption by birds in relation to fat content of pulp. *Am. Midl. Nat.* 199:121-127.
- BROWN, R. G. B. 1974. The bird damage problem in southern Ontario. *Can. Wildl. Serv. Rep. Ser.* 27: 1-56.
- BRYAN, J. E., AND P. A. LARKIN. 1972. Food specialization by individual trout. *J. Fish Res. Bd. Canada* 29:1615-1624.
- COCK, M. J. W. 1978. The assessment of preference. *J. Anim. Ecol.* 47:805-816.
- DENSLOW, J. S. 1987. Fruit removal rates from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Can. J. Bot.* 65:1229-1235.
- 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.
- DENSLOW, J. S., AND T. C. MOERMOND. 1982. The

- effect of accessibility on rates of fruit removal from tropical shrubs: An experimental study. *Oecologia* (Berlin) 54:170-176.
- FORBES, S. A. 1880. The food of birds. Bull. Ill. State Lab. Nat. Hist. 1:80-148.
- GOCHFELD, M., AND J. BURGER. 1984. Age differences in foraging behavior of the American Robin (*Turdus migratorius*). *Behaviour* 88:227-239.
- GOSLER, A. G. 1987. Pattern and process in the bill morphology of the Great Tit *Parus major*. *Ibis* 129:451-476.
- GRANT, P. R. 1981. The feeding of Darwin's finches on *Tribulus cistoides* (L.) seeds. *Anim. Behav.* 29:785-793.
- GRIEG-SMITH, P. W., AND M. F. WILLSON. 1985. Influences of seed size, nutrient composition and phenolic content on the preferences of Bullfinches feeding in ash trees. *Oikos* 44:47-54.
- GRUNDEL, R. 1990. The role of dietary diversity, prey capture sequence and individuality in prey selection by parent Mountain Chickadees (*Parus gambeli*). *J. Anim. Ecol.* 59:959-976.
- HAMILTON, W. J., JR. 1940. Summer food of the robin determined by fecal analyses. *Wilson Bull.* 52:179-182.
- HAUSER, E. 1966. The natural occurrence of a hybrid honeysuckle (*Lonicera × bella*) in Ohio and Michigan. *Mich. Bot.* 5:211-217.
- HEINRICH, B. 1976. The foraging specializations of individual bumblebees. *Ecol. Monogr.* 46:105-128.
- HEPPNER, F. H. 1965. Sensory mechanisms and environmental clues used by the American Robin in locating earthworms. *Condor* 67:247-256.
- HERRERA, C. M. 1978. Individual dietary differences associated with morphological variation in robins *Erithacus rubecula*. *Ibis* 120:542-545.
- HERRERA, C. M. 1982. Defense of ripe fruit from pests: Its significance in relation to plant-disperser interactions. *Am. Nat.* 120:218-241.
- HERRERA, C. M. 1985. Habitat-consumer interactions in frugivorous birds. Pages 341-365 in *Habitat selection in birds* (M. L. Cody, Ed.). Academic Press, Orlando.
- HERRERA, C. M., AND P. JORDANO. 1981. *Prunus mahaleb* and birds: The high-efficiency seed dispersal system of a temperate fruiting tree. *Ecol. Monogr.* 51:203-218.
- HIRTH, D. H., A. E. HESTER, AND F. GREELEY. 1969. Dispersal and flocking of marked young robins (*Turdus m. migratorius*) after fledging. *Bird-Banding* 40:208-215.
- INMAN, A. J., L. LEFEBVRE, AND L. GIRALDEAU. 1987. Individual diet differences in feral pigeons: Evidence for resource partitioning. *Anim. Behav.* 35:1902-1903.
- JACOBS, J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. *Oecologia* (Berlin) 14:413-417.
- JAMES, F. C., AND C. E. MCCULLOCH. 1985. Data analysis and the design of experiments in ornithology. *Curr. Ornithol.* 2:1-63.
- 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.
- 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.
- JONES, E., AND N. T. WHEELWRIGHT. 1987. Seasonal changes in the fruits of *Viburnum opulus*, a fleshy-fruited temperate-zone shrub. *Can. J. Bot.* 65:2291-2296.
- JORDANO, P. 1987. Frugivory, external morphology and digestive system in Mediterranean sylviid warblers *Sylvia* spp. *Ibis* 129:175-189.
- KEAR, J. 1964. Colour preference in young Anatidae. *Ibis* 106:361-369.
- KING, T. R., AND H. E. MCCLURE. 1944. Chemical composition of some American wild feedstuffs. U.S. Dep. Agric. Res. Serv. (Rep.) 69:33-46.
- KLEINBAUM, D. G., AND L. L. KUPPER. 1978. Applied regression analysis and other multivariate methods. Duxbury Press, North Scituate.
- KREFTIN, L. W., AND E. I. ROE. 1949. The role of some birds and mammals in seed germination. *Ecol. Monogr.* 19:271-285.
- LEVEY, D. J. 1987a. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129:471-485.
- LEVEY, D. J. 1987b. Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *Auk* 104:173-179.
- LEVEY, D. J., AND A. GRAJAL. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. *Am. Nat.* 138:171-189.
- LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106:675-686.
- 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.
- MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants. McGraw-Hill Book Co., New York.
- 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.
- MASON, J. R., AND R. F. REIDINGER, JR. 1981. Effects of social facilitation and observational learning on feeding behavior of the Red-winged Blackbird (*Agelaius phoeniceus*). *Auk* 98:778-784.
- MCPHERSON, 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.
- 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., AND J. S. DENSLow. 1985. Neotropical avian frugivores: Patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Pages 865-897 in *Neotropical ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and N. G. Smith, Eds.). *Ornithol. Monogr.* 36.
- MOERMOND, T. C., J. S. DENSLow, D. J. LEVEY, AND E. SANTANA C. 1986. The influence of morphology on fruit choice in Neotropical birds. Pages 137-146 in *Frugivores and seed dispersal* (A. Estrada and T. H. Fleming, Eds.). *Tasks for vegetation science*, vol. 15. Dr. W. Junk Publ., Dordrecht.
- MOERMOND, T. C., J. S. DENSLow, D. J. LEVEY, AND E. SANTANA C. 1987. The influence of context on choice behavior: Fruit selection by tropical birds. Pages 229-254 in *Quantitative analyses of behavior*, vol. 6 (M. L. Commons, A. L. Kacelnik, and S. J. Shettleworth, Eds.). Lawrence Erlbaum Assoc., Hillsdale, New Jersey.
- MORTON, S. R., AND P. H. DAVIES. 1983. Food of the Zebra Finch (*Poephila gutta*), and an examination of granivory in birds of the Australian arid zone. *Aust. J. Ecol.* 8:235-243.
- NORUSIS, M. J. 1988. SPSS/PC+ V2.0, V3.0/3.1 for the IBM PC/XT/AT and PS/2. SPSS Inc., Chicago.
- PASZKOWSKI, C. A. 1982. Vegetation, ground, and frugivorous foraging of the American Robin. *Auk* 99:701-709.
- PASZKOWSKI, C. A., AND T. C. MOERMOND. 1984. Prey handling relationships in captive Ovenbirds. *Condor* 86:410-415.
- PIEROTTI, R., AND C. ANNETT. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. Pages 417-442 in *Foraging behavior* (A. C. Kamil, J. Krebs, and H. R. Pulliam, Eds.). Plenum Press, New York.
- PETRIDES, G. A. 1986. A field guide to trees and shrubs: Northeastern and north-central United States and southeastern and south-central Canada, 2nd ed. Houghton Mifflin Co., Boston.
- POWERS, L. R. 1973. Record of a robin feeding shrews to its nestlings. *Condor* 75:248.
- PRICE, T. D. 1987. Diet variation in a population of Darwin's finches. *Ecology* 68:1015-1028.
- PRICE, T. D., AND P. R. GRANT. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* 38: 483-494.
- RABINOWITCH, V. 1969. The role of experience in the development and retention of seed preferences in Zebra Finches. *Behaviour* 33:222-236.
- RICHMOND, M. L. 1975. American Robin feeds garter snake to its nestlings. *Wilson Bull.* 87:552.
- RINGLER, N. H. 1983. Variation in foraging tactics of fishes. Pages 159-171 in *Predators and prey in fishes* (D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward, Eds.). Dr. W. Junk Publ., Dordrecht.
- RINGLER, N. H. 1985. Individual and temporal variation in prey switching by brown trout, *Salmo trutta*. *Copeia* 1985:918-926.
- RISSING, S. W. 1981. Foraging specializations of individual seed-harvester ants. *Behav. Ecol. Sociobiol.* 9:149-152.
- 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. dissertation, Cornell Univ., Ithaca, New York.
- SIEGEL, S. 1956. *Nonparametric statistics: For the behavioral sciences*. McGraw-Hill Book Co., New York.
- SLINKER, B. K., AND S. A. GLANTZ. 1985. Multiple regression for physiological data analysis: The problem of multicollinearity. *Am. J. Physiol.* 249 (Regulatory Integrative Comp. Physiol. 18):R1-R12.
- SMITH, J. N. M., AND R. ZACH. 1979. Heritability of some morphological characters in a Song Sparrow population. *Evolution* 33:460-467.
- SMITHE, F. B. 1975. *Naturalist's color guide*. Am. Mus. Nat. Hist., New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman and Co., San Francisco.
- SORENSEN, A. E. 1983. Taste aversion and frugivore preference. *Oecologia* (Berlin) 56:117-120.
- SORENSEN, A. E. 1984. Nutrition, energy and passage time: Experiments with fruit preference in European Blackbirds (*Turdus merula*). *J. Anim. Ecol.* 53:545-557.
- WAINIO, W. W., AND E. B. FORBES. 1941. The chemical composition of forest fruits and nuts from Pennsylvania. U.S. Dep. Agric. Res. Serv. (Rep.) 62: 627-635.
- WERNER, T. K., AND T. W. SHERRY. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin finch" of Cocos Island, Costa Rica. *Proc. Natl. Acad. Sci. USA* 84:5506-5510.
- WEST, L. 1986. Interindividual variation in prey selection by the snail *Nucella (=Thais) emarginata*. *Ecology* 67:798-809.

- WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808-818.
- WHEELWRIGHT, N. T. 1986. The diet of American Robins: An analysis of U.S. Biological Survey records. *Auk* 103:710-725.
- WHEELWRIGHT, N. T. 1988. Seasonal changes in food preferences of American Robins in captivity. *Auk* 105:375-377.
- 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.
- WHEELWRIGHT, N. T., AND G. H. ORIANS. 1982. Seed dispersal by animals: Constraints with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* 119:402-413.
- WHITE, D. W., AND E. W. STILES. 1985. The use of refractometry to estimate nutrient rewards in vertebrate-dispersed fruits. *Ecology* 66:303-307.
- WIENS, J. A., AND J. T. ROTENBERRY. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecol. Monogr.* 50: 287-308.
- WILLSON, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. *Curr. Ornithol.* 3:223-279.
- 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.
- 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.
- WONNACOTT, R. J., AND T. H. WONNACOTT. 1985. *Introductory statistics*, 4th ed. John Wiley and Sons. New York.
- YOUNG, H. 1955. Breeding behavior and nesting of the eastern Robin. *Am. Midl. Nat.* 53:329-352.

APPENDIX 1. Fruit consumption and morphometric data for 35 American Robins.

Bird	Capture date	Sex <sup>a</sup>	Fruit <sup>b</sup>				Wing chord (cm)	Tarsus length (mm)	Bill			Middle toe-hallux (mm)	Mass <sup>c</sup> (g)	
			M	H	D	T			length (mm)	width (mm)	depth (mm)		1	2
26	30 June	M	24	0	0	24	12.5	32.8	19.1	5.3	6.5	—	76.0	72.0
51	26 June	M	20	0	0	20	13.1	33.8	20.5	5.6	6.1	—	84.5	80.0
52	27 June	M	7	0	2	9	13.0	33.1	19.8	5.9	6.3	—	76.5	77.0
53	28 June	F	27	0	1	28	12.9	34.9	19.0	5.2	6.7	38.5	82.5	81.0
54	28 June	F	10	12	4	26	13.0	33.8	20.1	5.6	6.1	34.9	—	77.0
55	29 June	F	3	0	0	3	12.8	31.1	18.7	5.2	5.9	33.1	70.0	64.0
56	01 July	M	0	0	4	4	12.7	33.3	20.0	5.4	6.6	36.0	75.0	77.2
57	01 July	F	0	0	0	0	12.7	32.6	19.5	5.8	6.5	33.5	93.0	82.0
58	02 July	J	13	6	4	23	13.1	36.1	18.0	4.6	5.7	37.5	77.0	82.0
59	06 July	J	12	0	2	14	13.1	32.5	20.1	5.3	6.4	33.3	74.5	73.0
60	08 July	M	5	0	0	5	12.8	33.7	21.1	5.5	6.7	—	72.0	71.0
61	09 July	M	1	0	40	41	12.7	33.7	19.6	5.0	6.1	35.7	72.5	70.0
62	10 July	M	26	7	0	33	12.7	34.1	21.2	5.9	6.7	35.0	80.0	—
63	10 July	F	8	0	0	8	12.7	33.2	20.1	5.4	6.5	32.3	76.0	79.2
64	10 July	J	1	0	0	1	12.7	30.5	19.0	4.6	5.9	30.7	76.5	85.0
65	10 July	J	11	0	2	13	12.2	30.4	18.5	4.5	5.9	30.4	71.0	78.0
66	11 July	J	0	0	0	0	12.7	34.5	19.6	5.6	6.7	39.0	78.0	75.0
67	11 July	J	12	0	1	13	12.9	34.3	18.1	4.9	5.9	34.6	72.0	71.0
68	17 July	J	4	0	59	63	12.7	33.6	18.7	5.3	5.4	36.1	70.2	70.0
69	17 July	J	8	1	11	20	12.9	33.1	19.6	5.7	6.4	35.5	76.5	75.0
70	20 July	J	10	0	0	10	12.2	32.5	18.0	5.4	6.2	34.9	70.0	81.5
71	20 July	J	5	0	7	12	12.4	32.4	19.2	5.2	6.0	34.9	73.5	71.0
72	20 July	J	0	0	0	0	12.1	32.6	17.8	5.5	6.0	32.6	71.9	76.0
73	20 July	J	4	0	0	4	12.9	34.7	18.6	5.1	6.2	37.8	70.2	75.0
74	20 July	M	8	0	1	9	12.9	33.2	21.9	5.5	6.3	36.6	78.0	79.0
76	22 July	J	0	0	0	0	12.7	34.0	19.6	4.8	6.0	33.3	70.0	77.0
77	26 July	J	18	2	2	22	12.7	34.2	18.8	4.8	5.8	37.3	84.0	78.0
78	26 July	J	14	0	0	14	12.3	31.9	18.5	5.7	6.1	34.7	78.5	72.5
79	27 July	J	3	0	0	3	12.6	33.9	20.0	5.5	5.9	36.7	76.0	83.0
80	29 July	J	24	0	0	24	12.1	33.9	20.7	4.8	6.2	35.0	76.5	79.5
81	29 July	F	17	0	1	18	12.8	32.9	20.1	6.0	6.0	35.9	35.9	83.0
82	30 July	M	8	0	4	12	13.0	33.9	19.2	5.6	6.1	36.9	80.0	81.0
83	30 July	J	0	0	1	1	12.8	30.1	17.8	5.4	5.6	35.6	73.5	77.5
84	30 July	J	14	0	4	18	12.5	32.9	20.1	5.5	5.8	37.9	78.3	83.0
85	30 July	F	1	0	0	1	12.3	34.2	19.4	5.4	6.0	36.8	75.0	70.0

<sup>a</sup> M = male; F = female; J = juvenile.

<sup>b</sup> M = mulberry; H = honeysuckle; D = dogwood; T = total.

<sup>c</sup> 1 = mass at capture; 2 = mass at release.

APPENDIX 2. Numbers of fruits eaten in individual trials.<sup>a</sup>

Bird	Date <sup>a</sup>	Trial 1			Trial 2			Trial 3			Trial 4			Trial 5			Trial 6			Preferred fruit <sup>b,c</sup>	P
		M	H	D	M	H	D	M	H	D	M	H	D	M	H	D	M	H	D		
51	1	4	0	0	0	0	0	7	0	0	4	0	0	2	0	0	3	0	0	M	0.002
52	1	1	0	2	2	0	0	2	0	0	1	0	0	1	0	0	0	0	0	M	0.017
26	4	8	0	0	3	0	0	5	0	0	1	0	0	3	0	0	4	0	0	M	<0.001
56	6	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0.017
60	12	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	2	0	0	—	—
61	14	0	0	0	0	0	4	0	0	6	0	0	10	1	0	9	0	0	11	D	0.002
62	14	2	0	0	2	1	0	3	3	0	6	2	0	6	1	0	7	0	0	M	0.002
74	24	1	0	1	1	0	0	3	0	0	3	0	0	0	0	0	0	0	0	—	—
82	34	0	0	0	1	0	4	1	0	0	1	0	0	2	0	0	3	0	0	M	0.017
53	3	4	0	0	5	0	1	5	0	0	2	0	0	5	0	0	6	0	0	M	<0.001
54	3	1	0	0	3	2	4	1	4	0	4	3	0	0	0	0	1	3	0	—	—
55	4	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0.017
57	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.001
63	14	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	6	0	0	0	<0.001
81	34	2	0	1	3	0	0	5	0	0	3	0	0	3	0	0	1	0	0	M	<0.001
85	34	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002
58	7	1	1	0	2	0	0	1	2	0	2	2	1	4	1	3	3	0	0	—	—
59	11	2	0	1	3	0	1	4	0	0	2	0	0	0	0	0	1	0	0	M	0.002
64	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0.002
65	14	3	0	1	1	0	1	0	0	0	0	0	0	2	0	0	5	0	0	—	—
66	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.001
67	16	2	0	0	0	0	0	3	0	1	4	0	0	1	0	0	2	0	0	M	0.002
68	21	2	0	10	0	0	11	0	0	10	0	0	7	0	0	8	2	0	13	D	<0.001
69	21	5	1	8	0	0	0	0	0	0	0	0	1	0	3	2	0	0	—	—	
70	24	1	0	0	1	0	0	1	0	0	7	0	0	0	0	0	0	0	0	M	0.017
71	24	0	0	1	0	0	0	0	0	0	3	0	1	1	0	1	1	0	4	—	—
72	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.001
73	24	0	0	0	1	0	0	1	0	0	2	0	0	0	0	0	0	0	0	—	—
76	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.001
77	30	3	0	0	5	0	0	4	0	0	2	0	0	1	2	1	3	0	1	M	0.002
78	30	0	0	0	2	0	0	3	0	0	1	0	0	6	0	0	2	0	0	M	0.002
79	31	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0.017
80	34	6	0	0	5	0	0	5	0	0	3	0	0	3	0	0	2	0	0	M	<0.001
83	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.002
84	34	1	0	2	1	0	2	4	0	0	4	0	0	0	0	0	4	0	0	—	—

<sup>a</sup> Date of first trial (1 = 29 June 1990).

<sup>b</sup> M = mulberry; H = honeysuckle; D = dogwood.

<sup>c</sup> 0 = no preference; dash indicates test for preference not possible.