

SEASONAL FRUIT PREFERENCES FOR LIPIDS AND SUGARS BY AMERICAN ROBINS

CHRISTOPHER A. LEPCZYK,¹ K. GREG MURRAY, KATHY WINNETT-MURRAY,
PAUL BARTELL,² ERIC GEYER,³ AND TIMOTHY WORK⁴

Department of Biology, Hope College, Holland, Michigan 49423, USA

ABSTRACT.—Fruit preference by birds is a complex process based upon the morphology and spatial arrangement of fruits and on the physiological needs and capabilities of birds. In North America, most fruits can be divided into two groups based on nutritional content: those rich in sugars relative to lipids, and those rich in lipids relative to sugars. To investigate how fruit preference may change seasonally and to determine if it is correlated with physiological state, we designed a simple laboratory experiment using American Robins (*Turdus migratorius*) and artificial fruits. During summer and autumn, we offered eight robins a choice between synthetic sugar-rich and lipid-rich fruits of equal caloric value and then measured food intake and assimilation efficiency for each fruit type. Overall, robins preferred sugar-rich to lipid-rich fruits during both seasons. Robins had a higher assimilation efficiency for sugars than for lipids during both seasons, although assimilation efficiency of lipids increased significantly from summer to autumn. During experiments, robins consumed significantly more sugar-rich than lipid-rich fruits in summer but not in autumn. Coupling fruit intake with assimilation efficiency indicates that in summer, robins had a higher rate of energy gain from sugars than from lipids, but by autumn the rate of energy gain from lipids increased to nearly the same level as that from sugars. Our results suggest that robins prefer sugar-rich fruits because of their simple and fast rate of digestion, enabling higher rates of energy gain, but that lipid-rich fruits become important with the onset of autumn. *Received 5 February 1999, accepted 14 December 1999.*

ONE MECHANISM used by plants to disperse their seeds is the reward of fleshy fruit pulp to frugivorous animals (Howe 1986). In turn, this reward provides a primary source of energy for the frugivore. Hence, frugivory has concomitant consequences for plant and animal. Because of these consequences, the question of what determines fruit preference and selection by frugivores has long been a central question of foraging ecology.

Most studies of fruit selection by frugivorous birds have approached the question as an optimal foraging problem. Frugivores are expected to choose the most profitable fruits, and

studies have found preferences based on caloric content (Sorensen 1984, Johnson et al. 1985, McPherson 1987), concentration of major nutrients (Denslow 1987, Levey 1987, Jung 1992), pulp-to-seed ratio (Howe and Vande Kerckhove 1980, Herrera 1982, Murray et al. 1993), fruit size (Paszkowski 1982), seed-passage rates (Sorensen 1984, Levey and Grajal 1991), fruit color (Turček 1963, Wheelwright and Janson 1985, Willson et al. 1990), secondary chemicals (Sorensen 1983, Cipollini and Levey 1997, Levey and Cipollini 1998), microbial infection (Buchholz and Levey 1990), abundance/crop size (Snow 1971, Howe and Estabrook 1977, Murray 1987, Sallabanks 1992), and accessibility (Denslow and Moermond 1982, Moermond and Denslow 1983). Furthermore, fruit selection is not based solely on characteristics of the fruit itself, but also on the bird's ability to digest the fruit (Levey and Karasov 1989, Martínez del Rio and Karasov 1990). Thus, fruit selection is a complex process that is based on interactions among the morphology and spatial arrangement of fruits and the physiological needs and capabilities of birds.

As seasons change, corresponding changes

¹ Present address: Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, Michigan 48824, USA. E-mail: lepczykc@pilot.msu.edu

² Present address: Department of Biology, University of Virginia, Charlottesville, Virginia 22903, USA.

³ Present address: Department of Forest Resources, Oregon State University, Corvallis, Oregon 97331, USA.

⁴ Present address: Department of Entomology, Oregon State University, Corvallis, Oregon 97331, USA.

occur in the physiological needs of frugivorous birds (Terrill 1990). One notable change occurs in late summer and early autumn when migratory birds build energy reserves to prepare for departure (Bairlein and Gwinner 1994). However, just as the physiological needs of the birds change seasonally, so do the fruits themselves. Specifically, fruits in North America can be divided into two broad groups based on nutritional content: those that are high in sugar relative to lipids, and those that are high in lipids relative to sugars (Stiles 1980, Herrera 1982). These two classes of fruits have a slight temporal difference in their occurrence, with sugar-rich fruits being common throughout the fruiting season (i.e. summer through early winter) and lipid-rich fruits being common primarily in late summer through early winter (Stiles 1980, Herrera 1982). Notably, the lipid-rich fruiting season is most prominent during the time when autumn migration occurs, suggesting a potential mutualistic relationship. Because most migratory birds depend on internally stored fat for fuel, they must accumulate large reserves prior to migration (Bairlein and Gwinner 1994). As such, a dietary preference may exist for lipid-rich fruits in the weeks or days before migration. Moreover, because lipids (ca. 39 kJ/g) contain more energy per unit mass than sugars (ca. 17 kJ/g; Guyton 1986), foraging theory predicts that lipid-rich fruits would be preferred to sugar-rich fruits, all else being equal, during all seasons. However, the efficiency with which lipids and sugars are digested and assimilated may differ. Thus, the question of which nutrients migratory birds select is of key interest in terms of foraging theory and bird physiology.

To investigate if fruit preferences change seasonally and are related to digestibility, we designed a simple laboratory experiment using migratory American Robins (*Turdus migratorius*). Because fruit choice may result from the combined effects of nutritional and non-nutritional factors (Baird 1980, Foster 1990), we eliminated as many extrinsic factors as possible by constructing synthetic fruits of equal caloric value that differed only in the relative amounts of sugars and lipids. We predicted that robins would choose the fruits that were most profitable (i.e. producing the highest rate of energy gain) during each season, and that during au-

tumn the most profitable fruits would be the lipid-rich ones.

METHODS

Study site.—We captured nine adult American Robins in mist nets between 7 and 30 April 1992 near Holland, Michigan, and maintained them in walk-in aviaries on the Hope College campus. All birds exhibited some mass loss after capture, but body mass leveled off within two weeks. When birds were not being tested, they were maintained on a synthetic diet of bananas and soy protein (Denslow et al. 1987) and provided water *ad libitum*. Birds were exposed to the natural light-dark cycle. Housing and care of birds was done with the approval of the Hope College Institutional Animal Care and Use Committee and under proper state and federal permits.

Artificial fruits.—To test for lipid and sugar preferences in robins, we developed two synthetic fruits of equal caloric value (on a fresh matter basis) that were either rich in lipids or in sugars. To maintain equal caloric values, the recipes for synthetic sugar-rich and lipid-rich fruits were based on a mass-percent method, with the total wet mass equaling 100 g (excluding an emulsifier of polyoxyethylensorbatan monooleate [tween 80] that prevented separation of lipid and aqueous components). The percentage of reducing sugars (i.e. glucose and fructose) and lipids in the two fruit types was based on the dry-mass composition of wild sugar-rich (3.3 to 53.1%, median 11.35%) and lipid-rich fruits (0.36 to 39.86%, median 0.77%) in eastern North America (see Stiles 1980, Johnson et al. 1985). We chose corn oil for our lipid component because it has a very similar fatty acid profile (ca. 50% oleic acid and 34% linoleic acid) to wild fruits (Zurovchak 1997). Sugar-rich fruits (40% sugar, 5% lipid) were prepared by boiling 51 mL of H₂O and adding in the following order: 40 g sugar (20 g glucose, 20 g fructose), 5 g corn oil, 0.5 mL tween 80, 2 g agar, and 2 g (30 drops) of food coloring. Fruits were colored red for the first set of preference experiments and purple (2:1 red:blue food coloring) for the reciprocal preference experiments. The hot solution was then injected into the wells of ELISA microplates (each well = 0.3 mL; total wells/batch = 225) and cooled in an ice bath. Lipid-rich fruits (20% lipid, 6% sugar) were prepared by boiling 70 mL of H₂O and adding 6 g sugar (3 g glucose, 3 g fructose), 20 g corn oil, 0.5 mL tween 80, 2 g agar, and 2 g of food coloring (purple for the first set of experiments and red for the reciprocals). The mixture was then treated in the same manner as the sugar-rich fruits. Both artificial fruits had similar textural consistencies and held their shape.

Fruit-preference experiments.—Because fruit availability affects fruit consumption by birds (Sallabanks 1992), we chose to eliminate differential availability

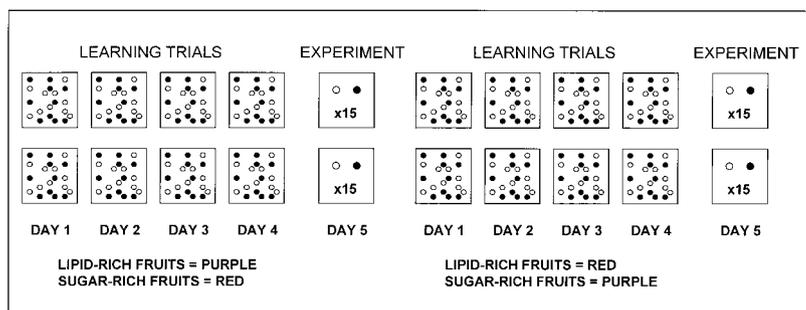


FIG. 1. Experimental design of fruit-preference experiments for individual American Robins during one season. Lipid-rich and sugar-rich fruits are depicted as filled and empty circles, respectively.

by designing preference experiments in which birds were always offered the same number of fruits. Thus, our experiments were designed to assess fruit preference (the likelihood of a fruit being chosen if offered on an equal basis with others) and not fruit selection (if a fruit is chosen disproportionately to its availability; Johnson 1980). The fruit preference and assimilation-efficiency experiments were conducted in small ($50 \times 30 \times 46$ cm) cages that contained one-way mirrors and an attached feeding dish. Summer experiments were conducted from 16 June to 24 July 1992. Birds were without food for one-half hour before each trial. Each bird was given at least 8 two-hour trials (two trials per day) with 20 fruits (10 lipid rich and 10 sugar-rich) to "learn" (Willson 1994) the composition of the two fruit types (Fig. 1). For the first set (≥ 8) of learning trials, lipid-rich fruits were colored purple and sugar-rich ones were colored red. The number of each fruit type eaten and the number dropped was recorded every 15 to 20 min during each two-hour trial. Between learning trials, birds were fed the maintenance (banana) diet. Following the last day of learning trials, we performed two sets of 15 pairwise tests (in which each bird had to choose between one fruit of each type) on each bird, one starting at 0930 EST and the second starting one hour after the 0930 test was completed (Fig. 1). The pairwise tests lasted between 1.5 and 3.5 h, depending on how long it took an individual to consume all 15 fruits. Beginning the week following completion of the first set of experiments, we performed at least eight reciprocal learning trials in which the color of lipid-rich and sugar-rich fruits was switched to attempt to remove color as a variable. After the reciprocal learning trials, each bird was again subjected to two sets of 15 pairwise tests, this time with the new color \times nutrient combinations (Fig. 1). Preference experiments were repeated from 13 to 23 September 1992 (i.e. autumn experiments) using the same nine individuals from the summer experiments. Learning trials and pairwise preference tests with reciprocal color \times nutrient combinations were performed in the same manner as in summer.

Assimilation efficiencies.—We measured assimilation efficiency (i.e. percent of ingested nutrient that did not appear in the fecal material during steady-state feeding) on 29 July, 6 August, 1 October, and 8 October 1992. Fruits were sugar-rich for experiments on 29 July and 1 October and lipid-rich for those on 6 August and 8 October. Food was removed 2 h before the start of experiments, which began at 1000 and lasted for 6 h. All nine birds were given 20 fruits (always colored red) in petri dishes. At hourly intervals, the number of fruits eaten was recorded, all fecal remains were scraped off the plastic lining at the bottom of the cages, and consumed fruits were replaced. Fecal remains were placed in marked aluminum weighing boats with several milliliters of 70% ethanol to kill any bacteria. Samples were then dried to constant mass at 55°C .

We analyzed concentrations of glucose and fructose with a colorimetric method (Snell and Snell 1937). Briefly, dried fecal samples were diluted with 10 mL distilled water, homogenized, heated in a warm water bath to allow solids to dissolve, and centrifuged. A 0.5-mL aliquot was then taken and mixed with 1.5 mL of reagent solution (2,4-dinitrophenolate and sodium potassium tartrate). The mixture was then heated in a boiling water bath for 6 min, followed by 3 min of cooling to room temperature. After cooling, samples were read in a spectrophotometer (Hewlett-Packard 8452A) at a wavelength of 515 nm to measure absorbency, from which sugar concentration was estimated (see Snell and Snell 1937). If an aliquot was too concentrated to measure absorbance, the original sample was further diluted with known quantities of distilled water and the process repeated. Lipids were extracted from dried fecal samples with a hexane:isopropanol (3:2) solvent (with 0.5% HCl to facilitate recovery of free fatty acids; Radin 1981). After a first extraction with 10 mL of solvent, solids were removed by centrifugation. Solids were then resuspended in 5 mL solvent and centrifuged again. The solvent was then allowed to evaporate (at 25°C) until the remaining residue (lipid) reached constant mass (modified from Radin

1981). Assimilation efficiency (%) was then calculated separately for sugar- and lipid-rich fruits using [(slope of cumulative dry mass consumed – slope of cumulative dry mass voided)/slope of cumulative dry mass consumed] \times 100, where the slopes were calculated on the cumulative masses each hour. We chose this method of calculating assimilation efficiency over the conventional method of measurement [i.e. (total dry matter consumed – total dry matter voided)/total dry matter consumed] because we were interested in measuring assimilation efficiency during steady-state feeding, which is not possible without using a marker (e.g. dye or radioisotope) and interrupting the feeding schedule.

The assimilable energy in kJ derived from each fruit type consumed during an experiment was calculated as [(no. of fruits) \times (g lipid assimilated/fruit) \times (kJ/g lipid) + (no. of fruits) \times (g sugar assimilated/fruit) \times (kJ/g sugar)]. The rate of energy gain was then calculated as the assimilable energy gain per 6 h (i.e. length of assimilation-efficiency experiment). Because both fruit types consisted of sugars and lipids and were consumed simultaneously, the assimilable energy was not based on the instantaneous rate of assimilation (i.e. the rate of assimilation of a single nutrient). Hence, assimilable energy simply indicates how much energy was assimilated from each fruit type. Only seven individuals were analyzed for assimilation efficiency, and six individuals for rate of energy gain, because the other individuals had been excluded from at least one of the experiments. Individuals were excluded from analysis if they failed to eat any of the artificial fruits during any of the experiments.

Data analysis.—To investigate overall bird behavior, we analyzed fruits taken as a function of color, nutrient, and time of year using a saturated hierarchical log-linear model (Bishop et al. 1975). This model produces a multiway contingency table in which significance tests are based on the marginal totals for each factor. We used a chi-square test to determine if individual robins preferentially selected one type of fruit based on nutrient versus color. Chi-square tests were run on each individual as well as on the combined data set for all birds. *P*-values $<$ 0.05 indicated a preference for a nutrient or color and are reported simply as “preferred.”

We used a one-factor repeated-measures ANOVA to analyze changes in assimilation efficiencies for a given nutrient over the two time periods. We used paired *t*-tests to compare rates of fruit consumption during assimilation-efficiency experiments and rates of assimilable energy gain from the two fruit types within a season and two-sample *t*-tests to compare across seasons within a fruit type. All *t*-tests were two-tailed, except in the case of assimilable energy gain across seasons for lipid-rich fruits, in which we used a one-tailed test because of the *a priori* prediction that the rate would increase during autumn. All

analyses were performed with SYSTAT (Wilkinson 1992).

RESULTS

Fruit preferences.—Nine robins were used for preference experiments in both seasons, but one bird failed to feed during some experiments and was excluded from analysis. During the summer test period, four birds preferred sugar-rich to lipid-rich fruits, and four showed no significant preference (Fig. 2). In the autumn test, five birds preferred sugar-rich to lipid-rich fruits, and three showed no significant preference (Fig. 2). Only three individuals showed a consistent preference from summer to autumn (Fig. 2). On average, robins preferred sugar-rich fruits to lipid-rich fruits during summer and autumn (Fig. 2).

Individuals that showed no preference based on nutrient content showed a distinct preference for color (Fig. 2). During the summer test, three birds preferred red fruits, one preferred purple fruits, and the remaining four showed no preference for color (Fig. 2). During the autumn test, two birds preferred red fruits, one preferred purple fruits, and five showed no preference (Fig. 2). Of the individuals that selected fruits based on color, only one bird showed a consistent preference during both time periods. On average, robins preferred red fruits to purple fruits in summer but showed no overall preference in autumn (Fig. 2).

The saturated log-linear model indicated that nutrient ($\chi^2 = 260.48$, *df* = 1, *P* $<$ 0.00005) and color ($\chi^2 = 39.30$, *df* = 1, *P* $<$ 0.00005) had a significant effect on fruit preference. The only significant interactions between factors were color \times season ($\chi^2 = 18.75$, *df* = 1, *P* $<$ 0.00005) and color \times nutrient ($\chi^2 = 9.12$, *df* = 1, *P* = 0.0025). Overall, season had no significant effect on preference ($\chi^2 = 0.28$, *df* = 1, *P* = 0.598) except for the loss of a preference for red fruit from summer to autumn. The color \times nutrient interaction indicated that the preference for sugar-rich fruits was stronger when fruits were red than when they were purple. Furthermore, the interaction suggested that color preferences overrode nutrient preferences in some individuals.

Assimilation efficiencies and total energy gain.—During summer, mean assimilation efficiency was $97.8\% \pm$ SE of 0.28 for sugars and $76.6 \pm$

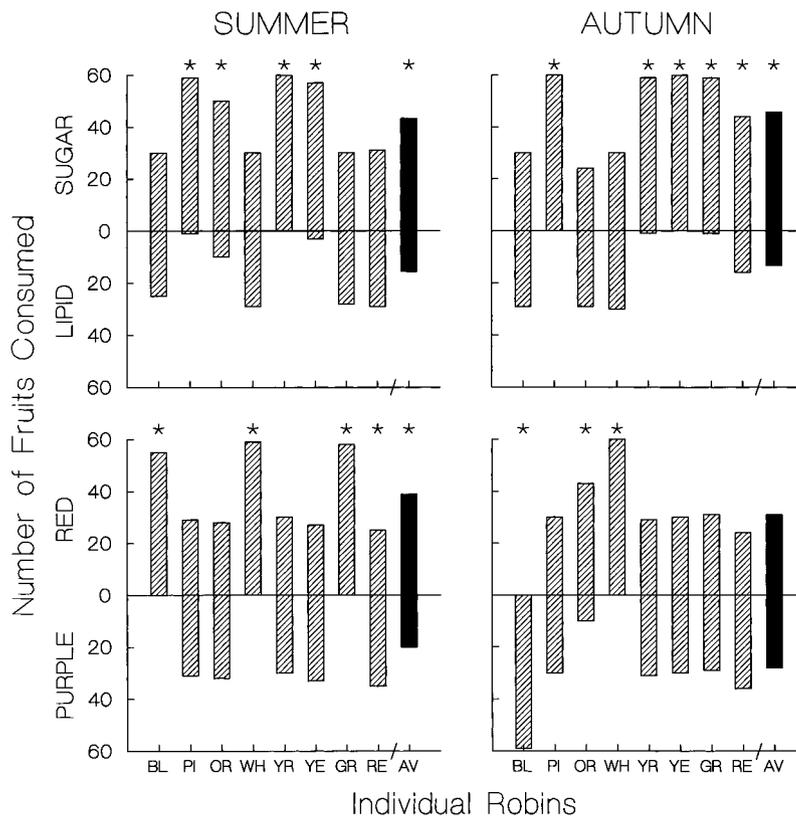


FIG. 2. Fruit preferences based on major nutrient (top row) and color (bottom row) for individual American Robins during summer and autumn. AV is the average number of fruits consumed by all individuals. Asterisks denote significant preference for a fruit type ($P < 0.05$).

3.85 for lipids. Autumn assimilation efficiency was $96.6\% \pm 0.44$ for sugars and $90.7\% \pm 1.24$ for lipids. The decrease in assimilation efficiency for sugars and the increase for lipids from summer to fall were statistically significant (sugar, $F = 21.4$, $df = 1$ and 6 , $P = 0.0036$; lipid, $F = 25.0$, $df = 1$ and 6 , $P = 0.0025$).

Consumption rates were significantly higher for sugar-rich fruits than for lipid-rich ones during summer assimilation-efficiency experiments ($\bar{x} = 26.5 \pm 3.22$ vs. 15.3 ± 2.11 fruits per 6 h; $t = 2.9$, $df = 10$, $P = 0.016$). During the autumn experiments, however, differences in consumption rates of sugar-rich and lipid-rich fruits were not statistically different ($\bar{x} = 28.0 \pm 2.83$ vs. 22.3 ± 2.93 fruits per 6 h, respectively; $t = 1.39$, $df = 10$, $P = 0.194$). Robins increased consumption rates of sugar-rich fruits from summer to fall only slightly (6%; $t = 0.35$, $df = 10$, $P = 0.704$), but increased consumption of lipid-rich ones more substantially (46%; $t =$

1.94, $df = 10$, $P = 0.081$). In neither case were the increases statistically significant, however.

During summer, the rate of assimilable energy gain from sugar-rich fruits was significantly higher than that from lipid-rich ones ($\bar{x} = 13.9 \pm 1.64$ vs. 6.8 ± 0.86 kJ/h; $t = 3.84$, $df = 10$, $P = 0.003$). In autumn, however, the rate of energy gain was only marginally (but not significantly) higher from sugar-rich fruits ($\bar{x} = 13.1 \pm 1.16$ vs. 9.8 ± 1.17 kJ/h; $t = 2.03$, $df = 10$, $P = 0.07$). Within fruit types, the rate of assimilable energy gain showed no seasonal change for sugar-rich fruits ($t = 0.39$, $df = 10$, $P = 0.70$) but increased significantly for lipid-rich fruits from summer to autumn (one-tailed $t = 2.07$, $df = 10$, $P = 0.033$).

DISCUSSION

Although the fruits used in this study were of equal caloric value, all robins that showed a

preference chose sugar-rich fruits over lipid-rich fruits during both seasons. Moreover, the preference for sugar-rich fruits was significant when averaged across all birds (Fig. 2). All individuals that did not show a preference based on nutritional content exhibited a color preference. During summer, the color preference was strong enough to yield an overall preference for red fruits across individuals (Fig. 2). However, by autumn fewer birds selected fruits based on color, and one actually switched preferences from red to purple. This strong initial preference for red during summer followed by a decrease in color preference during autumn is very similar to that found in Cedar Waxwings (*Bombycilla cedrorum*; McPherson 1988). Such strong color preferences may have had the effect of overriding nutrient preferences. Notably, all of the robins showed a distinct preference based on either nutritional content or color during each season (Fig. 2).

Although the role of color was not the focus of this study, color proved to play an important role in fruit selection. In previous studies investigating color in fruit selection, no single color was preferred absolutely to all others (Willson et al. 1990), but some were definitely avoided (e.g. yellow and green fruits). In the wild, the most common colors for ripe fruits are dark purple and red (Janson 1983, Wheelwright and Janson 1985, Willson 1986). Given that we used purple and red fruits, color preferences may have developed based on experiences with fruits in each individual's natal home range, or preferences simply may be a behavioral or genetic factor that is not related to fruit quality. In a previous study with the same local population of robins, we found similar distinct color preferences and color switching (Murray et al. 1993).

We expected robins to show a strong preference for lipid-rich fruits during summer or autumn because of the greater energy density per unit mass and as a source for premigratory fattening. In fact exactly the opposite was true, because more robins preferred sugar-rich fruits in autumn than in summer. Similarly, Whelan and Willson (1994) found no preference for lipid-rich fruits during autumn migration. However, robins had a marked increase in the assimilation efficiency of lipids from summer to autumn as well as in the overall assimilable energy gain from lipids. The change in energetic

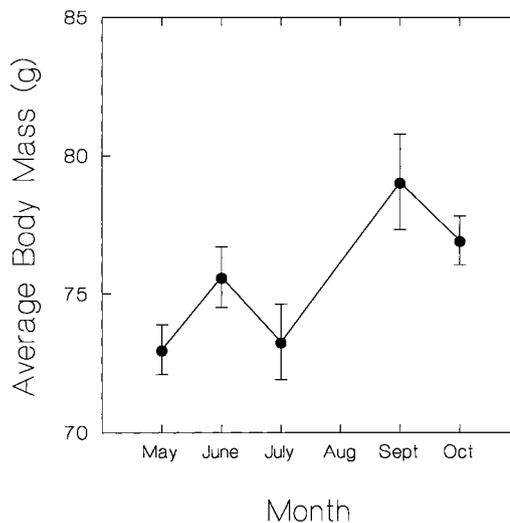


FIG. 3. Average monthly body mass (\pm SE) of nine (seven for June) captive American Robins. No masses were recorded during August.

gain across seasons can be attributed to a change in the intake rate of lipid-rich fruits and to an increase in assimilation efficiency. Specifically, an increase in intake during the autumn assimilation-efficiency experiments, coupled with a significant increase in assimilation efficiency of lipids, resulted in a similar total assimilable energy gain from lipid-rich and sugar-rich fruits during the assimilation-efficiency experiments. Moreover, although robins showed an increase in assimilation efficiency of lipids across seasons, they showed no preference for lipid-rich fruit, irrespective of the color cue used. The lack of preference for lipid-rich fruits may have resulted from several factors. First, robins may use sweetness as the primary indicator of fruit quality. Previous studies have shown that birds can differentiate fruits based on sweetness (Levey 1987) and can distinguish between types of sugars and agar cubes with and without sugar (Martínez del Río et al. 1989). Thus, if robins used sweetness as a primary indicator of quality, they might not be readily influenced by lipids, which agrees with previous observations (Borowicz 1987). Second, our preference experiments were conducted after the birds had experienced their autumn increase in body mass (Fig. 3). As a result, robins may not have chosen lipid-rich fruits because they had already completed premigratory fattening. Third, carbohydrates and lipids are di-

gested through very different pathways. Lipids require a multistep biochemical process of emulsification, hydrolysis, and absorption (Griminger 1986, Karasov 1988, Afik and Karasov 1995), which tends to increase the retention time of digesta in the gut, whereas simple sugars are absorbed immediately via active transport and passive absorption (Caviedes-Vidal and Karasov 1996, Levey and Cipollini 1996, Afik et al. 1997), resulting in shorter retention times. Although the exact reason for the lack of preference for lipids is unknown, the most plausible explanation is that lipids are more energetically expensive to process and require more time than simple sugars, resulting in fewer fruits being consumed in any given period of time.

Although the robins in our study did not prefer lipid-rich fruits, they exhibited a marked increase in assimilation efficiency of lipids during autumn. Because digestion represents a tradeoff between the length of time digesta (e.g. fruit pulp) are in the gut and the thoroughness of digestion (Robbins 1993), such an increase in assimilation efficiency of lipids could result from a reduction in intake of lipid-rich fruits, as has been demonstrated in American Robins and other thrushes (Witmer and Van Soest 1998). In other words, because fewer fruits are consumed, they may reside in the gut longer, allowing for more complete digestion. Indeed, Zurovchak (1997) recently found that American Robins increased retention time of digesta and decreased consumption rate with increasing dietary lipid content, resulting in a constant assimilation efficiency for lipids of approximately 75%. Although our measure of lipid assimilation efficiency in summer mirrors that of Zurovchak, our autumn measures clearly do not. Furthermore, robins consumed 46% more fruit during the autumn assimilation-efficiency experiments than during the summer experiments, which arguably could have decreased retention times. Thus, given that the intake of lipid-rich fruits increased, the finding that 91% of lipids were assimilated during autumn seems counter to the constant lipid assimilation efficiency found by Zurovchak (1997).

Witmer and Van Soest (1998) found similar assimilation efficiencies in American Robins that were maintained on lipid-rich *Viburnum dentatum* fruits (86%) or were conditioned to a

fatty diet (87%). Concordant with the increase in assimilation efficiency in our study was the impending autumn migration; robins gained body mass from summer to autumn (Fig. 3), suggesting that they underwent premigratory fattening. Because the birds were eating only synthetic banana mash but were exposed to natural light and temperature regimes in their aviaries, the increase in lipid assimilation efficiency could not have been induced by changes in composition of wild fruit. Furthermore, Herrera (1998) recently found that the percent of fruit in the diet and nutritional characteristics of the fruit had no significant effect on deposition of body fat in autumn. Thus, although the increase in lipid assimilation efficiency may be essential to building and maintaining fat stores in autumn, it appears to be decoupled from diet. Therefore, the change in lipid assimilation efficiency appears to be based on an extrinsic cue (e.g. photoperiod or temperature) that signals the need to build fat in preparation for migration. One caveat is that because the individuals in our experiments were long-term captives, we did not directly examine the preferences of premigratory or migrating birds that would have been faced with the need to build energy reserves quickly.

Our results suggest that American Robins preferred fruits that were the easiest to digest and that conferred the greatest rate of energy gain. Although the rate of energy gain from lipid-rich fruits increased significantly from our summer to autumn experiments, the mean energy gain was slightly greater from sugar-rich fruits. Robins predominantly selected sugar-rich fruits, but their assimilation efficiency of lipids increased significantly in autumn, indicating a potential seasonal shift in preparation for migration. We also note that preference for sugar-rich fruits may have consequences for fruit-producing plants. Specifically, plants that produce sugar-rich fruits and depend on avian dispersal of their seeds may experience higher rates of fruit removal by robins than do plants that produced lipid-rich or sugar-poor fruits. Thus, our results have important ramifications not only for foraging theory, but for plant population dynamics.

ACKNOWLEDGMENTS

We thank David Netzly for the use of his laboratory, Rod Boyer for advice on lipid recovery, and

Christopher Barney for critical discussions. Steve Lugo and Kim Scott provided invaluable assistance with bird maintenance and experiments. The manuscript was greatly improved by comments from Carlos Bosque, William Karasov, Doug Levey, Scott McWilliams, Terry Root, Rex Sallabanks, and an anonymous reviewer. Funding was provided by a National Science Foundation Research Experience for Undergraduates grant (NSF REU BIO 9100398) to Christopher Barney and Anthony Nieuwkoop.

LITERATURE CITED

- AFIK, D., B. W. DARKEN, AND W. H. KARASOV. 1997. Is diet shifting facilitated by modulation of intestinal nutrient uptake? Test of an adaptational hypothesis in Yellow-rumped Warblers. *Physiological Zoology* 70:213–221.
- AFIK, D., AND W. H. KARASOV. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76:2247–2257.
- BAIRD, J. W. 1980. The selection and use of fruit in an eastern forest. *Wilson Bulletin* 92:63–73.
- BAIRLEIN, F., AND E. GWINNER. 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Review of Nutrition* 14:187–215.
- BISHOP, Y. M. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. *Discrete multivariate analysis*. MIT Press, Cambridge, Massachusetts.
- BOROWICZ, V. A. 1987. Fruit consumption by birds in relation to fat content of pulp. *American Midland Naturalist* 119:121–127.
- BUCHHOLZ, R. J., AND D. J. LEVEY. 1990. The evolutionary triad of microbes, fruits, and seed dispersers: An experiment in fruit choice by Cedar Waxwings, *Bombycilla cedrorum*. *Oikos* 59:200–204.
- CAVIEDES-VIDAL, E., AND W. H. KARASOV. 1996. Glucose and amino acid absorption in House Sparrow intestine and its dietary modulation. *American Journal of Physiology* 271R:561–568.
- CIPOLLINI, M. L., AND D. J. LEVEY. 1997. Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology* 78:782–798.
- DENSLOW, J. S. 1987. Fruit removal rates from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 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 Bulletin* 99:131–134.
- DENSLOW, J. S., AND T. C. MOERMOND. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: An experimental study. *Oecologia* 54:170–176.
- FOSTER, M. F. 1990. Factors influencing bird foraging preferences among conspecific fruit trees. *Condor* 92:844–854.
- GRIMINGER, P. 1986. Lipid metabolism. Pages 345–358 in *Avian physiology* (P. D. Sturkie, Ed.). Springer-Verlag, New York.
- GUYTON, A. C. 1986. *Textbook of medical physiology*, 7th ed. W. B. Saunders, Philadelphia, Pennsylvania.
- HERRERA, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63:773–785.
- HERRERA, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: A 12-year study. *Ecological Monographs* 68:511–538.
- HOWE, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Pages 123–189 in *Seed dispersal* (D. R. Murray, Ed.). Academic Press, New York.
- HOWE, H. F., AND G. F. ESTABROOK. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111:817–832.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1980. Nutmeg dispersal by tropical birds. *Science* 210:925–927.
- JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219:187–189.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- 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.
- JUNG, R. E. 1992. Individual variation in fruit choice by American Robins (*Turdus migratorius*). *Auk* 109:98–111.
- KARASOV, W. H. 1988. Nutrient transport across vertebrate intestine. Pages 131–172 in *Advances in comparative and environmental physiology* (R. Gilles, Ed.). Springer-Verlag, Heidelberg, Germany.
- LEVEY, D. J. 1987. Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *Auk* 104:173–179.
- LEVEY, D. J., AND M. L. CIPOLLINI. 1996. Is most glucose absorbed passively in Northern Bobwhite? *Comparative Biochemistry and Physiology* 113A:225–231.
- LEVEY, D. J., AND M. L. CIPOLLINI. 1998. A glycoalkaloid in ripe fruit deters consumption by Cedar Waxwings. *Auk* 115:359–367.
- LEVEY, D. J., AND A. GRAJAL. 1991. Evolutionary implications of fruit processing limitations in Cedar Waxwings. *American Naturalist* 138:171–189.
- LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive re-

- sponses of temperate birds switched to fruit or insect diets. *Auk* 106:675-686.
- MARTÍNEZ DEL RIO, C., AND W. H. KARASOV. 1990. Digestive strategies in nectar- and fruit-eating birds and the sugar composition of fruit rewards. *American Naturalist* 136:618-637.
- 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.
- MCPHERSON, J. M. 1987. A field study of winter fruit preferences of Cedar Waxwings. *Condor* 89:293-306.
- MCPHERSON, J. M. 1988. Preferences of Cedar Waxwings in the laboratory for fruit species, colour and size: A comparison with field observations. *Animal Behaviour* 36:961-969.
- MOERMOND, T. C., AND J. S. DENSLow. 1983. Fruit choice in Neotropical birds: Effects of fruit type and accessibility on selectivity. *Journal of Animal Ecology* 52:407-420.
- MURRAY, K. G. 1987. Selection for optimal fruit crop size in bird-dispersed plants. *American Naturalist* 129:18-31.
- MURRAY, K. G., K. WINNETT-MURRAY, E. A. CROMIE, M. MINOR, AND E. MEYERS. 1993. The influence of seed packaging and fruit color on feeding preferences of American Robins. *Vegetatio* 107/108:217-226.
- PASZKOWSKI, C. A. 1982. Vegetation, ground, and frugivorous foraging of the American Robin. *Auk* 99:701-709.
- RADIN, N. 1981. Extraction of lipids from tissues with hexane-isopropanol. *Methods in Enzymology* 72:5-7.
- ROBBINS, C. T. 1993. *Wildlife feeding and nutrition*. Academic Press, San Diego, California.
- SALLABANKS, R. 1992. Fruit fate, frugivory, and fruit characteristics: A study of hawthorn, *Crataegus monogyna* (Rosaceae). *Oecologia* 91:296-304.
- SNELL, F. D., AND C. T. SNELL. 1937. *Colorimetric methods of analysis*, vol. 2. Van Nostrand, New York.
- SNOW, D. W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.
- SORENSEN, A. E. 1983. Taste aversion and frugivore preference. *Oecologia* 56:117-120.
- SORENSEN, A. E. 1984. Nutrition, energy and passage time: Experiments with fruit preference in European Blackbirds (*Turdus merula*). *Journal of Animal Ecology* 53:545-557.
- STILES, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* 116:670-688.
- TERRILL, S. B. 1990. Ecophysiological aspects of movements by migrants in the wintering quarters. Pages 130-143 in *Bird migration* (E. Gwinner, Ed.). Springer-Verlag, New York.
- TURČEK, F. J. 1963. Color preference in fruit-and seed-eating birds. Pages 285-292 in *Proceedings XIII International Ornithological Congress* (C. G. Sibley, Ed.). Ithaca, New York, 1962. American Ornithologists' Union, Washington, D.C.
- WHEELWRIGHT, N. T., AND C. H. JANSON. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *American Naturalist* 126:777-799.
- WHELAN, C. J., AND M. F. WILLSON. 1994. Fruit choice in migrating North American birds: Field and aviary experiments. *Oikos* 71:137-151.
- WILKINSON, L. 1992. SYSTAT for Windows, version 5 ed. SYSTAT, Inc., Evanston, Illinois.
- WILLSON, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. *Current Ornithology* 3:223-279.
- WILLSON, M. F. 1994. Fruit choices by captive American Robins. *Condor* 96:494-502.
- 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.
- WITMER, M. C., AND P. J. VAN SOEST. 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12:728-741.
- ZUROVCHAK, J. G. 1997. Nutritional role of high-lipid fruits in the diet of migrant thrushes. Ph.D. dissertation, Rutgers University, New Brunswick, New Jersey.

Associate Editor: C. Bosque