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NUTRITIONAL VALUES OF WILD FRUITS AND CONSUMPTION BY MIGRANT FRUGIVOROUS BIRDS[1]

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Abstract. To learn some of the bases for consumption of temperate fleshy fruits by birds, we examined nutritional and morphological traits of temperate fleshy fruits and made laboratory observations on consumption of individual fruit species using 18 fruit species and 11 migrant frugivorous bird species in Illinois. The only seasonal trends in fruit traits were interspecific increases in absolute quantity of potassium and protein per fruit. Fruit energy content did not differ among species having bicolored vs. monochrome or small vs. large fruit displays. The fruit mass consumed was correlated best with dry pulp mass per fruit, providing significant positive correlations in 6 of 11 frugivorous species. Large fruit size relative to bill size did not appear to affect fruit consumption over the range of fruit sizes and bird species used. Because retained energy was correlated with mass consumed, the fruit pulp mass consumed was in most cases a good index of the energy obtained. Some significant differences occurred in digestive efficiency of a bird species eating different fruit species, and among different bird species eating a single fruit species, but no trends were apparent.

Regurgitated seeds generally spent less time in a bird than did defecated seeds, facilitating more rapid disposal of seed ballast. Smaller birds defecated only small seeds and regurgitated some small seeds as well as all large ones, whereas larger birds defecated all smaller seeds and many larger ones. Consequently, resultant seed shadows may depend upon both bird and seed size.

Key words: avian morphology; cations; digestibility; frugivore; nutrients; seed defecation; seed regurgitation; single-species fruit consumption; temperate fleshy fruits.

INTRODUCTION

Most fleshy fruited plants in temperate latitudes rely on migrating birds to disperse their seeds (Snow 1971, Thompson and Willson 1979, Stiles 1980, Herrera 1981). Migrants stop at rest sites for up to several days to replenish nutrients and energy and are confronted with a broad range of fruits differing in morphology and nutrient content. Migrant birds clearly eat some fruits more readily than others (Thompson and Willson 1978, Sorensen 1981, 1983), but the bases for avian selection of temperate fleshy fruits are poorly known. The theoretical literature suggests that nutritional qualities and morphology, such as fruit and seed size, are important in fruit selection (Snow 1971, McKey 1975, Howe and Estabrook 1977, Howe and Vande Kerckhove 1980, Martin 1985).

This paper addresses the following sets of questions regarding interactions between fleshy fruits and migrating frugivorous birds in east-central Illinois:

1) To what extent do fruits vary in nutrition and morphology?

(a) Are there seasonal patterns in these traits? Snow (1971) suggested that early-maturing fruits should be more succulent and less nutritious (especially in proteins and lipids) than late-maturing species. Herrera's (1982) results supported Snow's contentions: summer-fruiting species in Spain produced watery fruits and winter fruits were high in lipids, corresponding to the presumed seasonal requirements of their avian seed vectors. Stiles (1980) and Stiles and White (1982) divided fruits into four categories: small- and large-seeded summer fruits and high- and low-quality fall fruits. These authors suggested that summer fruits are high in carbohydrates and low in lipids, and that high-quality fall fruits are dispersed or abscised quickly and have a high lipid content, whereas low-quality fall fruits are dispersed or abscised slowly and have a low lipid content.

(b) Is fruit quality correlated with aspects of the fruiting display that attract frugivorous birds? An inverse relationship between fruit quality and crop size or display color might be expected if one attractive feature can compensate for the lack of another.

2) How do fruit nutrients (and, indirectly, energy), cations, and morphology affect avian fruit consumption? We can examine two important relationships:

(a) Do birds consume more low-quality fruits to compensate for lower reward levels? Or do birds consume more high-nutrition fruits? If so, what aspects of quality seem most important?

(b) Is the fruit pulp mass consumed a good index of the energy obtained by avian consumers, or do differences in digestive efficiency (among bird species and

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among fruit species) mean that intake is a poor measure of energy obtained?

3) Does fruit or seed size affect the probablility of seed regurgitation vs. defecation? How does method of voiding seeds affect the time seeds are carried inside the avian consumer and potential dispersal agent?

METHODS

Fruit morphology and chemistry

Whole fresh fruit, fresh seed, and seedless pulp dry mass of 22 of the area's most common fruit species were measured on 1411 ripe fruits collected from areas near Urbana, Illinois, USA. Dried pulp from 20 fruit species was analyzed for nutrients (lipids, nitrogen, reducing sugars, energy content) and cations (Na, K, Ca, Mg). Lipid content was determined gravimetrically after two extractions with petroleum ether (the second time overnight) and drying in nitrogen gas (E. Weber, *personal communication*). Percent total nitrogen was estimated by the micro-Kjeldahl method (Horwitz 1970); protein content was calculated by multiplying by 4.4 (Milton and Dintzis 1981). We measured reducing sugars instead of total available carbohydrates because reducing sugars are more rapidly available as an energy source for migrating birds than are nonreducing sugars. Reducing sugars were separated from the ground pulp with two extractions (15 min each) in 80% ethanol over a steam bath (A. Felsot, *personal communication*). The solutions were processed by the methods of Moore (1974) and read at 700 nm on a Beckman model 25 spectrophotometer. Percent reducing sugars was determined by extrapolating the spectrophotometric readings for the pulp extractions onto a standard curve. Energy content was determined using a Phillipson oxygen microbomb calorimeter according to the methods of Phillipson (1964) until values differing by <5% were obtained. Cation content was determined by placing 0.1 g of dried pulp in a muffle furnace at 500°C for 5–9 h. Acid extracts of ashed samples were measured on a Perkin Elmer 360 atom adsorpter.

Interspecific seasonal trends in fruit morphology and chemistry were analyzed by regressing each fruit characteristic (dependent variable) on the species' median fruiting dates (independent variable) as determined from herbarium specimens; median fruiting dates ranged from 4 August to 9 October. Because collection of specimens often does not reflect field abundance, some error is necessarily inherent in these estimates; use of a median rather than a mean helps reduce that error. In any event, the results would not change if the fruiting order of several species was switched.

Feeding trials

Migrant avian frugivores were mist-netted in Champaign County, Illinois, in 1976 and 1977 and held in outdoor aviaries for varying lengths of time from late August through October. Birds were successfully maintained on a diet of cottage cheese mixed with Gerber's high-protein cereal and Gerber's fruit-flavored baby food, supplemented with hard-boiled eggs, raisins, mealworms, and wild fruits not used in feeding trials the following day. The latter two items were used to entice the birds to peck at the artifical diet. This worked well; once one or two birds in an aviary began feeding, the others usually quickly followed suit.

Birds to be tested were removed from aviaries and placed (at ≈0700) singly in a small wire-mesh cage covered on the top and all sides except the observer's side. Each cage contained a known number of a single fruit species; all fruits were detached from their stems. The fruit mass presented in the trials usually exceeded consumption and was similar for all fruit species. The order of fruit presentation was randomized before each trial series. An individual bird was tested twice with the same fruit species (still in randomized order) when possible. Food was removed from the aviaries the evening before each trial to allow evacuation of the digestive tract. This period was sometimes inadequate; in at least 20 trials, birds retained a small number of identifiable seeds from the maintenance diet for >12 h. Fruit pulp, however, appeared to be excreted in <12 h, since the feces did not change color during a feeding trial. No corrections were made in these instances. A total of 66 individuals of 11 bird species was tested and up to 18 fruit species were used in 405 feeding trials. From 5 to 16 fruit species were offered to each bird species. Fruits used in the feeding trials were picked at the same time and from the same plants as those fruits used in the nutrient and cation analyses.

Birds were observed continually during each trial for 2 h or until all fruits were eaten, whichever time was shorter. Information on how fruits were ingested and on method (regurgitation vs. defecation) and timing of seed loss were obtained by recording when each fruit was eaten, when seeds were regurgitated, and when defecation occurred. After 2 h, uneaten fruit was removed and weighed; the test birds remained in the cages for ≈2 h more. Feces passed during the 4-h period were collected, dried to constant mass in a drying oven, and weighed. No trials were run to determine length of time to void fruits completely, nor are there data indicating passage rates, though fruits probably pass faster than other food types (G. Walsberg, *personal communication*). Consumption of each fruit species was measured as the mean pulp dry mass eaten (whole wet mass eaten × percent dry pulp) by individuals of each bird species.

Retained energy was calculated for individual birds as energy ingested minus energy excreted. Digestive efficiency was calculated for individual birds as retained energy/energy ingested.

Morphological variables were obtained from fruit and bill dimensions. Bill dimensions were measured on specimens at the Field Museum of Natural History in Chicago, Illinois, the collection of Jean and Richard Graber at the Illinois Natural History Survey, and the Illinois Natural History Museum at the University of Illinois. Bill length, width, and depth were measured as distance from the lower bill tip to the corner of the gape, width at gape, and depth at gape, respectively. These dimensions were used in lieu of traditional morphological criteria because they seemed more significant in limiting the upper size of food items that could be ingested (R. Graber, *personal communication*). Diameters of field-collected fruits were measured with calipers. The size of nonspherical fruits (diameters usually differing by 1–2 mm) was calculated as the mean of length and width measurements ($N = 30$ for each species) rather than the smallest fruit diameter. Measuring only the smallest fruit diameter assumes that birds handle fruits perfectly, but this was never observed in the feeding trials. Each bill dimension used in the analysis was represented as the fruit size minus the respective bill measure to give an index of relative fruit size. All three bill measurements were used because only gape and depth were intercorrelated ($r = 0.78$, $P < .01$, $N = 11$). This also allowed us to see if one bill dimension was consistently related to fruit consumption.

The mean mass of each fruit species consumed by each bird species (dependent variable) was regressed (SAS, Barr et al. 1979) on each of four sets of independent variables: the percentage and absolute amount of several nutrients (mass of dry pulp, protein, lipids, reducing sugars) per fruit and the percentage and absolute amount of several cations (Na, K, Ca, Mg) per fruit. The morphological variable previously determined to be correlated most highly with consumption was also used as an independent variable. Including a morphological variable allows us to discern if different factors affect fruit consumption over a range of fruit sizes. Energy content (in joules per gram) was not included as an independent variable because it was strongly correlated ($r = 0.90$, $P < .001$, $N = 19$) with percentage of lipids. Each bird species was analyzed separately. Trials in which a bird ate nothing (56 of 405) were deleted because of uncertainty about why the bird failed to eat.

RESULTS

Nutritional content of fruits

We analyzed morphological features, and nutrient, energy, and cation content for the pulp of 22 native fleshy fruits (Appendix). No seasonal trends appeared for fruit mass, pulp wet mass, pulp dry mass, percent dry pulp per fruit, or percent water. The absolute quantity of protein and potassium per fruit (but not the percentage) increased later in the year ($r = 0.44$, $P < .05$, $N = 20$ and $r = 0.67$, $P < .01$, $N = 18$, respectively). No seasonal trends occurred for lipids, reducing sugars, energy content per fruit, Na, Ca, or Mg.

Fruit energy content was compared among species having different types (bicolor vs. monochrome: Willson and Thompson 1982) and sizes (large vs. small) of fruit displays (Appendix). Energy content per unit mass did not differ (t test) among either grouping (bicolor, $\bar{X} = 20\,628$ J/g; monochrome, $\bar{X} = 20\,332$ J/g; large, $\bar{X} = 22\,279$ J/g; small, $\bar{X} = 17\,941$ J/g).

Nutrient and cation content of six fruit species were compared with values from the literature, and some marked differences occurred. Our values for protein content in *Vitis vulpina, Prunus serotina,* and *Celtis occidentalis* were considerably lower than Halls (1977) (2.2 vs. 5.4–9.8%; 2.0 vs. 13.9%; 3.5 vs. 9.5%, respectively). Our lipid values are similar to those of Stiles and White (1982) for *Lindera benzoin* (33.2 vs. 34.6%), *Sambucus canadensis* (2.8 vs. 4.9%), and *Celtis occidentalis* (0.4 vs. 0.7%), but much lower than those of Halls (1977) and Wainio and Forbes (1941). We also obtained lower lipid values than Halls (1977) for *Prunus serotina* (0.4 vs. 7%) and some *Vitis vulpina* (0.8 vs. 0.9–9.5%). Our Ca value for *C. occidentalis* is much lower than Halls (1977) (0.4 vs. 11.8%). Sources of such differences could lie in technique or in genetic, seasonal, habitat, or regional differences in the fruits. Considerable intraspecific variation occurred in our nutrient and cation contents (Appendix). Whatever the source of variation, such differences necessitate caution in interpretation.

Fruit traits and avian consumption

Total fruit consumption in 2 h was correlated significantly with the pulp dry mass per fruit in 6 of the 11 frugivore species tested (Table 1). Seed mass per fruit (PF) and per seed (PS), which both increased with pulp dry mass per fruit ($r = 0.56$, $P < .01$, $N = 22$ and $r = 0.69$, $P < .001$, respectively), were positively correlated with mean pulp dry mass consumed per bird species (dependent variable) in four of the six species: Swainson's Thrush, $r = 0.56$, $P < .05$, $N = 13$ (PS); American Robin, $r = 0.75$, $P < .01$, $N = 15$ (PS); $r = 0.72$, $P < .01$ (PF); Brown Thrasher, $r = 0.83$, $P < .01$, $N = 10$ (PS); Hermit Thrush, $r = 0.69$, $P < .01$, $N = 13$ (PF). (Scientific names are given in Table 1.) Ability to regurgitate seeds rapidly undoubtedly contributed to ingestion of more pulp dry mass.

No simple relationship existed between fruit chemistry and fruit mass consumed in the feeding trials. Amount of one or more cations was correlated with pulp dry mass consumed for most bird species (Table 1). The inconsistency among bird species as to the particular cation or direction of the relationship implies that the correlations are a byproduct of pulp dry mass ingested. Protein content per fruit was correlated with fruit consumption in three species; the slope was positive for the Veery and negative for the Brown Thrasher and Cardinal (Table 1). Reducing-sugar content per fruit was positively correlated with fruit consumption for the Gray-cheeked Thrush. Lipid content

TABLE 1. Multiple regression results for fruit mass consumption by bird species.

Bird species*	Number of individuals	Bird mass (g)	Fruit pulp nutrients†			Fruit pulp cations†		
			Variables‡	Direction	R^2	Variables‡	Direction	R^2
Cardinal (*Cardinalis cardinalis*)	2	44	dry pulp per fruit and protein mass	+ −	= 0.65	NS		
Veery (*Catharus fuscescens*)	8	33	protein mass and fruit diameter − bill length	+ −	= 0.50	% K	−	0.36
						% K and % Na	− +	= 0.62
						% K and % Na and fruit diameter − bill depth	− + +	= 0.82
Hermit Thrush (*C. guttata*)	15	31	dry pulp per fruit	+	0.53	NS		
Gray-cheeked Thrush (*C. minima*)	5	30	sugar mass and fruit diameter − bill length	+ −	= 0.43	Ca mass	−	0.49
Swainson's Thrush (*C. ustulata*)	6	32	dry pulp per fruit	+	0.50	Mg mass	+	0.44
			dry pulp per fruit and fruit diameter − bill length and % protein	+ − +	= 0.85			
Gray Catbird (*Dumetella carolinensis*)	5	39	dry pulp per fruit	+	0.55	% K	−	0.35
Wood Thrush (*Hylocichla mustelina*)	6	50	dry pulp per fruit	+	0.87	Mg mass	+	0.77
Scarlet Tanager (*Piranga olivacea*)	1	32	NS			% K	−	0.78
Brown Thrasher (*Toxostoma rufum*)	2	72	dry pulp per fruit	+	0.45	Mg mass	+	0.43
			dry pulp per fruit and protein mass	+ −	= 0.74			
American Robin (*Turdus migratorius*)	10	77	dry pulp per fruit	+	0.70	fruit diameter − bill depth	+	0.50
						fruit diameter − bill depth and Mg mass	+ +	= 0.67
Red-eyed Vireo (*Vireo olivaceous*)	6	18	NS			% Ca	−	0.59

* Bird species are arranged alphabetically by genus.

† Analyses using pulp nutrients and cations were performed using both the percent and absolute amount (mass) in each fruit, as well as with the bill dimension most highly correlated with fruit consumption.

‡ Multiple regression variables are included if $P \leq .05$ and are listed in descending order of inclusion into the regression. Nonsignificance of all variables is denoted by NS.

per fruit was not correlated with fruit consumption for any avian species. Use of percentages instead of absolute quantity in these correlation analyses did not change the results. Fruit consumption was negatively correlated with energy per gram of dry fruit pulp for the Wood Thrush ($r_s = -0.68$, $P < .05$, $N = 9$) and Scarlet Tanager ($r_s = -0.89$, $P < .05$, $N = 5$).

The relationship between relative fruit size (a combination of fruit and bill dimensions) and fruit consumption was significant only for the American Robin,

TABLE 2. Significant differences (ANOVA; Student-Newman-Keuls test) in digestive efficiencies (DE) among fruit species within a bird species and among bird species within a fruit species, for fruit species with $N \geq$ three trials per bird species.*

Fruit species	Brown Thrasher	Gray Catbird	Gray-cheeked Thrush	American Robin	Hermit Thrush	Swainson's Thrush	Veery	Wood Thrush	Red-eyed Vireo	$\bar{X}$ DE of fruit species
Parthenocissus	0.463	0.418^{b}								0.441
Menispermum				0.406^{ab}	0.620^{ab}					0.513
Smilax lasioneura				0.509^{b}	0.536^{b}					0.523
Arisaema					0.605^{ab}					0.605
Polygonatum		0.403_{d}^{b}		0.688_{d}^{a}	0.758_{c}^{a}	0.648_{d}	0.727_{d}			0.645
Prunus	0.454_{d}	0.582_{d}^{ab}	0.462_{d}	0.762_{d}^{a}	0.744_{d}^{ab}	0.661_{d}	0.772_{d}		0.825_{c}	0.658
Lindera	0.623	0.657^{ab}				0.716	0.761	0.849		0.721
S. hispida				0.760^{a}	0.713^{ab}					0.737
Phytolacca	0.805	0.588^{a}	0.781	0.743^{a}	0.714^{ab}	0.745	0.887			0.752
Euonymus					0.752^{a}					0.752
Celtis				0.785^{a}	0.753^{a}		0.741			0.760
Smilacina		0.655_{cd}^{ab}		0.807_{cd}^{a}	0.627_{d}^{ab}	0.736_{cd}	0.897_{c}		0.827_{c}	0.763
Cornus		0.820^{a}		0.771^{a}	0.800^{a}	0.676				0.767
Sambucus					0.666_{d}^{ab}		0.821_{d}		0.895_{c}	0.794
Vitis		0.834_{c}^{a}			0.717_{d}^{ab}		0.884_{c}		0.885_{c}	0.830
$\bar{X}$ DE of bird species	0.586	0.620	0.622	0.692	0.693	0.702	0.811	0.849	0.858	

* Fruit and bird species are listed in order of ascending mean DE from top to bottom and left to right, respectively. Significantly different DE among fruit species within a bird species are indicated in each column by the superscripts a and b: a > b. Significantly different DE among bird species within a fruit species are indicated in each row by the subscripts c and d: c > d. Values that do not differ significantly have the same super- or subscript.

the largest species tested (fruit diameter − bill depth, $R^2 = 0.50$; see Table 1). The slopes were positive, indicating that more fruit was eaten as fruit size increased.

Pulp dry mass consumption was positively correlated (Spearman rank correlation, $P < .05$) with retained energy in 9 of 11 bird species (all but Swainson's Thrush and Scarlet Tanager). When all birds were tested in a single regression, an individual's fruit consumption was positively correlated with the retained energy during a feeding trial ($r = 0.87$, $P < .0001$, $N = 349$). Energy extracted per gram of pulp dry mass ingested was greatest in fruits with high (>25%) lipid content (Appendix). Almost all birds (19 of 21) obtained >16 720 J/g, and most (13 of 21) extracted >20 900 J/g from high-lipid fruits. No more than 16 302 J/g were extracted from low-lipid fruits. This suggests that high-lipid fruits could, if available, replenish the birds' fat reserves most rapidly. Yet within this group of fruits, the range of digestive efficiencies was wide (0.44 for *Parthenocissus* to 0.78 for *Cornus,* Table 2).

Of all variables, digestive efficiency was correlated only with protein content per fruit in the Gray-cheeked Thrush ($r = -0.83$, $P < .01$, $N = 12$). Thus, neither the percent nor absolute amount of nutrients (lipids, protein, reducing sugars, joules per gram of dry pulp) per fruit appeared to affect digestive efficiency. The pulp dry mass consumed was correlated with digestive efficiency in the Wood Thrush ($r_s = 0.71$, $P < .05$, $N = 9$) and Swainson's Thrush ($r_s = -0.60$, $P < .05$, $N = 13$).

Differences in digestive efficiency were examined both within each bird species (separated by fruit species) and within each fruit species (separated by bird species) for fruits with at least three trials per bird species (one-way ANOVA followed by a Student-Newman-Keuls test). These results, however, provide only a preliminary estimate of digestive efficiencies in migrating birds because the trials were on recently captured birds with unknown histories. The Veery, Swainson's Thrush, Gray-cheeked Thrush, Red-eyed Vireo, and Brown Thrasher had similar digestive efficiencies on all fruits tested. The Hermit Thrush, American Robin, and Catbird, on the other hand, digested some fruits significantly better than others, but the array of fruits digested well differed among these three species (Table 2).

Some fruit species were digested more efficiently by some bird species than by others (Table 2). For example, Red-eyed Vireos had significantly higher efficiencies on *Sambucus* and *Prunus* than did other bird species, and Hermit Thrushes had higher efficiencies on *Polygonatum* and lower efficiencies on *Vitis* than did other bird species. Other fruit species were digested with similar efficiency by all bird species tested. This similarity is especially noteworthy in *Phytolacca, Lindera,* and *Cornus,* in which the digestive efficiencies of fruits with quite different composition were similar for birds in two or three avian families.

Fruit and seed handling

The thrushes, mimids, and the vireo typically swallowed the fruits and later voided the seeds. The Scarlet Tanager often picked the pulp off the seed, letting the seed drop. The Cardinal commonly crushed and presumably digested the seeds, at least of large-seeded species such as *Lindera.*

The seeds of most plant species sometimes were regurgitated, a fact long known for small temperate birds (e.g., Kerner 1895, Bailey 1897, Proctor 1897, Herrera and Jordano 1981, Sorensen 1981). Time between ingestion and seed regurgitation was not related to the mass per seed for any bird species (two-tailed Spearman rank correlation, $P > .05$). Amount of fruit eaten did not affect the probability of regurgitating or defecating seeds for any bird species ($P > .05$).

Method of voiding seeds may be related to frugivore size. Red-eyed Vireos (≈ 18 g) defecated only the smallest seeds, such as elderberry (*Sambucus*), and regurgitated some small seeds, as well as all larger ones. In contrast, American Robins (≈ 77 g) defecated seeds as large as black cherry (*Prunus*) and sometimes regurgitated seeds smaller than dogwood (*Cornus*). The other tested birds, which ranged from ≈ 30 g (Gray-cheeked Thrush) to ≈ 72 g (Brown Thrasher), showed no interspecific differences in seed treatment. Variation among conspecifics was sometimes marked.

Regurgitated seeds generally spent less time in a bird than did defecated seeds. The most extensive data (using only individuals voiding seeds of one plant species both ways) are for Hermit Thrushes and American Robins: we recorded the time from the first fruit eaten to the first regurgitation and first defecation. For Hermit Thrushes, the time from consumption to defecation averaged almost three times that to regurgitation; median times differed significantly (median test: median between 10 and 11 min vs. median between 30 and 31 min, $P < .05$, $N = 28$) for all fruit species combined. Time to defecation exceeded time to regurgitation in 25 of 28 matched pairs (sign test, $P < .05$, two or three trials per fruit species). Regurgitation was consistently faster than defecation for *Cornus, Vitis, Polygonatum,* and *Euonymus* (Mann-Whitney U test, no overlap, $P < .05$, one-tailed, $N = 3$ comparisons per fruit species) and did not differ significantly in *Smilacina, Smilax* (two species), or *Menispermum,* although the same trend was evident. For American Robins, seed regurgitation ($\bar{X} = 19$ min) usually occurred sooner than seed defecation ($\bar{X} = 30$ min) over the entire sample (sign test, $P < .05$, $N = 23$). Regurgitation was consistently faster than defecation for *Vitis* and *Smilax hispida* seeds (Mann-Whitney U, $P < .05$, no overlap, one-tailed, $N = 3$), and did not differ in *Cornus, Smilacina,* and *Smilax lasioneura.*

For six Hermit Thrushes eating smaller seeds (*Phytolacca, Solanum*), the time between ingestion and first regurgitation or defecation of a seed did not differ consistently, though the proportion of all seeds voided by regurgitation during a feeding trial generally was higher than the proportion of all seeds defecated for a given time interval. Four individuals voided a consistently higher proportion of *Phytolacca* seeds by regurgitation than by defecation in the first 30 min after ingestion (68% vs. 33%, 20% vs. 0%, 67% vs. 47%, 41% vs. 2%); similar differences were apparent in the second 30 min after ingestion. Similarly, two Hermit Thrushes eating *Solanum* voided the seeds sooner by regurgitation than by defecation. Maximum recorded times for seed voiding were 90 min for regurgitation and 12 h for defecation (averages cannot be calculated for all seeds ingested because the exact order of each seed's input and output was unknown).

DISCUSSION

Nutrient composition of native fruits varied considerably. The only seasonal trends in fruit traits were increases in absolute amount of protein and potassium per fruit. These trends do not correspond with the predictions of Snow (1971) or Herrera (1982) for seasonal trends of European fleshy fruits. Herrera's predictions, however, may not be applicable, since birds in Spain are commonly under summer water stress, while birds in Illinois probably are not. Nor do our results support the contention (Stiles 1980, Stiles and White 1982) that carbohydrate levels are higher in summer- than in fall-maturing fruits in the North American eastern deciduous forest. The few trends in fruit nutritional values suggest either that fruits do not match the possibly changing seasonal nutritional requirements of birds, or that the seasonal requirements of birds do not change greatly. The birds' ability to supplement nutritional demands with insects, which reach peak densities in Illinois at the same time as peak bird migration (Kendeigh 1979), may relax selection pressures on fruit species to produce sufficient nutrients to satisfy completely the nutritional requirements of their avian seed vectors.

If bird-dispersed plants compete for dispersers (as suggested by Herrera 1981, Stapanian 1982*a*), then low-nutrition fruits might be subject to greater selection for conspicuous fruiting displays and, conversely, conspicuous displays might permit the evolution of lower nutritional value. Displays in which the ripe fruit color contrasts with associated structures or unripe fruits (bicolored displays: Willson and Thompson 1982) are generally conspicuous, at least to humans, and apparently also to birds (Willson and Melampy 1983). However, these fruits are not less nutritious than those of monochrome displays (Appendix). Low-nutrition fruits might also be favored on plants producing large fruit crops if the large crop itself attracts birds (but see Stapanian 1982*b*), but there is no inverse relationship between fruit crop size and nutritional values of single fruits (Appendix).

Pulp dry mass per fruit was the most important factor correlated with fruit consumption in these experiments. Other fruit nutrients or cations were inconsistently correlated. Higher correlations with pulp dry mass per fruit than with relative fruit size suggest that differences in treatment of individual fruits, i.e., storage in the crop vs. passage to the gizzard, may be important. In only a few cases did birds eat more of a less nutritious fruit type, indicating that they seldom compensated for low-quality fruits with greater quantity.

Relative fruit size did not appear to affect fruit consumption over the range of fruit sizes and bird species used in this study. The apparent lack of morphological constraints on fruit consumption, combined with the array of fruit sizes presented in the feeding trials, indicate that most migrant frugivore species are able to consume and disperse most fleshy fruit species available during fall migration. Seed size did not noticeably affect fruit consumption.

In most cases, the mass eaten was a good index of energy obtained, since most birds showed retained energy correlated with mass consumed, and since digestive efficiency was only sometimes different. Nevertheless, the mass eaten is not always a good index of energy obtained. For instance, consumption of high-lipid fruits yielded more retained energy per gram of dry pulp than did low-lipid fruits, even though digestive efficiency was uncorrelated with fruit nutrients and especially energetic content. In many cases, birds obtained more joules per gram of dry pulp from high-lipid fruits than possible with 100% digestive efficiency of low-lipid fruits. Thus, high-lipid fruits are the most rewarding to the birds when all other fruit traits are equal. However, in the laboratory these migrants did not eat more of high-lipid fruits; instead, consumption of a fruit species was usually related to pulp dry mass per fruit, which may be more easily assessed by a feeding bird than is nutrient content. Consuming fruits with more pulp dry mass minimizes the number of fruits needed to reach satiation and the length of exposure to predators (see Howe 1979). Also, less energy may be expended handling fewer and larger fruits, giving the bird a higher net yield (Emlen 1968, Martin 1985).

Regurgitation rather than defecation of large seeds (depending partly on frugivore size) makes deposition closer to the source more likely; small seeds, in contrast, have a higher probability of being transported away from the source. Dispersal by several bird species might produce a seed shadow that varies with body size of the avian consumer as well as with seed size (see also Sorensen 1981). Variation in disperser quality also affects the seed shadow (see Howe and Primack 1975, Howe 1977). In our trials, the feeding behavior of the Scarlet Tanager, and especially the Cardinal, makes them poor dispersal agents of at least some fruit species.

What is apparent overall from these analyses is that patterns of fruit consumption and seed voiding are highly variable among temperate bird species. Generalizations on bird-fruit interactions require a more refined understanding of the kinds of variation that occur among these interactions.

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APPENDIX

Variation in mass and morphology, cation content, and nutrient content of individual fruits collected in central Illinois (except *A. rubra* in Minnesota). Fruit species are arranged from early to late median fruiting dates.

	Fruit size (mm)		Mean whole-fruit properties (±1 SE)				
Fruit species*	*N*	$\bar{X}$ ± SE	*N*	Fresh mass (g)	Pulp dry mass (g)	Number of seeds	Total fresh seed mass (g)
(Summer)							
Rubus allegheniensis (B)	···	···	37	0.759 (0.029)	0.035 (0.002)	35.892 (1.814)	0.132 (0.009)
Arisaema triphyllum (M, S)	30	7.17 (0.16)	80	0.203 (0.009)	0.011 (0.001)	1.501 (0.092)	0.083 (0.005)
Caulophyllum thalictroides (B, S)	30	8.60 (0.36)	41	0.347 (0.020)	0.026 (0.002)	1.000 (···)	0.189 (0.009)
Prunus serotina (B, L)	30	7.50 (0.08)	60	0.463 (0.013)	0.057 (0.003)	1.000 (···)	0.104 (0.004)
Sambucus canadensis (B, L)	30	5.05 (0.05)	51	0.059 (0.003)	0.004 (0.000)	3.451 (0.085)	0.034 (0.003)
(Fall)							
Cornus racemosa (B, L)	30	6.39 (0.09)	130	0.157 (0.003)	0.027 (0.001)	1.000 (···)	0.041 (0.001)
Smilacina racemosa (B)	30	6.58 (0.28)	132	0.178 (0.006)	0.020 (0.001)	1.197 (0.036)	0.055 (0.002)
Polygonatum commutatum (M, S)	30	10.19 (0.19)	150	0.551 (0.016)	0.059 (0.002)	8.687 (0.227)	0.218 (0.006)
Phytolacca americana (B, L)	30	7.86 (0.11)	150	0.302 (0.005)	0.019 (0.001)	9.680 (0.068)	0.089 (0.001)
Acetaea rubra (M, S)	30	8.56 (0.17)	20	0.305 (0.017)	0.013 (0.001)	8.650 (0.509)	0.112 (0.007)
Parthenocissus quinquefolia (B)	30	7.48 (0.16)	20	0.254 (0.020)	0.027 (0.001)	2.100 (0.204)	0.078 (0.007)
Solanum americanum (B)	30	8.10 (0.14)	20	0.360 (0.027)	0.030 (0.002)	16.450 (2.067)	0.034 (0.004)
Celastrus scandens (B)	···	···	10	0.302 (0.016)	0.048 (0.003)	4.400 (0.340)	0.054 (0.006)
Panax quinquefolius (M, S)	···	···	31	0.291 (0.017)	0.007 (0.000)	2.000 (0.066)	0.125 (0.005)
Vitis vulpina (M)	30	7.68 (0.12)	42	0.277 (0.002)	0.035 (0.003)	1.595 (0.137)	0.050 (0.006)
Celtis occidentalis (M, L)	30	9.80 (0.07)	30	0.443 (0.021)	0.127 (0.012)	1.000 (···)	0.199 (0.006)
Lindera benzoin (M)	30	8.53 (0.20)	72	0.380 (0.011)	0.040 (0.001)	1.000 (···)	0.145 (0.003)
(Winter or persistent)							
Menispermum canadense (M)	30	7.98 (0.11)	78	0.609 (0.017)	0.067 (0.003)	1.000 (···)	0.109 (0.003)
Smilax hispida (M)	30	7.29 (0.18)	82	0.300 (0.012)	0.040 (0.001)	1.146 (0.046)	0.098 (0.004)
Smilax lasioneura (M)	30	7.73 (0.12)	120	0.429 (0.014)	0.046 (0.001)	3.308 (0.126)	0.149 (0.006)
Euonymus atropurpurea (B)	30	7.70 (0.18)	40	0.181 (0.012)	0.026 (0.002)	1.250 (0.069)	0.096 (0.007)
Rhus radicans (M, L)	···	···	15	0.028 (0.001)	0.001 (0.000)	1.000 (···)	0.025 (0.007)

* Bicolored fruiting displays are marked with a B, monochrome ones with an M; very small displays (≤50 fruits) are indicated by an S, very large ones (≥500 fruits) with an L (see also Willson and Thompson 1982).

† Percent lipids and reducing sugars are the mean of two sample determinations; percent protein is from one sample determination.

‡ The small fruit mass of some species necessitated using several fruits rather than individual fruits.

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APPENDIX Continued

Mean cation content (%, ±1 SE)					Mean nutrient content (%)†			Energy content of dry pulp‡ (J/g)	
N	Sodium	Potassium	Calcium	Magnesium	Protein	Lipids	Reducing sugars	*N*	$\bar{X}$ ± 1 SE
10	0.096 (0.016)	2.074 (0.173)	0.406 (0.047)	0.265 (0.062)	…	…	…	3	18 170 (322)
14	0.117 (0.012)	3.005 (0.213)	1.433 (0.259)	0.333 (0.026)	5.54	3.52	35.9	1	19 207 (…)
9	0.064 (0.010)	4.508 (0.498)	0.354 (0.104)	0.063 (0.013)	5.24	1.62	3.3	6	18 689 (410)
10	0.053 (0.006)	1.391 (0.295)	0.131 (0.030)	0.058 (0.011)	2.02	0.42	19.9	9	16 967 (418)
5	0.695 (0.143)	2.528 (0.121)	0.446 (0.186)	0.380 (0.045)	7.08	2.80	12.6	2	21 130 (1045)
15	0.095 (0.010)	1.785 (0.121)	0.761 (0.123)	0.466 (0.053)	3.26	39.86	10.0	2	28 374 (347)
29	0.065 (0.009)	2.060 (0.230)	0.084 (0.010)	0.051 (0.004)	1.63	0.54	12.6	2	18 551 (184)
14	0.013 (0.002)	1.371 (0.098)	0.149 (0.026)	0.050 (0.004)	5.41	1.61	47.2	6	18 505 (485)
19	0.400 (0.062)	5.018 (0.738)	0.154 (0.019)	0.201 (0.044)	5.37	0.73	53.1	3	18 706 (456)
…	…	…	…	…	5.41	1.64	5.1	2	14 944 (163)
10	0.070 (0.010)	3.193 (0.245)	1.679 (0.272)	0.296 (0.029)	3.85	25.66	11.1	1	23 412 (…)
10	0.077 (0.014)	3.142 (0.181)	0.110 (0.014)	0.075 (0.010)	8.56	0.61	14.0	1	20 260 (…)
…	…	…	…	…	8.18	3.92	…	3	19 303 (815)
5	0.185 (0.026)	6.108 (0.142)	0.192 (0.014)	0.148 (0.014)	9.24	…	…	1	18 350 (…)
5	0.045 (0.002)	1.457 (0.153)	0.255 (0.034)	0.066 (0.009)	2.24	0.81	12.4	2	18 354 (782)
5	0.030 (0.005)	1.892 (0.694)	0.412 (0.100)	1.892 (0.354)	3.48	0.36	11.6	9	18 563 (314)
19	0.055 (0.008)	3.714 (0.216)	0.121 (0.018)	0.076 (0.007)	4.22	33.24	3.4	2	26 748 (1484)
15	0.032 (0.003)	2.101 (0.128)	0.043 (0.004)	0.024 (0.006)	4.75	0.86	23.2	6	20 775 (485)
15	0.040 (0.006)	2.567 (0.232)	0.325 (0.071)	0.307 (0.068)	3.96	0.84	8.2	12	19 705 (481)
18	0.068 (0.009)	4.051 (0.300)	0.145 (0.019)	0.028 (0.006)	4.09	0.73	15.0	6	18 559 (431)
5	0.299 (0.162)	8.678 (4.076)	0.777 (0.321)	0.497 (0.249)	9.15	31.16	4.7	6	23 366 (1626)
14	0.072 (0.015)	1.481 (0.105)	0.756 (0.133)	0.189 (0.012)	…	…	…	1	29 937 (…)