

DO SEEDS HINDER DIGESTIVE PROCESSING OF FRUIT PULP? IMPLICATIONS FOR PLANT / FRUGIVORE MUTUALISMS

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ABSTRACT.—The seeds of bird-dispersed fruits could impose significant costs on frugivores if seed bulk reduces the effective capacity of the gut and, hence, reduces the rate of nutrient intake. This has led to the notion that avian frugivores pass food through their digestive tracts rapidly to minimize the effects of seeds on nutrient acquisition. Consequently, avian frugivores are thought to utilize fruit sugars inefficiently, because this permits higher intake and sugar-assimilation rates from a supposedly energy-dilute food. I evaluated the influence of seed bulk on intake and absorption of sugars from chokecherry fruits (*Prunus virginiana*) by Cedar Waxwings (*Bombycilla cedrorum*), American Robins (*Turdus migratorius*), Wood Thrushes (*Hylocichla mustelina*), Gray-cheeked Thrushes (*Catharus minimus*), and Hermit Thrushes (*Catharus guttatus*). I compared Cedar Waxwings with thrushes to determine if they differed in how seed bulk affects digestion of fruit. Cedar Waxwings have higher mass-specific intake rates of sugary fruits than do thrushes; because waxwings defecate all seeds, whereas thrushes regurgitate many seeds, the difference in intake of sugary fruits between waxwings and thrushes may result from ingestion / fruit-processing limitations associated with mode of seed processing. For all species, seeds did not reduce rates of intake and sugar absorption from chokecherry fruit pulp. All birds assimilated sugars from chokecherry fruits efficiently, and digestive processing of seeds did not reduce sugar absorption. Rates of fruit processing were closely tied to rates of sugar absorption, rather than to the physical composition of the diet. My results suggest that current models of digestive function in avian frugivores are seriously flawed. Because differences in intake rates of sugary fruits between waxwings and thrushes were independent of the presence of seeds, these differences were not due to different modes of seed processing. *Received 13 January 1997, accepted 18 August 1997.*

THE MUTUALISTIC RELATIONSHIP between plants that produce fleshy fruits and vertebrate seed dispersers is well known (Snow 1971, McKey 1975, Pijl 1982, Wheelwright and Orians 1982). Dispersers benefit from the nutrient rewards of fruit pulp, primarily sugars and lipids (Herrera 1987, White 1989, Witmer 1996), whereas plants benefit from the deposition of seeds in suitable habitat away from the vicinity of parent plants. Many studies have demonstrated increased survival of seeds and seedlings away from parent plants (Janzen 1972, Howe and Primack 1975, Webb and Willson 1985). The specialized dispersal systems of mistletoes illustrate the important role of dispersers in depositing seeds at appropriate sites (Reid 1989, Murphy et al. 1993, Sargent 1995, Martínez del Rio et al. 1996). In addition to the benefits accrued by fruiting plants and frugi-

vores, theoretical considerations have argued that there are costs to mutualistic partners. Presumably, the cost to plants is in the resources that they allocate to producing fruit pulp that has no purpose other than to attract dispersers (Howe 1993). Some fruits are photosynthetic, suggesting a mechanism by which plants may minimize the costs of fruit production (Cipolini and Levey 1991). Seed dispersers are thought to incur costs associated with ingestion of seeds in at least three ways: (1) the energy required to carry seeds in the gut, (2) the energy required to manipulate seeds, and (3) the occupation of gut volume with indigestible bulk that reduces the rate at which fruit pulp can be processed and nutrients assimilated (Snow 1971, McKey 1975, Howe and Vande Kerckhove 1980, Herrera 1981, Sorensen 1984, Levey and Grajal 1991, Murray et al. 1993). Measurements of these costs are scarce (see Levey and Grajal 1991, Murray et al. 1993), and no work has addressed how seeds in natural fruits affect avian dispersers. Here, I evaluate

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the hypothesis that seeds limit ingestion and assimilation rates of sugars from fruit pulp by frugivorous birds.

Several studies have developed the idea that the indigestible seed bulk of fruits reduces rates of nutrient assimilation by birds. Levey and Grajal (1991) found that Cedar Waxwings (*Bombycilla cedrorum*) fed two kinds of artificial diets with different seed sizes but equal seed loads (seed volume per total fruit volume; seed load held constant by adjusting the numbers of seeds per fruit) passed large seeds faster than small seeds and consumed the large-seeded fruits at faster rates. This result led them to propose that Cedar Waxwings are process-rate limited when eating sugary fruits, i.e. that waxwings ingest fruits as fast as they can process them through the gut, and that seeds represent a significant cost because gut volume that could contain nutritious fruit pulp is occupied by indigestible seeds. In a parallel study, Murray et al. (1993) found that American Robins (*Turdus migratorius*) consumed large-seeded fruits faster than small-seeded fruits. They also invoked gut-processing limitations, attributing their result to the fact that robins regurgitated seeds of large-seeded fruits and defecated seeds of small-seeded fruits. The idea of limitation of gut-processing rate has fostered the contention that avian frugivores process foods rapidly through their guts and utilize fruit nutrients inefficiently. Presumably, rapid gut-processing rates are a result of selective pressures to reduce the retention time of indigestible seeds within the digestive tract because of high energy requirements and volumetric constraints on gut capacity of frugivorous birds. One hypothesized consequence of this scenario is the evolution of rapidly assimilated simple sugars as nutrient rewards in fruit pulp. Even so, avian frugivores are reputed to utilize fruit sugars inefficiently, presumably because this permits rapid fruit-processing rates that result in higher rates of sugar assimilation from supposedly energy-dilute fruits.

Differences in dietary specialization and modes of seed processing between waxwings and thrushes suggest that seed bulk has different consequences for digestive processing of fruit by these two groups of birds. In the wild, Cedar Waxwings select a diet dominated by sugary fruits, whereas thrushes consume both sugary and fatty fruits (Witmer 1996). Associ-

ated with this nutrient-based pattern of diet selection, waxwings have higher (ca. 1.5 times) mass-specific intake rates of sugary fruits than do thrushes, and waxwings always pass seeds through the digestive tract, eliminating them by defecation. In contrast, thrushes regurgitate most medium to large seeds (>90% for chokecherry fruits), a trait that may be associated with efficient digestive processing of fatty diets (Witmer 1994). The hypothesis that passage of seeds through the digestive tract reduces rates of nutrient intake and absorption (Levey and Grajal 1991, Murray et al. 1993) leads to the prediction that seeds should reduce sugar-assimilation rates to a greater degree in Cedar Waxwings than in thrushes. Alternatively, unidirectional passage of seeds within fruits containing readily assimilated simple sugars may enable birds to achieve higher rates of fruit intake and processing than when seeds are regurgitated; i.e. flow of food through the digestive tract can proceed uninterrupted by the reversal of flow from stomach to mouth that occurs during regurgitation. If passage of seeds through the digestive tract functions to permit high intake and processing rates of sugary fruits, then removal of seeds should reduce differences in intake rates between Cedar Waxwings and thrushes.

METHODS

I evaluated the influence of seed bulk on intake and assimilation rates of sugars from a natural fruit diet, chokecherry (*Prunus virginiana*), by Cedar Waxwings (mean body mass = $36.0 \pm$ SD of 3.5 g, $n = 4$), American Robins ($72.0 \pm$ SD of 6.6 g, $n = 4$), Wood Thrushes (*Hylocichla mustelina*; $60.0 \pm$ SD of 11.4 g, $n = 4$), Gray-cheeked Thrushes (*Catharus minimus*; $38.7 \pm$ SD of 4.1 g, $n = 2$), and Hermit Thrushes (*Catharus guttatus*; $28.3 \pm$ SD of 1.0 g, $n = 2$). These North American frugivores commonly eat cherries in the wild (Martin et al. 1951, Wheelwright 1986, Witmer 1996). Birds were long-term captives (more than one year) that had been maintained on a diet of moistened Eukanuba Brand Small Bites Puppy Chow and wild fruits. Chokecherry fruits were collected in September 1990 and stored frozen until the experiment. Because of the relatively small gape width of Hermit Thrushes and Gray-cheeked Thrushes, these two species were fed fruits of a smaller average size than those fed to the other species. Both fruit batches were collected from single shrub clusters at peak ripeness to maximize uniformity among individual fruits. Thawed chokecherries were similar in appearance and texture to fresh

fruits. Water content of fruit pulp from the batch fed to Cedar Waxwings, American Robins, and Wood Thrushes was 72%, and sugar content of the dry pulp was 63%. Water content of fruit pulp from the batch fed to *Catharus* spp. thrushes was 70%, and sugar content of the dry pulp was 60%. Similar values of 76% water and 58% sugar in dry pulp were reported by Witmer (1996), whereas White (1989) reported higher water (81%) and lower sugar (43% sugar in dry pulp) contents. Estimates of the relative amounts of fruit pulp and seed bulk of fruits by mass and volume were the same. Seeds comprised 11.5% of fresh mass (or volume) and 33% of dry mass of fruits fed to Cedar Waxwings, American Robins, and Wood Thrushes. Seeds comprised 19.7% of fresh mass (or volume) and 47% of dry mass of fruits fed to *Catharus* thrushes.

Birds were held individually in stainless steel cages (30 × 45 × 45 cm) with subtending collection pans in artificially lighted rooms maintained at 16°C. Birds were weighed daily, 2 h after nightfall. Water was available *ad libitum* at all times. Birds were fed whole chokecherry fruits for two days prior to the experiment to acclimate them to this diet. Each bird was alternately tested with whole and pitted fruits of chokecherry, fed *ad libitum* for the 10 daylight hours in two consecutive 24-h feeding trials (16 to 17 February 1991). Trial order was split evenly among randomly chosen individuals of each bird species. For each 24-h trial, food intake was quantified and feces were collected, frozen, and freeze-dried for chemical analyses. Because of the potential for birds to compensate for dilution of the diet by increasing the duration of their daily feeding periods, fruit intake was measured at hourly intervals to assess short-term patterns of consumption. I quantified food consumption by counting remaining fruits at each hourly check, returning dropped fruits to food dishes. To insure that birds did not select among fruits offered, I replenished diets when only a few fruits remained from the previous feeding. Pulp intake was estimated from the average values for batches of fruits fed to birds, accounting for losses of pulp when fruits were pitted. Sugar content of fruits and feces was measured by the Anthrone procedure (Yemm and Willis 1951) after extraction of samples with 80% ethanol.

To illustrate the potential effect of total intake on retention time of food within the intestines of Cedar Waxwings, the change in mean turnover time was estimated from fresh-mass (=volumetric) intake rate and intestinal volume (volume divided by intake rate; Van Soest 1994). This method assumes constant gut volume and continual processing of fruit food through the gut, consistent with the hypothesis of bulk-processing limitation (Levey and Grajal 1991). Intestinal volumes were measured on salvaged birds with relaxed tissues (Witmer 1994); thus, *in vivo* intestinal volume may have been lower. Although this

may inflate estimates of turnover time, the method is intended only to show the approximate direction and magnitude of change in retention time with changes in bulk intake under an assumption of continuous flow through a fixed gut volume.

Because sugar digestive efficiency is a proportion, this measure was arcsine-transformed for statistical analysis. Unless otherwise noted, data were analyzed by repeated-measures ANOVA because individual birds were tested on both diets (species as the between-factor and diet treatment as the within-factor). When ANOVA revealed significant differences among species, post-hoc differences between pairs of species were assessed by Fisher's protected least significant difference test (Fisher's PLSD). Because of the differences in how Cedar Waxwings and thrushes process seeds, I also performed planned comparisons between Cedar Waxwings and the four thrushes to evaluate whether waxwings responded differently than thrushes to removal of seeds from fruits.

RESULTS

There were no significant effects of trial day on total intake of fresh fruit ($F = 0.03$, $df = 1$ and 11, $P = 0.61$), pulp intake ($F = 2.55$, $df = 1$ and 11, $P = 0.14$), sugar digestive efficiency ($F = 0.01$, $df = 1$ and 11, $P = 0.95$), or total sugar assimilated ($F = 3.05$, $df = 1$ and 11, $P = 0.11$). Therefore, trial day was eliminated as a factor from subsequent analyses. Cedar Waxwings and thrushes responded in parallel ways to diet treatments (species × diet treatment interactions, $P_s > 0.30$; planned comparison × diet treatment interactions, $P_s > 0.50$).

Relative mass changes during the 24-h trials were not different among species ($F = 2.13$, $df = 4$ and 11, $P = 0.15$), nor did Cedar Waxwings differ from thrushes (planned comparison, $F = 2.86$, $df = 1$ and 11, $P = 0.12$). Relative mass changes of birds fed whole fruits versus pitted fruits did not differ significantly (whole fruits: $\bar{x} = -2.8 \pm SD$ of 1.4%; pitted fruits: $\bar{x} = -2.3 \pm 1.7\%$; $F = 1.05$, $df = 1$ and 11, $P = 0.33$).

For all species, daily mass-specific intake rates of wet matter (fruit pulp and seeds combined) were higher for whole fruits than for pitted fruits ($F = 22.86$, $df = 1$ and 11, $P < 0.001$), but intake rates of fruit pulp from these two diets were not statistically different ($F = 0.16$, $df = 1$ and 11, $P = 0.69$; Fig. 1). Pulp intake rates among thrush species were the same, whereas the intake rate by Cedar Waxwings was higher than that of each thrush species ($F = 10.89$, $df = 1$ and 11, $P < 0.001$; Fisher's PLSD for each

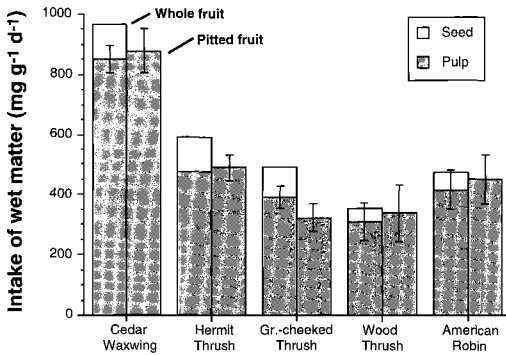


FIG. 1. Daily intake rates ($\bar{x} \pm SE$) of wet matter (fruit pulp and seeds) by five frugivores fed pitted versus whole chokecherry fruits.

comparison, $P_s \leq 0.008$). Patterns of hourly intake of pulp over the course of the feeding day were indistinguishable between treatments for all species ($F < 0.01$, $df = 1$ and 22 , $P = 0.99$; Fig. 2).

Under the assumptions of constant gut volume and continual flow, estimated mean retention time of *Prunus* pulp in the intestines of Cedar Waxwings should have decreased from about 63 to 57 min with the inclusion of seeds (Fig. 3). This effect would have been smaller for thrushes because they regurgitate most *Prunus* seeds. If sugar absorption is closely linked to retention time, seed bulk should have reduced sugar digestive efficiency for Cedar Waxwings to a greater degree than for thrushes. However, digestive efficiencies of sugars were similar for whole fruits ($96.4 \pm 0.9\%$) and pitted fruits ($96.6 \pm 0.8\%$; $F = 4.37$, $df = 1$ and 11 , $P = 0.061$; Fig. 4), and the response to diet treatment did not differ significantly among bird species. Digestive efficiencies of sugars were not different among bird species ($F = 0.52$, $df = 4$ and 11 , $P = 0.72$; planned comparison between Cedar Waxwing and thrushes, $F = 1.12$, $df = 1$ and 11 , $P = 0.31$).

Daily rates of sugar assimilation, the product of intake rate and digestive efficiency, were not significantly different for pitted and whole fruits ($F = 0.12$, $df = 1$ and 11 , $P = 0.73$; Fig. 5). Parallel with results for daily intake patterns of fruit pulp, hourly patterns of sugar assimilation were not influenced by the presence of seeds ($F = 0.66$, $df = 1$ and 22 , $P = 0.43$). Rates of sugar assimilation were the same among thrush species but higher for Cedar Waxwings than for each of the thrushes ($F = 9.66$, $df = 4$

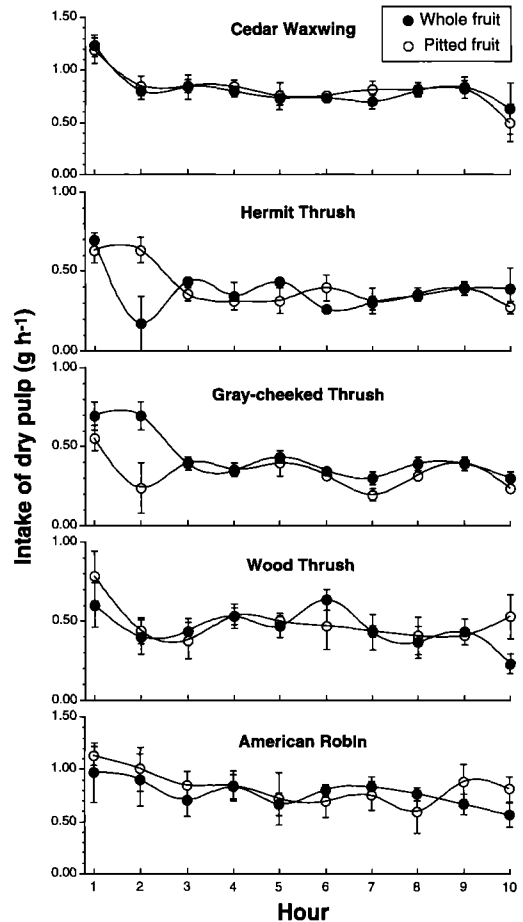


FIG. 2. Hourly patterns of pulp consumption ($\bar{x} \pm SE$) of pitted (open circles) and whole (filled circles) fruits by five frugivores.

and 11 , $P = 0.001$; Fisher's PLSD, $P_s \leq 0.010$). Because chokecherry fruit pulp contains primarily sugars, with only minute amounts of lipids and protein (3.0 and 2.6%, respectively; Witmer 1996), rates of sugar assimilation closely approximated rates of energy assimilation. Energy assimilation (from sugars) among thrush species was scaled to body mass to the 0.74 power (sugar assimilated = $2.24 \times \text{body mass}^{0.74}$), similar to the value reported among passerines (0.724, $n = 35$ species; Lasiewski and Dawson 1967). Compared with the allometric pattern among thrushes, daily sugar assimilation was higher for Cedar Waxwings (planned comparison, $F = 39.5$, $df = 1$ and 14 , $P < 0.001$; Fig. 5).

Given the absence of detectable differences

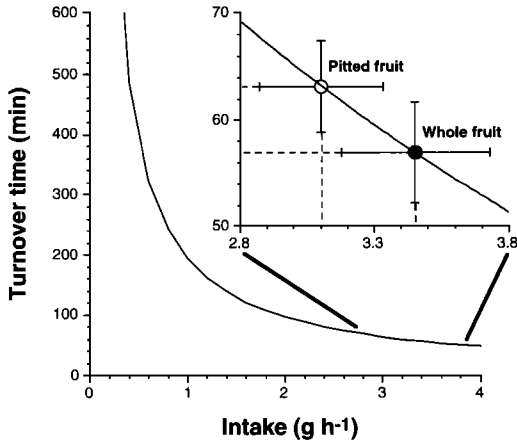


FIG. 3. Estimated effect of seed bulk on the retention time of fruit pulp by Cedar Waxwings under a model of continuous flow through an inflexible system. Values for inset are $\bar{x} \pm SE$. See Methods for details and assumptions.

among species in digestive responses to dietary seed bulk, the overall probability of falsely accepting the null hypothesis if total intake was reduced in proportion to dilution of the diet with wet bulk (Type II error) was 16% ($n = 16$); the Type II error under the expectation of intake reductions proportional to dry matter of the chokecherry diet was well below 1% (Miller et al. 1990). This experiment was statistically powerful enough to detect an effect of seeds on fruit-pulp intake of 6.6%, adequate for effects on intake proportional to wet or dry pulp mass. This was demonstrated by the significant effect of seed bulk on total intake.

DISCUSSION

Digestive responses to seed bulk.—Frugivorous birds compensated for dietary seed bulk by passing (Cedar Waxwings) or regurgitating (thrushes) seeds efficiently enough that the rates of processing and assimilating fruit-pulp sugars were not depressed (Figs. 1, 2, 5). Compensation even at 1-h intervals suggests that chokecherry seeds did not constrain instantaneous rates of intake or sugar absorption. Unidirectional processing of seeds through the digestive tract by Cedar Waxwings may be an efficient mode of processing bulky diets of readily assimilated simple sugars in an aqueous medium. Regurgitation by thrushes may eliminate seeds from the stomach so that entry of

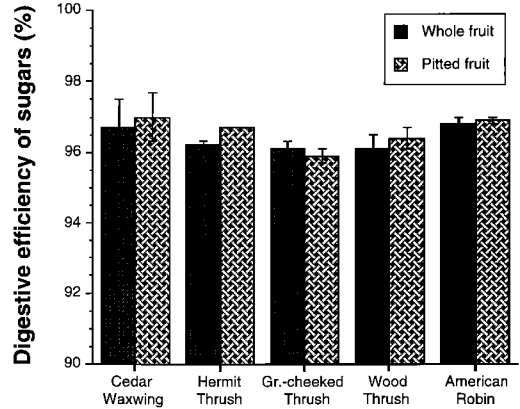


FIG. 4. Digestive efficiencies of sugars ($\bar{x} \pm SE$) by five frugivores fed pitted versus whole chokecherry fruit diets.

pulp into the intestine is not affected by seed bulk (see Levey and Grajal 1991). Equivalent rates of sugar absorption by frugivorous birds eating seedless pulp versus whole fruits suggest that intake and assimilation of fruit-pulp sugars were cued to, or limited by, the rate of sugar absorption or energy assimilation, rather than by the physical composition of these diets. Cedar Waxwings and thrushes also show compensatory digestive responses to dilution of artificial sugary diets, increasing intake rate and passage speed as sugar concentration declines to regulate daily rates of sugar uptake to constant levels (Witmer unpubl. data).

Birds eating whole and pitted chokecherry

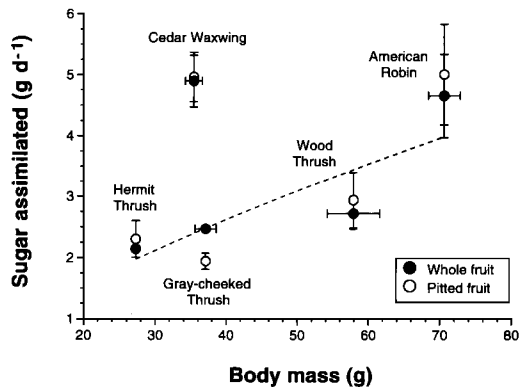


FIG. 5. Daily rates of sugar assimilation ($\bar{x} \pm SE$) by five frugivores fed pitted versus whole fruits. Sugar assimilation was not affected by the presence of seeds in fruits. Dashed line shows allometric pattern of sugar assimilation among the four thrush species.

fruits performed equally well on these diets, showing the same degree of mass loss (<3%). Thus, seed processing does not appear to have exacted significant energetic costs to birds, but this remains to be quantified.

Implications for frugivore digestive function and nutrient assimilation from fruits.—The high digestive efficiencies of sugars by the five frugivores I studied are comparable to those shown by frugivorous manakins (Worthington 1989) and nectarivorous hummingbirds (Hainsworth 1974, Karasov et al. 1986), contradicting the contention that frugivores assimilate fruit nutrients inefficiently (e.g. Karasov and Levey 1990, Levey and Duke 1992). The lack of an effect of indigestible bulk intake on digestive efficiency, regardless of seed-processing mode, challenges current ideas of how frugivores process fruits. Because the simple sugars (glucose and fructose) in aqueous solutions of fruit pulp do not require digestion and are readily absorbed by active and passive mechanisms (Pappenheimer and Reiss 1987), birds rarely may face tradeoffs between intake and nutrient absorption from sugary fruit diets under natural levels of dietary dilution with indigestible bulk (Witmer and Van Soest 1998). Rapid digestive processing of sugary fruits is expected because glucose and fructose are easily absorbed nutrients. Indeed, previous contentions that frugivores have intrinsically rapid passage rates may have resulted from effects of experimental diet type, rather than animal dietary habits; passage rates for Cedar Waxwings and thrushes eating the same diets are not different (Witmer 1994). Thus, fast passage of fruit diets does not appear to be a trait of frugivores that results in impaired nutrient utilization, but a result of how rapidly fruit sugars can be thoroughly absorbed (compared with lipid- and/or protein-rich foods). Rapid passage of seeds relative to pulp through the intestines of Cedar Waxwings (Levey and Duke 1992) probably functions to minimize the time that indigestible seeds are retained within the absorptive portion of the gut, while permitting retention of pulp until absorption of nutrients is complete. The ability of frugivorous birds to compensate for seeds also suggests that their guts distend to accommodate indigestible bulk, as well as the possibility that frugivore guts process fruit foods discretely, rather than continuously.

Do seeds affect interspecific patterns of fruit consumption and sugar assimilation?—My results do

not suggest that seed-processing mode accounts for the intake differences of sugary foods between Cedar Waxwings and thrushes (Figs. 1 and 5). Similarly, Cedar Waxwings ingest and assimilate sugary, low-protein artificial diets at higher rates than thrushes (ca. 1.5 times; Witmer unpubl. data). These rates of sugar assimilation approximate maintenance-energy intake by these species under the same conditions of captivity, suggesting that frugivores are not energy-limited when eating sugary fruits (Witmer 1994). Cedar Waxwings appear to have higher rates of energy metabolism when eating sugary, low-protein diets than do more omnivorous frugivores. The relatively wide intestinal morphology of waxwings is implicated as a trait that enables this species to achieve high intake rates of bulky, sugary fruits (Witmer 1994). For lipid-rich fruits, which are not normally eaten by waxwings and which require longer retention times for digestion and absorption (Mateos and Sell 1981, Afik and Karasov 1996, Witmer and Van Soest 1998), seed bulk may have a much stronger negative effect on ingestion and/or absorption rates than it does for sugary fruits.

Seed loads of fruits and the evolution of plant/frugivore mutualisms.—Differences in seed loads may account for the contrasting results between my study and those of Levey and Grajal (1991) and Murray et al. (1993). Seeds comprised about 28% (by volume) of artificial diets in the previous studies versus 12 to 20% of the natural diet in my study. In fact, the seed loads used in the other two studies that reported effects of seed bulk on fruit intake appear to be higher than those typically found in sugary, bird-dispersed fruits (Fig. 6). The ability of the digestive systems of avian frugivores to compensate for seed bulk may explain the results of studies in which birds did not discriminate on the basis of seed load (McPherson 1987, Willson and Comet 1993, Willson 1994). Although fruit removal by birds has been correlated with the seed-to-pulp ratio of natural fruits (Howe and Vande Kerckhove 1980, 1981, Sallabanks 1993), my results suggest that the causes of such correlations remain obscure.

My results suggest that seeds of bird-dispersed fruits often do not impose bulk-processing limitations on frugivores. The ways in which seeds influence fruit-intake rates potentially depend on the physical and chemical

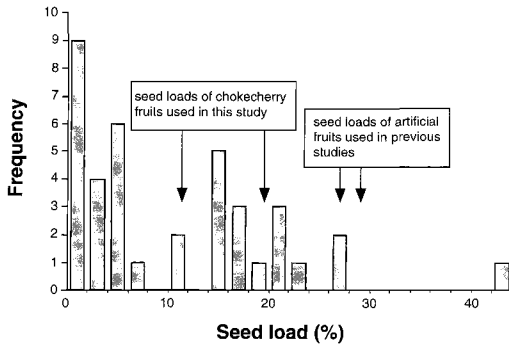


FIG. 6. Distribution of seed loads (g seeds per g whole fruit, fresh mass) for sugary fruits of 38 plant species from the eastern United States (9 species from Witmer [1996a], 29 species from White [1989]). Bold arrows show seed loads of chokecherry fruits used in this study and artificial fruits used by Levey and Grajal (1991) and Murray et al. (1993).

composition of fruits, energy demands on frugivores, and the digestive traits of particular species. The conditions under which food composition may cause bulk-processing limitations for fruit-eating birds need to be clarified in order to understand the extent to which the composition (nutrient type and concentration, water content, and seed load) of natural fruits may limit rates of nutrient assimilation.

The mutualistic nature of plant/frugivore interactions would be expected to have molded frugivores and fruiting plants to minimize the costs of seeds to nutrient uptake from fruit diets. Because fruits are produced by plants as rewards to attract seed dispersers, natural selection should favor the packaging of seeds within fruits to reduce the effects of seeds on nutrient digestion and/or absorption by frugivores. From the perspective of seed dispersers, natural selection likewise should be expected to produce digestive modifications to minimize effects of seeds on ingestion and absorption of fruit-pulp nutrients. Frugivorous birds have a diversity of apparent digestive modifications associated with processing fruit pulp and seeds (e.g. Wetmore 1914, Wood 1924, Walsberg 1975). Comparisons in a phylogenetic framework of the ability of frugivorous and non-frugivorous birds to compensate for indigestible bulk in natural and artificial fruit diets will be necessary to resolve the extent to which modes of seed processing by frugivorous birds represent mutualistic adaptations to fruit diets.

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