

# CO-OCCURRENCES OF FOODS IN STOMACHS AND FECES OF FRUIT-EATING BIRDS<sup>1</sup>

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**Abstract.** Short-term dietary mixing by American Robins (*Turdus migratorius*) and other fruit-eating birds in eastern North America was examined using 5,697 records of stomach contents for 11 bird species and 3,618 avian fecal droppings from New Jersey. Avian seed budgets were estimated by using fruit morphological data to relate foraging observations to seed counts from stomachs and feces.

Remnants of multiple taxa of foods were found commonly in individual feces and stomachs although these samples held only 0.25–2 times the seeds consumed during a typical feeding bout. Depending on bird taxon, seeds from different fruit species were mixed in 1.5–39.6% of feces and 4.2–41.6% of stomachs, and fruit and animal material were mixed in 24–59% of stomachs.

Frequency of mixed seeds was positively correlated with proportion of fruit in the stomach and with seed concentration of fruits in the diet. For birds overwintering in the United States, seed mixing in stomachs peaked in winter when birds were most dependent on fruit, not in fall when fruit abundance and diversity were greatest. Thus, estimates of dietary mixing may be biased by seasonal or habitat-related trends in avian fruit dependence or fruit morphology. Furthermore, mixing was no less common in feces than in comparable stomachs even though stomachs contained three to four times more seed mass. This finding along with our observations of seed treatment by birds suggested that mixing was amplified by shuffling of seeds and fruits in the upper gut and by variability of seed transit times through the intestines.

**Key words:** Avian frugivores; feces; fruit; mixed diets; seed dispersal; stomach contents.

## INTRODUCTION

Diets of fruit-eating bird species in the temperate zone typically include fruits from many plant species (Ridley 1930, Martin et al. 1951, Herrera 1984a), reflecting the accessibility and simple morphology of most temperate fruits. Indeed, the mechanisms and selective pressures for plants to “target” fruits for specific bird species appear limited (see Herrera 1982a, Janson 1983, Moermond and Denslow 1983, Pratt 1983, Gautier-Hion et al. 1985, Herrera 1985, Wheelwright 1985) compared to pollen dispersal systems (Wheelwright and Orians 1982). The broad fruit diets attributed to bird species result in part from lumping dietary records across individuals, habitats, seasons, and regions (cf. Wheelwright 1986). Although relevant to questions of avian behavior, nutrition, and seed dispersal, little is known about the extent to which individual birds vary their fruit diets over brief periods.

Fruits of different species vary in potential nutritional rewards for birds (Herrera 1982b, Stiles

and White 1982, Johnson et al. 1985, Debussche et al. 1987, Herrera 1987), and neotropical birds show preferences between fruit species in paired feeding trials (Moermond and Denslow 1983). Nevertheless, reasons exist for individual birds in the field to eat fruits of different species (or insects instead of fruits) in consecutive feeding bouts. Birds may seek mixed meals to sample available resources, balance nutrient intake (Berthold 1976a, 1976b; Jordano 1987, 1988; also see Westoby 1974), or limit intake of certain toxins (Herrera 1982a). Mixing may also be related to bird movements because a bird's proximity to, and preference for, various foods may change (Levey et al. 1984) when it “fearfully” abandons a feeding site (Moore 1978, Howe 1979, Pratt and Stiles 1983, Snow and Snow 1984).

Frequent mixing of fruit meals could be significant for seed-dispersal interactions in several ways (Herrera 1984a, Stiles and White 1986, Jordano 1987). Rapid switches in food use by birds might increase the removal rate of low-quality fruits located near high-quality ones (cf. Fleming et al. 1977) and reduce the probability of seeds being deposited under parent or conspecific plants where predation and competition would be most

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intense (Janzen 1970, Pratt and Stiles 1983). Mixed meals may also lead to seeds of two or more species being deposited together, which in turn might affect probabilities of seed predation, seedling competition, and, ultimately, plant community structure (Herrera 1988). Finally, dietary patterns of Mediterranean sylviid warblers suggest that birds lacking access to a variety of fruits necessary to balance their nutrient intake may limit their overall fruit consumption (Jordano and Herrera 1981; Jordano 1987, 1988).

Diversity in the diets of individual birds has been assessed through observations of consecutive feeding bouts (Hoppe 1987) and analyses of stomach (Wheelwright 1986), gut (i.e., stomach plus intestines; Herrera 1984a, Jordano 1987) and fecal contents (Sorensen 1981). Inferences have also been drawn from seed trap data (Stiles and White 1986). Observing consecutive foraging bouts in free-ranging, nonterritorial, forest birds is difficult and open to observer bias (Hoppe 1987). The degree of diet mixing reflected by seeds in guts and feces depends on the bird's seed budget, that is, the number of feeding bouts and defecations needed to fill and empty the gut, and the extent to which seeds of different species are shuffled or retained differentially in the gut (Sorensen 1984; Johnson et al. 1985; Levey 1986, 1987). Diet diversity may be underrepresented by seed contents of guts and feces because larger, regurgitated seeds are discharged by birds about twice as quickly as smaller, defecated seeds (6–15 vs. 12–50 min, respectively; combined data from Webber 1895, Nice 1941, Walsberg 1975, Herrera 1981, Sorensen 1984, Johnson et al. 1985). All else being equal, seed-mixing frequencies should increase with increasing gut and fecal volume and decreasing fruit and seed size.

We examine here the extent and variability of seed mixing in stomachs of important avian frugivores in North America and in autumn fecal droppings from central New Jersey.

## METHODS

We compiled data on stomach (i.e., proventriculus plus ventriculus) contents for 5,697 individuals from 11 seed-dispersing bird species (see Table 1 and Fig. 2 for specific epithets and sample sizes) from records of individual assays originally conducted by the Bureau of Biological Survey (later the United States Fish and Wildlife Service, Department of the Interior). Bird species

chosen for study included major North American frugivores from three families (Mimidae, two species; Muscicapidae, six species; and Bombycillidae, one species; Thompson and Willson 1979, Baird 1980, Stiles 1980) and a picid and an emberizid species important in New Jersey field studies (see below, White 1989). Records for these species, stored at Patuxent Wildlife Research Center, Laurel, Maryland, represent a fraction of the ca. 250,000 birds collected from throughout North America between 1876–1950 in a massive food-habits study designed primarily to assess the impact of wildlife on agricultural pests and crops (McAtee 1912, Beal 1915, Martin et al. 1951). Advantages and shortcomings of the data set were discussed recently by Wheelwright (1986). The information recorded for each stomach included collection site and date, stomach fullness and proportion of fruit material by volume, and the identity and, when recorded, number of seeds of each fruit taxon present. Seeds were enumerated infrequently in the original records; however, the spotty data apparently reflects protocol differences among survey personnel rather than a biasing tendency to record only unusual numbers of seeds.

Fruit foraging and seed deposition were studied September through December, 1979–1982, on three sites in central New Jersey: a mixed-aged woodland (Institute Woods, Princeton), a 30- to 50-year-old field with herbaceous and low woody vegetation (Franklin Township, Somerset County), and a mature oak-dominated woodland and adjacent 1- to 20-year-old fields (William L. Hutcheson Memorial Forest, East Millstone). Detailed habitat descriptions were included in Bard (1952), Horn (1971), Baird (1980), and McDonnell and Stiles (1983). In aggregate over each fall season, birds used fruits from 20–27 plant taxa at each site (White 1989; cf. Baird 1980, McDonnell and Stiles 1983, McDonnell 1986). The number of fruits swallowed and the arrival-to-departure interval in seconds were recorded for feeding bouts of American Robins (*Turdus migratorius*) observed at each site.

Seeds were identified to plant species in 3,618 avian fecal droppings and 1,696 regurgitated seeds encountered on trails, fallen logs, and ground during regular transits of the study sites. Droppings could be recognized as originating from (1) Northern Flickers (*Colaptes auratus*), (2) Yellow-rumped Warblers (*Dendroica coronata*) or perhaps other Parulinae (Emberizidae), or (3) Amer-

ican Robins or other mid-sized members of the Turdinae (Muscicapidae), Mimidae, Bombycillidae, or Sturnidae based on feces thickness and surface texture. We refer here to these dropping types as "flicker," "warbler," and "thrush," respectively. A typical full-sized feces from an American Robin was 20–25 mm long by 4–5 mm in diameter; the end emerging from the cloaca first tended to be widest and was the locus of urates when they occurred. Northern Flicker feces were wider than robin feces, had a well-formed, grayish, surface layer, and often contained ants; warbler feces were narrow and short. The circumstances and moisture content of the majority of fecal droppings suggested deposition on the day of discovery; however, many droppings may have been older. To limit biases, we excluded evidently disturbed or completely dried droppings and droppings that were of ambiguous origin. No correction was made for possible differences in detectability of deposited seeds.

Although thrush droppings may have been deposited by 10 or more species (White 1989), observations of birds, dropping locations, and dropping phenology suggested that our sample was weighted heavily towards American Robins which foraged for animal matter on open ground. Robins were abundant on the study areas periodically through late fall. The influence of non-robins on thrush feces is uncertain. Most avian frugivores were smaller than American Robins and so may have deposited smaller feces with lower potentials for seed mixing. Nevertheless, results from stomach samples (detailed below) suggested only an intermediate rate of fruit mixing in diets of American Robins.

A bird may expel regurgitated seeds in temporal and physical proximity approaching that of a fecal dropping. However, because we could not confidently link individual regurgitated seeds in the field, we excluded such seeds from all analyses of co-occurrence frequencies. Records of regurgitated seeds were used only to calculate mean number of seeds per egestion (see Table 4); for that analysis, we assumed that seeds were expelled singly by a bird in the thrush category based on bird diets, seed size/regurgitation patterns, and fruit/gape-width restrictions (White 1989).

Seed co-occurrences examined here were likely a conservative estimate of dietary mixing (cf. Herrera 1984a, Jordano 1987) because birds sometimes process seeds more quickly than ac-

companying skin and pulp (Levey 1986) and because stomach and fecal samples represent only a portion of total gut contents.

To estimate avian seed budgets, we calculated total fruit mass consumed per feeding bout (number of fruits  $\times$  individual fruit mass; for American Robins) and total fruit mass represented by all seeds contained in a stomach or fecal dropping (here termed fruit mass equivalent) using data on fruit mass and seed number per fruit for ca. 50 plant species in New Jersey (White 1989). For stomach and fecal samples, fruit mass equivalent was estimated only when seeds were enumerated and fruit mass and seed number were known for all plant species.

## RESULTS

### AVIAN SEED BUDGETS

American Robins swallowed a median of 0.95 g of fruits per autumn feeding bout in New Jersey, the equivalent of three to four typical fruits (median species fruit mass: 0.29 g; Fig. 1A). The median fruit mass represented by seeds in American Robin stomachs collected by the Biological Survey in autumn in nine northeastern states was 1.39 g, similar to the fruit mass eaten in one to two feeding bouts (Fig. 1B). Fruit mass equivalent of stomach seeds in the whole sample (0.95 g) was less than that in the subsample above because animal material made up a large proportion of stomach contents in spring (Fig. 2). Median fruit mass represented by seeds in thrush fecal droppings examined in autumn in New Jersey was 0.33 g, or about the mass of a single fruit (Fig. 1C). Fruits used by birds in this study contained a median of 8.5 seeds per gram of fruit mass (range: 1.6–57.5; see Table 4).

Seeds in the intestines contribute to a bird's total seed burden. Fresh, whole fecal droppings known to come from American Robins were  $22 \pm 12$  mm long (mean  $\pm$  SD; range: 15–28 mm;  $n = 48$ ). Intestines of two salvaged American Robins were 230 and 257 mm long. Fecal droppings may be shaped by the large intestine: ceca-to-vent length in specimen two was 32 mm. Based on length, a robin's intestines might contain 10 fecal loads, equal to the seeds from about 3.3 g of fruit. This is likely an overestimate, however, because absorption of nutrients in the small intestine should concentrate seeds distally. Eurasian Blackbirds (*Turdus merula*) absorb 45–90% of ingested pulp dry mass (Sorensen 1984). Thus,

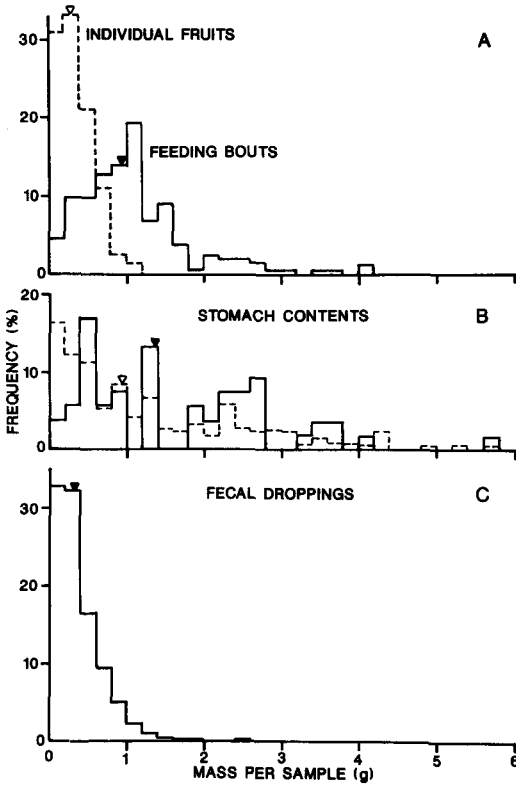


FIGURE 1. Frequency histograms of (A) mean species fruit mass for 81 native and naturalized species in New Jersey (dashed line) and total fruit mass consumed per autumn feeding bout of American Robins in New Jersey ( $n = 266$  bouts; solid line), (B) the fruit mass represented by seeds in American Robin stomachs collected year-round throughout North America ( $n = 221$  records with seeds enumerated fully; dashed line) or from September–December in New Jersey and eight surrounding northeastern states ( $n = 53$ ; solid line), and (C) fruit mass represented by seeds in thrush fecal droppings examined in autumn in New Jersey ( $n = 2,959$  droppings). Triangles indicate medians.

on average in American Robins, seeds in a full gastro-intestinal tract may represent  $< 4$  g of fruit and result from as few as four feeding bouts, or 13 median-sized fruits.

Fecal droppings of flickers and warblers contained seeds representing about one-third to one-fourth the fruit mass equivalent of corresponding stomach samples (medians: 0.34 vs. 0.91 and 0.03 vs. 0.13 g, respectively).

For the 11 avian frugivores examined here, strong positive correlation existed between the mean estimated fruit mass in the stomach and

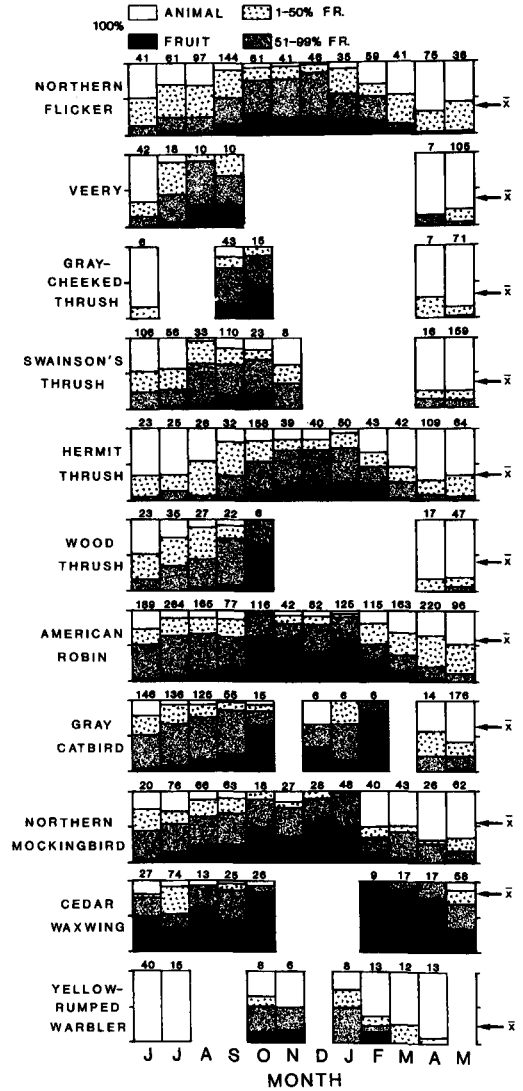


FIGURE 2. Monthly proportions of stomachs with specified volumes of fruit and/or animal matter for 11 bird species in North America. Individual stomachs contained pure animal (unfilled bars) or fruit (filled bars) matter or a mixture of both. In stomachs with mixed contents, animal (stippled) or fruit (shaded) matter predominated by volume. Sample size is shown above each bar; months with five or fewer stomach samples were omitted. Arrows indicate the weighted mean percentage fruit volume.

bird mass (Spearman's rank correlation:  $r_s = 0.945, P < 0.001, n = 11$ ). On average, estimated stomach fruit mass was  $1.72 \pm 0.66\%$  of bird mass.

TABLE 1. Fruit mass equivalents and plant-taxa mixing of seeds in stomachs and seed concentration of fruits in diets of seed-dispersing birds.  $n$  is number of stomachs with fruit. Bird species differed significantly in mean fruit mass equivalents ( $F_{10, 616} = 7.31, P < 0.0001$ ), mean plant taxa per stomach ( $F_{10, 3439} = 18.61, P < 0.0001$ ), and mean of log seeds per gram of fruit for each species occurrence in the diet ( $F_{10, 3918} = 23.94, P < 0.0001$ ); for these three variables, values not sharing a letter are significantly different (Duncan's test,  $P < 0.05$ ). Bird masses are from Clench and Leberman (1978).

Species	Bird mass (g)	Fruit mass equivalent (mg)	$n$	% stomachs with that number of taxa				Taxa/stomach	Seeds/g fruit in diet
				1	2	3	4		
Gray Catbird									
<i>Dumetella carolinensis</i>	36.9	60bcd	514	58.4	32.3	8.6	0.8	1.52a	21.8b
Northern Mockingbird									
<i>Mimus polyglottos</i>	48.5	97bcd	359	74.1	22.3	3.1	0.6	1.30b	19.0bc
Wood Thrush									
<i>Hylocichla mustelina</i>	47.4	125ab	86	74.4	25.6			1.26bc	16.4bcd
Veery									
<i>Catharus fuscescens</i>	31.2	67bcd	62	77.4	19.4	3.2		1.26bc	21.6b
Swainson's Thrush									
<i>Catharus ustulatus</i>	30.8	34cd	250	78.8	19.2	1.6	0.4	1.24bc	17.2bc
Northern Flicker									
<i>Colaptes auratus</i>	132.0	154a	419	79.2	18.4	2.4		1.23bc	13.9cde
Hermit Thrush									
<i>Catharus guttatus</i>	31.0	41cd	351	80.1	17.1	2.6	0.3	1.23bc	20.1bc
American Robin									
<i>Turdus migratorius</i>	77.3	135ab	1,085	82.8	15.7	1.6		1.19bcd	10.1e
Gray-cheeked Thrush									
<i>Catharus minimus</i>	32.8	53bcd	59	84.7	15.3			1.15bcd	11.4e
Cedar Waxwing									
<i>Bombycilla cedrorum</i>	33.1	96abc	230	90.0	7.8	1.7	0.4	1.13cd	10.6e
Yellow-rumped Warbler									
<i>Dendroica coronata</i>	12.6	9d	24	95.8	4.2			1.04d	32.0a

## STOMACH CONTENTS

*Mixing of fruit and animal material.* The bird species examined relied heavily on fruits (Fig. 2). Except for Yellow-rumped Warblers, the bird species used fruits in all sampled months including breeding periods, and a majority of birds had fruit-dominated diets in over half the bird species-by-month periods sampled (range among bird species: 29–100%). Thrushes that migrate from North America in winter continue to feed on fruits and insects in the neotropics (see Keast and Morton 1980).

Fruit and animal matter were mixed often in bird stomachs (Fig. 2; cf. Jordano 1982). The mean percentage of birds with both plant and animal material in their stomachs, weighted equally for months with five or more records, was 59% for Northern Flickers, 49% for six species of Turdinae (Veery *Catharus fuscescens* through American Robin), 53% for two mimid species (Gray Catbirds *Dumetella carolinensis* and Northern Mockingbirds *Mimus polyglottos*), 32%

for Cedar Waxwings (*Bombycilla cedrorum*), and 24% for Yellow-rumped Warblers. Additional instances of animal-plant mixing may have been missed because of rapid digestion of soft-bodied animals (i.e., earthworms; see Wheelwright 1986) or rapid regurgitation of large seeds. Stomachs with animal material exclusively were most common during the spring breeding season.

*Mixing of fruits from different species.* Frugivorous birds frequently carried seeds from two or more plant taxa simultaneously in their stomachs (Table 1). Fruit mixing was most common in the Mimidae, in which one-third of stomachs with fruits contained seeds of multiple taxa, and less common in Turdinae, in which seed taxa were mixed in only one-fifth of fruit-containing stomachs. Only 2.5% of fruit-containing stomachs (range: 0–3.7%) had seeds from more than two taxa, and no stomachs had more than four fruit taxa. Mean number of taxa per stomach was not significantly correlated with bird mass ( $r_s = 0.345, P > 0.30, n = 11$ ) or mean fruit mass

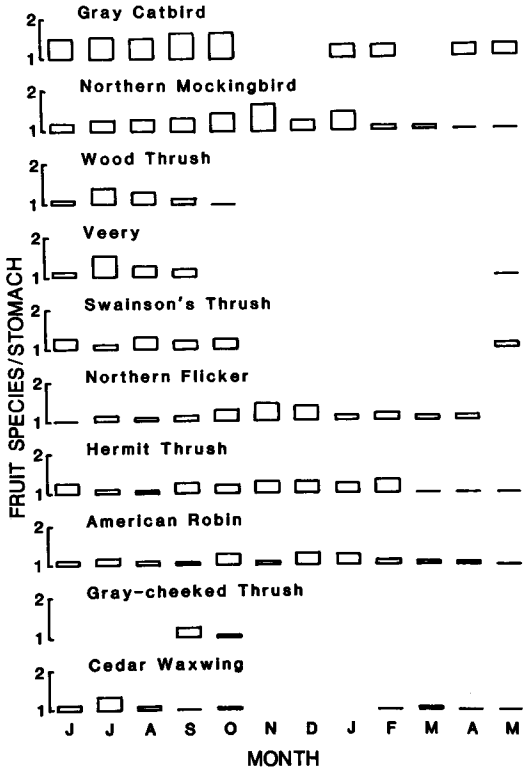


FIGURE 3. Mean number of fruit species per fruit-containing stomach in monthly samples from 10 bird species in North America. No bars are shown for months in which five or fewer fruit-containing stomachs were collected.

represented by seeds in the stomach ( $r = 0.273$ ,  $P > 0.40$ ,  $n = 11$ ), suggesting that differences among bird species in fruit mixing were not due simply to differences in stomach capacity.

Nevertheless, within bird species, stomach fruit mixing should be expected to increase with the quantity of fruit in the stomach and with the diversity of fruit taxa in the environment. In temperate North America, the number of plant species with ripe fruits peaks seasonally during August–October (Thompson and Willson 1979, Stiles 1980) while the importance of fruits in bird diets peaks often in winter (Fig. 2). To separate these factors, we examined number of plant taxa per stomach by season (August–October vs. November–July) and proportion of fruit in the stomach (1–50%, 51–99%, or 100%) for seven bird taxa using analysis of variance (Table 2). Number of plant taxa per stomach did not vary

TABLE 2. Results of ANOVAs of fruit taxa per fruit-containing stomach as a function of season (August–October vs. November–July) and proportion of fruit in the stomach (classed as 1–50%, 51–99%, and 100%) for birds in North America.

Bird taxa	Source of variation <sup>1</sup>		
	Season	Proportion fruit	Interaction
Gray Catbird	ns	*	ns
Northern Mockingbird	ns	*	ns
Migrant thrushes	ns	ns	ns
Northern Flicker	ns	***	ns
Hermit Thrush	ns	ns	ns
American Robin	ns	*	ns
Cedar Waxwing	ns	ns	**

<sup>1</sup> ANOVAs were based on Type III sums of squares. Number of stomachs per species are given in Table 1. "Migrant thrushes" lumps data for Veery, Gray-cheeked Thrush, Swainson's Thrush, and Wood Thrush, long-distance migrants collected in similar periods (see Fig. 1). ns  $P > 0.05$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

significantly with season for any bird taxon, but it did increase significantly with volume of fruit in the diet for four bird species. In Cedar Waxwings, a significant interaction existed between season and relative fruit content, but mixing tended to be lower in autumn than during the rest of the year (1.05 vs. 1.15 taxa per stomach, respectively). Proportion of fruit in the stomach was negatively (Northern Flicker, Swainson's Thrush *Catharus ustulatus*, Hermit Thrush *Catharus guttatus*) or insignificantly (other species) correlated with fullness of the stomach. Examination of monthly differences in fruit taxa per stomach showed that, for birds overwintering in North America, mixing was highest in winter (Fig. 3), a period of heavy dependence on fruits by birds (Fig. 2) in the face of declining numbers of fruits per plant as fall-ripening crops are depleted. For American Robins, this contrasts with the pattern for total number of insect-plus-fruit taxa per stomach which peaks later in April–June (Wheelwright 1986).

CONTENTS OF FECAL DROPPINGS

The frequency of fecal droppings with two or more individual seeds increased with bird size from 30% in warblers, to 70% in thrushes, to 84% in flickers (Fig. 4). The mean number of seeds per dropping increased from 1.4, to 3.9, to 9.2, respectively. The frequency of droppings with seeds from two or more species also increased with bird size from 1.5% in warblers, to 20.5% in thrushes, to 39.6% in flickers. Considering only

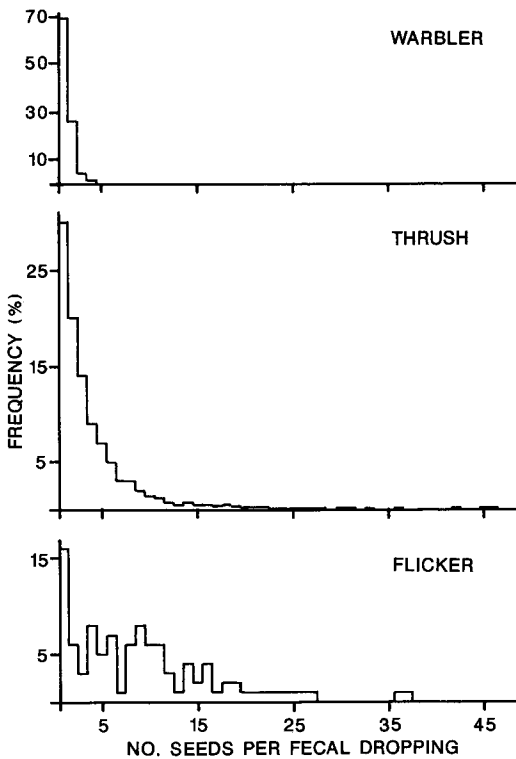


FIGURE 4. Frequency histograms of seed number per fecal dropping for three dropping types examined in autumn in New Jersey. There were 357 seeds in 260 warbler droppings, 12,613 seeds in 3,219 thrush droppings, and 1,276 seeds in 139 flicker droppings.

multiseeded droppings, the frequency of multi-species droppings increased from 4.9%, to 31.8%, to 46.1%, respectively (Table 3).

#### MIXING FREQUENCIES FOR INDIVIDUAL PLANT SPECIES

To determine if certain plant species were more likely than others to occur in mixed-species samples, we tallied the number of solitary and mixed-

species occurrences in feces and stomachs by plant taxa. Seed association frequencies in thrush droppings varied widely for 22 plant species with adequate data (Table 4). The percentage of seeds of a given species that were deposited with seed(s) of one or more other species ranged from 1.9–82.7% and was correlated significantly with the number of seeds per fresh gram of the reference fruit (termed fruit seed density;  $r_s = 0.668$ ,  $P < 0.002$ ), but not with the number of seeds per fruit ( $r_s = 0.342$ ,  $P > 0.10$ ). The mean number of conspecific seeds per egestion was correlated strongly with both fruit seed density ( $r_s = 0.899$ ,  $P < 0.001$ ) and seed number per fruit ( $r_s = 0.592$ ,  $P < 0.01$ ). Thus, besides bird-generated differences, a seed's depositional fellows also may depend on aspects of fruit design including seed and fruit mass and seed number.

Similarly, among 13 plant taxa common in September–December in bird stomachs in the northeast (Virginia, Kentucky, Missouri, Iowa, Minnesota, and Ontario and regions to the north and east), 20–60% of taxon occurrences were in stomachs with two or more plant taxa (Table 4). As in droppings, mixing frequency in stomachs correlated with fruit seed density ( $r_s = 0.897$ ,  $P < 0.001$ ).

The fact that mixing frequency varied among plant species with differences in fruit seed density suggests that variation among bird species in mean number of taxa per stomach may have reflected differences in the types of fruit being eaten instead of differences in dietary mixing per se. To examine this, we calculated mean fruit seed density for all taxon occurrences in stomachs of each bird species (Table 1). Fruit seed density ranged from 0.9–455.6 seeds per gram of fresh fruit (median = 13.6, mean = 37.5) in 64 plant taxa for which we had data (accounting for 90.3% of stomach fruit occurrences). Mean seed density of the diet differed significantly

TABLE 3. Frequency distribution of plant species per individual fecal dropping for three dropping types examined from September–December in central New Jersey. Dropping types differed significantly in mean number of species per dropping ( $F_{2, 3615} = 41.47$ ,  $P < 0.0001$ ); each mean was distinct (Duncan's test,  $P < 0.05$ ).

Dropping type	No. droppings	% multi-seeded	% droppings with that number of species				Species/dropping overall
			1	2	3	4	
Warbler	260	31.2	95.1%	4.9%			1.02
Thrush	3,219	70.0	68.2%	29.0%	2.6%	0.2%	1.24
Flicker	139	84.2	53.9%	41.9%	3.4%	0.9%	1.43

TABLE 4. Associations among thrush-deposited seeds in New Jersey and among fruit taxa in stomachs of 11 bird species in the northeast in autumn.  $n$  is number of thrush-deposited seeds or number of taxon occurrences in bird stomachs. Plant species differed significantly in the probability of a seed being deposited in feces with a seed of one or more other species (i.e., percentage seeds mixed;  $F_{21, 13313} = 68.51$ ,  $P < 0.0001$ ) and in mean number of conspecific seeds per egestion (fecal droppings plus seeds regurgitated singly; seed numbers log-transformed,  $F_{21, 4757} = 123.21$ ,  $P < 0.0001$ ); for these two variables, values not sharing a letter are significantly different (Duncan's test,  $P < 0.05$ ).

Reference taxon	Seeds/ fruit	Seeds/g fruit	Thrush-deposited seeds			Stomachs	
			Seeds mixed		Conspecific seeds/egestion ( $\bar{x} \pm SD$ )	Taxa mixed	
			$n$	(%)		$n$	(%)
<i>Prunus serotina</i>	1	1.6	64	3.1a	1.0 ± 0.0a	87	21.8
<i>Cornus florida</i>	1	2.2	262	11.5ab	1.1 ± 0.3a	117	20.5
<i>Nyssa sylvatica</i>	1	2.3	177	14.1ab	1.1 ± 0.4a	52	28.8
<i>Lindera benzoin</i>	1	2.7	631	1.9a	1.0 ± 0.2a	12	25.0
<i>Viburnum prunifolium</i>	1	2.9	416	17.1bc	1.4 ± 0.8ab		
<i>Cornus amomum</i>	1	4.9	43	11.6ab	1.9 ± 1.3bcd		
<i>Viburnum acerifolium</i>	1	5.0	25	48.0fg	1.1 ± 0.4a		
<i>Vitis</i> spp.	1.8	5.1	3,654	28.4cd	2.3 ± 1.6cdef	69	40.6
<i>Pyrus</i> sp.	3.2	6.2	87	40.2efg	2.1 ± 1.3cde		
<i>Pellodendron amurense</i>	4.0	6.7	75	46.7fg	2.7 ± 2.3def		
<i>Cornus racemosa</i>	1	8.0	27	44.4efg	1.5 ± 1.0ab		
<i>Aronia arbutifolia</i>	2.6	8.9	90	57.8gh	2.7 ± 2.2def		
<i>Rhamnus catharticus</i>	3.9	14.0	61	67.2h	1.8 ± 1.4bc		
<i>Parthenocissus quinquefolia</i>	3.0	17.5	641	31.7de	2.7 ± 2.2efg	54	44.4
<i>Ilex verticillata</i>	5.8	20.9				29	51.7
<i>Celastrus orbiculatus</i>	4.8	21.9	710	31.4de	3.8 ± 3.2gh		
<i>Phytolacca americana</i>	9.5	24.1	2,779	29.3cd	7.8 ± 7.3i	61	45.9
<i>Juniperus virginiana</i>	1.2	26.6	1,512	52.6fg	3.2 ± 2.5fgh	23	30.4
<i>Myrica pensylvanica</i>	1	33.2	216	48.1fg	4.2 ± 3.9gh	10	60.0
<i>Rosa multiflora</i>	4.6	38.6	1,010	28.8cd	7.3 ± 5.5i		
<i>Toxicodendron radicans</i>	1	45.7	474	53.0fg	4.7 ± 4.9h	42	52.4
<i>Sambucus canadensis</i>	3.8	47.8				30	60.0
<i>Lonicera japonica</i>	6.7	48.2	312	82.7i	4.2 ± 4.8h		
<i>Rhus</i> spp.	1	57.5	69	33.3de	3.0 ± 4.0cde	28	53.6

among bird species (Table 1; data log-transformed) even when distinctly narrow-gaped Yellow-rumped Warblers were omitted from the analysis ( $F_{9, 3897} = 25.61$ ,  $P < 0.0001$ ). Furthermore, significant positive correlation existed between fruit seed density in the diet and taxa mixing in the stomach ( $r_s = 0.758$ ,  $P < 0.05$ ), supporting the idea that mixing was food biased. Fruits with single, large seeds (e.g., *Prunus*, *Cornus*, *Nyssa*) were recorded often in diets of bird species with low mixing, while fruits with multiple small seeds (e.g., *Rubus*, *Sambucus*, *Vaccinium*, *Ilex*) were common in diets of bird species with high mixing. Because seed size varies with season and habitat (Stiles 1980), differences among bird species in stomach mixing rates may reflect temporal sampling biases and bird habitat preferences. Thus, mixing was high for Gray Catbirds, many of which were collected in summer

in shrubby habitats, and low for Gray-cheeked Thrushes, many of which were collected from forests in autumn (cf. Fig. 2 and Martin et al. 1951).

## DISCUSSION

### BIRD DIETS

Seeds from different plant species were mixed in high frequency in stomachs and feces given the small volume of these samples in relation to the quantity of fruit consumed in a typical single-species foraging bout. Plant and animal material were similarly highly mixed in stomachs. Co-occurrences of fruits in guts of nontropical, fruit-eating birds may be common. Eight bird species examined in Spanish scrublands contained seed or skin of 1.33–2.43 plant species per whole-gut sample (Herrera 1984a, Jordano 1987). In con-



trast, "very few" of the ca. 775 fruit-containing feces of British thrushes had mixed fruit species (Sorensen 1981, p. 246).

Co-occurrence of foods in stomachs and feces was not a sure measure of mixed meals (i.e., consumption of different foods in consecutive feeding bouts) for three reasons. First, mixing frequencies were affected by simple physical considerations, including stomach and dropping volume, proportion of stomach contents in fruit, and fruit size and seed number (Stiles and White 1986). Similar relationships existed for sylviid warblers in Spain where the number of fruit species per gut was positively correlated with bird mass and percentage fruit in the gut (Jordano 1987). Small bird size may also affect mixing indirectly through gape-size limitation of dietary diversity (Wheelwright 1985, Jordano 1987). This effect may be accentuated here because the Yellow-rumped Warbler, the smallest frugivore examined, also specializes on a few species of waxy fruits (White 1989). A likely result of these physical biases is that avian food habitat studies based on plant species occurrences in stomach, gut, or fecal samples will emphasize small- over large-seeded fruits.

Second, overestimation of fine-scale mixing in the diet may have resulted when slow-passing seeds or animal hard parts were mixed with recently eaten, fast-passing food. Seed transit times through vertebrate guts often have skewed distributions with long tails (e.g., Hoelzel 1930, Ridley 1930, Proctor 1968, Janzen 1981, Levey 1986, Braun and Brooks 1987). Thus, even in small passerine birds feeding on fruits of a single species, the slowest-passing seed was retained a median 3.1 times longer than the fastest-passing seed (range: 1.7–11.1,  $n = 15$  bird species; data assembled from Webber 1895; Nice 1941; Walsberg 1975; Herrera 1981; Levey 1986; White and Stiles, unpubl. data). Some insect parts may also pass slowly (Jordano and Herrera 1981). Overlapping transit times may account for the fact that fruit mixing appeared no less common in feces than in stomachs although stomachs contained three to four times more seed mass. Variation in transit intervals may arise from differences in seed size and processing mode (i.e., regurgitation vs. defecation; Sorensen 1984, Levey 1986), pulp texture and adherence to the seed (Levey 1986), and seed specific gravity and surface area (Hoelzel 1930, Janzen 1981).

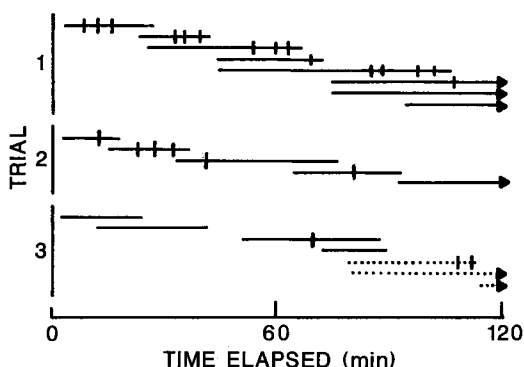


FIGURE 5. Retention times for seeds of *Sassafras albidum* (solid lines) and *Lindera benzoin* (dotted lines) eaten by a Veery during three 2-hr feeding trials in an indoor flight cage. The interval from drupe ingestion to seed regurgitation and expulsion or to the end of observation (arrowhead) for each fruit is represented by a horizontal line; for clarity, lines are offset within each trial. Crossbars indicate a fruit was visible for 1–10 sec when it was regurgitated into the bill and re-swallowed. Fruit skins had been painted contrasting colors to allow identification of reappearing fruits. Where seed fates were ambiguous, we assumed seeds were expelled in ingestion order (see Levey 1987). Note that misinterpreting the origin of a regurgitated seed as the most recently consumed fruit would result in a serious underestimate of seed retention time.

Fruits and seeds may also be shuffled from ingestion order by gizzard contractions and peristalsis in the upper gut. In a captive Veery, we observed that swallowed marked fruits with firm, oily pulp (cf. Stiles 1980) were often regurgitated into the bill, reswallowed, and transferred to the gizzard for separation of pulp and seed; the clean seeds, en route to being expelled, then passed by recently eaten fruits (Fig. 5; also see Levey 1987). We also saw fruits regurgitated and reswallowed in a Gray Catbird and American Robins in captivity and a Gray-cheeked Thrush (*Catharus minimus*) and robins in the wild. Although such "juggling" may arise simply from the difficulty of distinguishing internally between firm fruits and seeds destined for expulsion, it shows how readily seeds might be mixed in the upper gut.

Finally, observed mixing frequencies were a function of additional unquantified factors including the birds' overall diet breadth and local spatial and temporal patterns of fruit availability.

Why do birds mix their diets as much as they

do? A prevailing view is that mixed diets reflect selective feeding to balance nutrient intake (Bonaccorso and Gush 1987; Jordano 1987, 1988; Herrera 1988) or minimize effects of food-specific poisons and digestion inhibitors (Howe and Vande Kerckhove 1980, Herrera 1982a, Janzen 1983). The regularity with which insects and fruits were mixed in bird stomachs bolsters the idea that fruits are a readily accessible source of calories but an inadequate source of protein for most birds (Rowan 1967, Jordano and Herrera 1981, Jordano 1982, Wheelwright 1983, cf. Milton 1979, Mattson 1980). Mixed diets may also reflect a need for balanced uptake of minerals (cf. Bennetts and Hutto 1985, Johnson et al. 1985, Roze 1985, Herrera 1987), vitamins, carotenoids, and water (Herrera 1982a, 1982b; Debussche et al. 1987). Fruit pulp furthermore varies in plant secondary compounds (Herrera 1982a and included citations) and degradation products (Janzen 1977; Eriksson and Nummi 1982; but see Herrera 1984b, 1985) that may also promote mixing in bird diets.

Notwithstanding these nutritional factors, bird movement coupled with weak preferences among similar fruits may provide a simple alternative explanation for mixed-fruit meals. During autumn and winter, standing crops of ripe fruits on individual plants often exceed the meal size of individual birds (Stiles 1980), yet birds characteristically feed in distinct short visits to fruit patches (Herrera and Jordano 1981, Sorensen 1981, Jordano 1982, Paszkowski 1982, Snow and Snow 1986, Hoppes 1987). Birds sometimes leave fruiting plants when they fall from precarious feeding perches (Janzen 1983, Moermond and Denslow 1983) or are chased by fruit defenders (Moore 1978, Merritt 1980, Pratt and Stiles 1983, Snow and Snow 1984) or competitors (Herrera and Jordano 1981), but short visits appear mostly to be part of a suite of traits that reduce a bird's risk of predation (Howe 1979, McDonnell 1986, Snow and Snow 1986). Often birds take only a fraction of a full-sized meal before leaving a patch (e.g., Fig. 1), and in their first postforaging move, they may avoid fruiting, conspecific plants (Herrera and Jordano 1981, Jordano 1982, Hoppes 1987). Thus "fearful" movements (sensu Howe 1979) away from one plant may place a hungry bird near fruits of different species, and the simple proximity of these latter fruits may increase their attractiveness (Fleming et al. 1977, Levey et al. 1984).

#### AVIAN SEED DISPERSAL

For plants, there may exist a high premium on seed dispersal: it may allow seeds to escape predation and competition near parent and conspecific plants, and it may increase the chance seeds will colonize sites favorable for plant regeneration (see Howe and Smallwood 1982, and Janzen 1983 for reviews). The consumption by birds of fruits of different species, or fruit and insects, in temporal proximity might influence fruit removal rates, seed distribution patterns, seed predation, and seedling competition.

First, mixing of fruit meals will result in a degree of temporal overlap in dispersal periods of concurrently available fruits. Thus, within a habitat and range of fruit quality, fruits with low avian preference rankings (cf. Martin 1985) may have removal chronologies and spatial dissemination patterns (but not absolute removal rates) that parallel strikingly those of high-ranking fruits, at least while crops of the latter species remain (Fleming et al. 1977). So it may be advantageous for species with low-quality fruits or small fruit crops to mature fruits in synchrony with those of other species in the community (cf. Herrera 1988).

Second, dispersal of seeds away from conspecifics is a likely by-product of dietary mixing in birds. In Papua New Guinea, Pratt (1983) found that omnivorous birds of paradise may deposit a smaller fraction of seeds under fruiting trees than do entirely frugivorous fruit-pigeons and bowerbirds. In the current study, American Robins and Northern Flickers foraging for insects often deposited seeds in open areas that may be superior regeneration sites (also see Smith 1975). It seems unlikely, however, that fruit traits that may promote mixed diets evolved because of selection for wide seed dispersal. Instead, traits such as unbalanced pulp nutrients and toxins more likely reflect plant nutrient constraints or adaptations to deter nondispersing frugivores (Herrera 1982a).

Finally, seeds mixed with fecal droppings may interact to influence seed predation rates or seedling competition. From a plant's perspective, seed associations in bird feces were nonrandom but highly variable: number of conspecific seeds per dropping and frequency of mixing in droppings increased with bird size and fruit seed density (seeds per unit wet fruit mass). However, for seeds attractive to vertebrates (e.g., *Prunus*), risk of

predation for individual seeds may not increase when seeds are aggregated in a dropping if animals eat all seeds they encounter (Webb and Willson 1985). Additional experiments are needed to determine if seed composition of droppings influences detectability or predation risk for seeds that are comparatively unattractive to predators. The duration of close physical association among seeds deposited in a single dropping is uncertain. Secondary dispersal by rain, frost heaving, seed-caching animals, incidental animal activity, or other factors can separate seeds (Livingston 1972, Smith 1975, Janzen 1982). Moreover, seed associations in a given patch in autumn are a dynamic function of disperser input and predation (Stiles and White 1986); seed dormancy is common among northeastern plants (U.S. Department of Agriculture, Forest Service 1974). Thus, predation probabilities may vary with seed density over a temporal and spatial scale larger than that of a fecal dropping (Smith 1975). Similarly, eventual seedling competitors may reflect not just co-deposited seeds but an integrated seed pool.

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