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FORAGING ECOLOGY OF AVIAN FRUGIVORES AND SOME CONSEQUENCES FOR SEED DISPERSAL IN AN ILLINOIS WOODLOT[1]

PATTI KATUSIC MALMBORG[2] AND MARY F. WILLSON
Department of Ecology, Ethology, and Evolution, University of Illinois, Shelford Vivarium,
606 East Healey Street, Champaign, IL 61820

Abstract. A 3-year study of interactions between frugivorous birds (11 species) and fleshy-fruited plants with bird-dispersed seeds (eight species) documented the diffuseness of the mutualism between the taxa. We found considerable annual variation in degree of frugivory, principal fruits in the diet, and dietary diversity for most of the frugivores. There were no consistent correlations between fruit or seed size and gape width, body size, or diversity of consumers. Mutual dependency of bird species and plant species was very limited. The birds could usually obtain 1 to 2% of their metabolically effective body mass in fruit pulp/minute, but they did not concentrate their foraging on the fruits yielding the greatest intake rate.

Subcanopy and understory foragers seldom changed foraging stratum and may constitute two guilds of seed dispersal agents, from the perspective of the plants. These guilds differed consistently in average body size, tendency to void seeds by regurgitation, occurrence in years of low fruit abundance, frequency of foraging on clumped fruiting displays, and in speed of movement away from a fruit source. However, three of the five subcanopy species have increased dramatically in abundance in the past 100 to 150 years, and so the dispersal regime for plant species whose fruits are eaten by these species may be different now from what it was.

Most of the frugivores foraged preferentially in treefall gaps, and several species also shifted their foraging behavior toward increased fruit foraging in gaps. These observations reinforce other studies that have shown greater abundances of birds and greater rates of fruit removal in gaps. As a result of the preference for fruit foraging in gaps, bird-dispersed plants growing in gaps may achieve better seed dispersal than those in forest interior.

Frugivores usually left a fruit source soon after feeding, so most seeds were carried some minimum distance away from the parent plant. However, the probability of departure varied with bird species and plant species, and bird species also differed in probable sites of seed deposition. The most efficacious dispersal agents were not necessarily the most common dispersers of any of the plants.

Key words: Frugivory; foraging ecology; seed dispersal; mutualism; fleshy fruits; fruit-eating birds; feeding rates.

INTRODUCTION

Frugivory is common in temperate forest birds in North America (Willson 1986) and is most prevalent during late summer and fall (Sherburne 1972, Thompson and Willson 1979, Stiles 1980), the season of southward migration of many bird species. Many plant species of north-temperate forests produce fleshy fruits that are eaten by birds (Willson 1986), which disperse the enclosed seeds. Fruit-eating birds and fleshy-fruited plants participate in a diffuse mutualism in which neither birds nor plants usually exhibit highly specific associations (Thompson 1982; Wheelwright and Orians 1982; Herrera 1984a, 1984b; Moermond and Denslow 1985).

The objectives of this study were several: (1) description of the dietary and foraging ecology of avian frugivores in eastern Illinois forest with respect to degree of frugivory, diet composition and diversity, and fruit-feeding rates; (2) examination of spatial heterogeneity of foraging activity, and postforaging behavior; (3) assessment of the possible consequences of variation in avian foraging patterns for dispersal of seeds.

STUDY AREA AND METHODS

Fieldwork was conducted during the late summer and fall (15 August to 15 November) of 1980, 1981, and 1982 in Trelease Woods, a 22.4-ha woodlot about 5 km northeast of Urbana, Champaign County, Illinois (ca. 40°06′59″N,

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[1] Received 20 March 1987. Final acceptance 2 October 1987.

[2] Corresponding author. Present address: Faunistic Section, Illinois Natural History Survey, 607 E. Peabody Dr., Champaign, IL 61820.

TABLE 1. Body size, foraging stratum, and peak migration times of the eleven avian frugivores considered in this study. The first five species are passage migrants, and the remainder are summer residents, except for the introduced resident starling. Body size data from unpublished fall data of W. G. Hoppes except *Sturnus vulgaris* from the literature. Foraging stratum: U = understory, S = subcanopy (see Methods). Average peak abundance dates determined from unpublished field censuses of R. A. Johnson, J. N. Thompson, and Mary F. Willson; in any one year, peak times may differ by 1 to 2 weeks from the average, but the order of the peaks was usually similar from year to year. Species are presented in order of body size.

Frugivore	Average peak abundance	Ave. wt. (g)	Stratum (average rank)
Dendroica coronata	Oct. 20	13	S (2.5)
Catharus ustulatus	Sept. 9	30	U (1.9)
C. guttatus	Oct. 18	31	U (2.1)
C. minimus	Sept. 18	33	U (2.2)
C. fuscescens	Sept. 4	36	U (1.9)
Dumetella carolinensis	Sept. 28	38	U (1.9)
Hylocichla mustelina	Sept. 21	51	U (2.1)
Turdus migratorius	Oct. 9	71	S (2.9)
Sturnus vulgaris	Oct. 10	76	S (2.9)
Quiscalus quiscula	Oct. 14	100	S (2.9)
Colaptes auratus	Oct. 5	114	S (2.9)

88°14′36″W). A mesic woods with a canopy composed principally of *Acer, Celtis, Quercus, Fraxinus,* and *Tilia* (Boggess 1964), Trelease harbors a number of fleshy-fruited plants and avian frugivores (Thompson and Willson 1979), many of which are quite common there. This study focused on eight bird-dispersed shrubs or shrub-like herbs and vines* (*Sambucus canadensis, Phytolacca americana, Toxicodendron radicans,* Vitis vulpina,* Parthenocissus quinquefolia,* Smilax hispida,* Menispermum canadense,** and *Lindera benzoin;* herein referred to by the generic names) and 11 of the more abundant frugivore species (Table 1). *Vitis* and *Lindera* were the most common of the fruiting species studied and *Phytolacca* and *Sambucus* the rarest.

Foraging observations were recorded by two observers simultaneously moving in opposite directions along a transect (ca. 1 km long) consisting of 16 sites, 10 in treefall gaps and six in forest interior. During the years of this study, about 20% of the area of the woodlot was composed of treefall gaps (unpubl. data).

Sites were chosen on the basis of the presence of fruit crops of at least one species. Each gap site included the entire gap plus the fringing vegetation (vines, shrubs, and young trees) at the edge of the gap. Each interior site was centered on a group of fruiting plants and was located at least 20 m from the nearest gap or the edge of the woods. The maximum radius of a site was determined by the range of vision within which the observer had a good view of bird activities and did not exceed a distance of about 10 m. The number of fruiting species and the average abundance of fruiting plants per site were statistically similar in gap and interior sites. Observations were made between sunrise and 11:00 (CST). Over the 3 years of the study, treefall-gap sites were observed for 1,365 hr and forest-interior sites were observed for 819 hr, in total.

The observers stationed themselves at the observation point for each site and stood quietly for a standard 15-min observation period. Data collection began with the arrival of the first frugivorous bird. We recorded the following information for each foraging bird at each site: bird species, food type (fruit or insects), species of fruit consumed, number of fruits eaten, length of feeding bout (from first food item eaten until last item eaten before the bird's behavior changed markedly—either stopped foraging and rested, changed food type, or left the site), size of fruiting display (isolated fruiting stem vs. clumped conspecific fruiting stems with contiguous crowns, for both vines and shrubs), vegetation stratum, and postforaging movement.

Degree of frugivory (proportion of all foraging bouts devoted to fruit eating) in this study yields an overestimate of total frugivory by each bird species, because the observations were centered on fruiting plants. Our values for degree of frugivory reflect the given presence of fruit and so must be interpreted in that context. Nevertheless, the data described here indicate the relative importance of fruits in the diets of these birds and are useful for comparative purposes.

Four foraging strata were used initially: (1) ground cover (≤1 m), (2) shrub (>1 to 3 m), (3) lower subcanopy (>3 to 6 m), (4) upper subcanopy (>6 m). These four strata were later collapsed to two, on the basis of average rank (1 through 4) of foraging stratum: S = subcanopy (average rank ≥2.5) and U = understory (<2.5). No observations were made of birds foraging in crowns of tall trees comprising the forest canopy, although subcanopy foragers are known to forage there as well. Foraging birds could be observed well in both understory and subcanopy levels because of the observer's proximity to the fruiting plants at each station.

We ranked the 3 years of the study by fruit abundance (in August and September) as estimated by two independent observers, using field notes on number of species in fruit, number of individuals in fruit, and estimated number of fruits per individual along the transect. Estimated fruit abundance was low in 1980, high in 1981 (mostly due to *Vitis* and *Parthenocissus* crops), and intermediate in 1982. Because the yearly differences were dramatic, we have confidence in this ranking.

Gape widths of mist-netted birds were measured, with vernier calipers, at the commissure (W. G. Hoppes and J. G. Blake, unpubl. data). Although gape width was correlated significantly with body size (Kendall's tau, $n = 11$, $z = 2.57$, $P < 0.05$), it was not correlated with fruit or seed sizes of fruits consumed or degree of frugivory, so we do not present the gape-width data here.

We used the fraction of the fruit diet provided by each plant species as an index of fruit importance, because this simple measure was very closely correlated with a more complicated index similar to that used by Herrera (1984a).

Nonparametric statistics are used throughout the data analysis. All correlations were Kendall's tau. To locate differences among categories found to be significantly different by a Kruskal-Wallis ANOVA, we used the following procedure: ranking all categories in order of their means, consecutive Mann-Whitney U-tests were done, pooling categories wherever the Mann-Whitney test was not significant. This was done twice, from both ends of the ranking of means; in all cases, the differences were found in the same locations in the array of categories. This procedure is analogous to the SNK test following a parametric anova. Unless otherwise stated, we use a significance level of $P \leq 0.05$. To save space, we do not present the values of calculated statistics here when they are not significant.

RESULTS

The 11 avian frugivores considered in this study are shown in Table 1. *Quiscalus quiscula* is included here as a frugivore and seed disperser because, like the others, it gulped the fruit whole, but this bird species may destroy some seeds, unlike the other species considered. Because all bird species used similar foraging strata in all years (Kruskal-Wallis tests), assignment of birds to foraging-stratum categories (U or S) was straightforward.

DIET COMPOSITION

Degree of frugivory. The degree of frugivory differed significantly among the bird species in each year (Table 2), ranging from 33 to 100% (1980, $G_{3df} = 31.9$, $P \leq 0.001$; 1981, $G_7 = 34.1$, $P \leq 0.001$; 1982, $G_6 = 61.4$, $P \leq 0.001$). The degree of frugivory was not correlated with seasonal order of peak bird abundance in any year or in all years together. Degree of frugivory was correlated with average body size (ranking the three smallest *Catharus* species equally) in all years combined (tau = 0.54, $z = 2.31$, $P = 0.021$), but not in any year separately. The association of degree of frugivory with foraging site is discussed in the section on spatial heterogeneity.

There was no significant difference in degree of frugivory between subcanopy and understory birds in 1981 or 1982 (Mann-Whitney U). Comparisons were not possible in 1980 (low fruit year), because none of the five subcanopy species was seen sufficiently often to get a sample size of 10 foraging bouts. The subcanopy foragers included the four species with the largest body sizes, and therefore size and stratum effects were not separable.

Seven frugivores were sufficiently abundant in at least 2 years to allow statistical comparisons among years (Table 2). *Catharus guttatus* ($G_3 = 40.8$, $P \leq 0.001$), *C. ustulatus* ($G_3 = 32.5$, $P < 0.001$), and *Dendroica coronata* ($G_2 = 51.2$, $P < 0.001$) showed significant annual differences in degree of frugivory, although these annual differences were not correlated with estimated levels of fruit abundance.

Diet composition (fruits). Significant interspecific differences in fruit species consumed by the avian frugivores were seen in all 3 years (χ^2 contingency tables, after deleting bird and fruit species with small samples, to comply with Cochran's Rule: 1980, five birds and four fruits, $\chi^2_{12} = 242$; 1981, eight birds and three fruits, $\chi^2_{14} = 1,175$; 1982, seven birds and three fruits, $\chi^2_{12} = 328$, all $P \leq 0.0001$; see Table 3).

All 11 bird species tended to concentrate on one or two particular fruit species each year. The favored fruit species was seldom the same from year to year, although *Parthenocissus* and *Vitis* accounted for 21 of 30 principal fruit species. No consistent correlations were found between traits of the favored fruits (fruit size, seed size, average

TABLE 2. Degree of frugivory (% of all bouts; n) and frequency of foraging in and around treefall gaps (% of bouts, adjusted to equal number of gaps and interior sites) for 10 species of frugivores in Trelease Woods. Significant differences were found among species in all years. Percents for degree of frugivory in each year are calculated only when $n \geq 10$. The average weights all observed species equally. ** marks species with significant differences among years in degree of frugivory. * marks significant inequality of gap- and interior-foraging (χ^2 = 20.1, 11.4, 3.9, 73.4, 15.2, 8.7, 6.5, 17.0, 118.0, 23.2 in order, down the table, all $P < 0.05$); *Quiscalus quiscula* (n = 11, overall) foraged in gaps 44% of the time (n.s.).

Frugivore	Degree of frugivory (%)				Foraging in gaps (%)
	1980	1981	1982	Overall	
*Dendroica coronata***	—	100 (28)	0 (13)	50 (41)	96*
Catharus minimus	100 (11)	—	87 (15)	92 (26)	89*
*C. guttatus***	36 (59)	100 (21)	28 (40)	44 (120)	40*
*C. ustulatus***	33 (27)	88 (103)	82 (50)	79 (180)	90*
C. fuscescens	—	93 (28)	—	93 (28)	100*
Dumetella carolinensis	—	100 (13)	—	100 (13)	93*
Hylocichla mustelina	83 (18)	—	71 (17)	77 (35)	74*
Sturnus vulgaris	—	100 (27)	—	100 (27)	100*
Turdus migratorius	—	100 (168)	100 (52)	100 (220)	97*
Colaptes auratus	—	100 (31)	100 (26)	100 (57)	97*
Average (all spp.)	63%	98%	59%	84%	
Ranked abundance of fruit:	Low	High	Intermediate		

time of peak abundance—data from Johnson et al. 1985) and avian body size, gape width, or phenology. There was no tendency for large-seeded species to be consumed by fewer species of birds. Bird species that concentrated on the same fruit species in the same year were not similar in body size, gape width, or phenology (Goodman and Kruskal's gamma). Significant annual differences in fruits consumed were found for all seven bird species for which we had sufficient data in two or more years (χ^2).

There was some indication of reciprocal plant-bird dependency (Herrera 1984a) for certain combinations of fruit and bird species. That is, a certain fruit type formed a large proportion of the fruit in a particular bird species' diet, and that bird species was an important consumer of the fruits of that particular plant species. For our system, using average values for 3 years (as done by Herrera for 4 years of his study) and data from Tables 3 and 7, there were four such pairs: *Dendroica coronata* ($\bar{x}$ = 26% *Toxicodendron*)/*Toxicodendron* (71% by *D. coronata*), *Catharus ustulatus* (44%)/*Lindera* (62%), *C. guttatus* (37%)/*Menispermum* (84%), and *T. migratorius* (46%)/*Vitis* (66%). Other combinations of fruit species and bird species exhibited either low values of dependency (<20% for each of the pair of species) or only one member of the pair had a high value.

Fruit diversity. In general, dietary diversity was not correlated with avian body size (except in 1982, inversely, tau = −0.54, $z = -2.01$, $P = 0.044$), annual estimated fruit abundance, or bird phenology (except in 1980, with a higher diversity in earlier migrants, tau = 0.97, $z = 2.72$, $P = 0.012$). *Catharus minimus* and *C. ustulatus* exhibited the most consistently high relative diversities, and *Q. quiscula* the most consistently low values across years (Table 3). *Catharus guttatus* was greatly variable.

The six understory species had significantly more diverse diets overall (3 years) than subcanopy species (Mann-Whitney $U = 4$, $P \leq 0.018$), but this difference did not appear in any single year. Subcanopy foragers only occasionally descended to the understory to feed on fruit (see below, and also Hoppes 1985), although eight of the 11 fruit species occurred principally in that stratum. The more diverse diet of understory birds was associated with a higher number of fruiting species in that stratum.

FEEDING RATES

The average number of fruits consumed per minute was calculated for each bird species eating each fruit species. The variances for each year were large and only occasional significant differences among years emerged; therefore we pooled all years.

Parthenocissus and *Vitis* were consumed at the

TABLE 3. Frequency distribution (% of all fruits eaten) and relative diversities (J) of fruits eaten by 11 avian frugivores, 1980 to 1982. Values for the principal fruits in the diet each year are underlined. The denominator for J (H_{max}) was the log of the number of fruit species consumed by all birds in each time span (Pielou 1969). Significant differences among years are indicated (*): χ^2 contingency tables, *Catharus ustulatus*, $\chi^2_6 = 160$, $P \le 0.001$; *C. guttatus*, $\chi^2_6 = 133$, $P = 0.001$; *C. minimus*, $\chi^2_4 = 17$, $P \le 0.01$; *Hylocichla mustelina*, $\chi^2_2 = 78$, $P < 0.001$); *Sturnus vulgaris*, $\chi^2_1 = 21$, $P \le 0.001$; *Turdus migratorius*, $\chi^2_2 = 192$, $P \le 0.001$; *Colaptes auratus*, $\chi^2_2 = 101$, $P \le 0.001$.

Frugivore	Year	*Sambucus*	*Phytolacca*	*Toxicodendron*	*Vitis*	*Parthenocissus*	*Smilax*	*Menispermum*	*Lindera*	Total *n* (fruits)	J
Dendroica coronata	1981	—	—	$\underline{77}$	15	8	—	—	—	60	0.357
										All years	0.334
*Catharus ustulatus**	1980	—	—	—	$\underline{45}$	—	—	28	27	11	0.663
	1981	—	+	—	17	9	—	2	$\underline{71}$	173	0.441
	1982	—	—	—	20	$\underline{52}$	—	—	28	92	0.567
										All years	0.521
*C. guttatus**	1980	—	—	—	—	—	—	$\underline{100}$	—	45	0.0
	1981	—	—	—	$\underline{53}$	—	$\underline{35}$	12	—	43	0.489
	1982	—	—	—	$\underline{39}$	$\underline{48}$	4	—	8	23	0.597
										All years	0.624
*C. minimus**	1980	—	—	—	33	$\underline{57}$	—	6	4	49	0.613
	1981	—	—	—	$\underline{80}$	—	—	7	13	15	0.323
	1982	—	—	—	$\underline{28}$	$\underline{32}$	$\underline{25}$	—	15	28	0.837
										All years	0.577
C. fuscescens	1981	—	—	—	6	—	—	—	$\underline{94}$	47	0.122
										All years	0.114
Dumetella carolinensis	1980	$\underline{82}$	—	—	—	—	—	—	18	11	0.295
	1981	—	—	24	$\underline{74}$	2	—	—	—	42	0.303
	1982	—	—	—	$\underline{100}$	—	—	—	—	10	0.0
										All years	0.493
*Hylocichla mustelina**	1980	3	—	—	—	$\underline{58}$	—	—	39	38	0.484
	1981	—	—	—	20	—	—	—	$\underline{80}$	10	0.257
	1982	—	—	—	8	9	—	—	$\underline{83}$	23	0.362
										All years	0.479
*Sturnus vulgaris**	1981	—	—	—	20	$\underline{80}$	—	—	—	112	0.261
	1982	—	—	—	$\underline{77}$	23	—	—	—	13	0.336
										All years	0.277
*Turdus migratorius**	1981	—	—	—	$\underline{58}$	42	—	—	—	890	0.349
	1982	—	13	—	$\underline{81}$	6	—	—	—	211	0.379
										All years	0.363
Quiscalus quiscula	1981	—	—	—	—	$\underline{100}$	—	—	—	64	0.0
	1981	—	—	—	$\underline{100}$	—	—	—	—	7	0.0
										All years	0.088
*Colaptes auratus**	1980	—	—	—	$\underline{100}$	—	—	—	—	24	0.0
	1981	—	—	6	21	$\underline{73}$	—	—	1	144	0.386
	1982	—	—	—	$\underline{86}$	14	—	—	—	92	0.251
										All years	0.399

TABLE 4. Average rates of fruit ingestion (fruits/min) by avian frugivores for all fruit types with $n \geq 5$ feeding bouts; all years combined. The "mean" weights the value for each bird species equally.

	Fruits					
Frugivores	*Toxicodendron*	*Vitis*	*Parthenocissus*	*Smilax*	*Menispermum*	*Lindera*
Dendroica	4.1	6.0				
Catharus ustulatus		6.5	11.7			3.2
C. guttatus		5.6		3.0	2.1	
C. minimus		5.0		11.6		7.8
C. fuscescens						3.1
Dumetella		6.5				
Hylocichla						4.3
Sturnus		11.6	14.0			
Turdus		12.3	12.4			
Quiscalus			21.3			
Colaptes		10.0	13.3			
$\bar{x}$	4.1	7.9	14.5	7.3	2.1	4.6
Fruit size (mm)*	–	7.7	7.5	7.3	8.0	8.5
Seed size (g)*	0.025	0.031	0.037	0.086	0.109	0.145
Pulp dry mass (g)*	0.001	0.035	0.027	0.040	0.067	0.040

* Data from Johnson et al. 1985.

highest rate (Table 4). *Parthenocissus* was eaten significantly faster than *Vitis,* in general (Mann-Whitney $U = 1$, $P < 0.002$). Differences among *Lindera, Toxicodendron, Smilax,* and *Menispermum* were not statistically significant, at least in part because of the few bird species with adequate samples. Fruits with small seeds were ingested significantly more rapidly than those with larger seeds (tau = 0.73, $z = 2.06$, $P = 0.039$), but there was no significant relationship between fruit dimensions and speed of ingestion.

A Kruskal-Wallis ANOVA (see Methods) showed the following ranking of differences in average ingestion rates among bird species: *Q. quiscula* ≧ *T. migratorius* ≧ *Colaptes auratus* = *S. vulgaris* > *Catharus minimus* = *C. ustulatus* = *Dumetella carolinensis* = *Dendroica coronata* = *Hylocichla mustelina* > *Catharus guttatus* = *C. fuscescens* (the last two indicated differences were statistically significant at $P < 0.02$; the first two were marginal at $P = 0.06$). We then considered each fruit species separately, using the same procedure. No significant differences in feeding rates on *Lindera* were found. On *Parthenocissus, Q. quiscula* ate faster than all the others (Mann-Whitney $U = 301$, $P = 0.04$). *Turdus migratorius* and *S. vulgaris* ate *Vitis* faster than *C. auratus* ($U = 1{,}893$, $P = 0.05$), which was faster than *C. ustulatus* ($U = 219$, $P = 0.03$); all the remainder were similar and slower. *Catharus minimus* ate *Smilax* faster than *C. guttatus* ($U = 15$, $P = 0.03$). Of 15 possible comparisons among bird species within fruit types, five were significant, so it is unlikely that the observed differences are due to chance alone.

Parthenocissus and *Vitis* fruits were eaten significantly faster by larger frugivores (tau = 0.57, $z = 1.97$, $P = 0.049$; tau = 0.60, $z = 2.41$, $P = 0.032$, respectively), but there was no correlation of frugivore body size and ingestion rate for *Lindera.* No correlation of body size and ingestion rate was found when ingestion-rate ranks for all fruits eaten by a bird species were tested against body-size ranks.

At the observed average feeding rates for each bird species on each fruit species, most birds obtained 1 to 2% of their metabolically effective body mass (estimated as $W^{0.7}$) in dry fruit pulp/minute (using fruit pulp weights from Johnson et al. 1985). However, *C. ustulatus* could get almost 3% of its effective body mass in a minute from *Parthenocissus. Catharus minimus* could get about 4% from *Smilax hispida* and almost 3% from *Lindera* but only 0.6% from *Menispermum. Dendroica coronata* could get 3.5% from *Vitis,* but only 0.07% from *Toxicodendron.*

SPATIAL PATTERNS OF FORAGING

Nine of the 11 frugivore species foraged more often than expected (on the basis of relative area) in gaps as compared to interior sites (74 to 100%, Table 2). Overall, 83% of all observed foraging bouts occurred in gaps. In contrast to the general tendency, *C. guttatus* foraged significantly more

TABLE 5. Degree of frugivory in relation to foraging site (gap [G] vs. interior [I]). The proportion of fruit-feeding bouts is given (*n*); 1980: $\chi^2 = 38.9$ (*C.g.*), 1982: $\chi^2 = 14.1$ (*C.u.*), 18.3 (*C.g.*), Fisher exact test, C = 0 (*H.m.*); all years: $\chi^2 = 18.8$ (*C.u.*), 79.7 (*C.g.*), 13.4 (*H.m.*); all $P < 0.001$. Data are presented only when $n \geq 5$ bouts in both types of foraging site in each case; data for all years combined includes annual samples that were too small to analyze separately.

	Degree of frugivory (%)					
	1980		1982		All years	
	G	I	G	I	G	I
Catharus ustulatus	—	—	93 (41)	33 (9)	81 (170)	30 (10)
C. guttatus	81 (26)	0 (33)	65 (17)	0 (23)	83 (63)	2 (57)
Hylocichla mustelina	—	—	100 (12)	0 (5)	88 (34)	14 (7)

often (60%) than expected in interior sites (Table 2).

Overall, more fruit-feeding bouts (all bouts for all bird species) occurred in gaps in all 3 years (95% of 61 in 1980, 99% of 422 in 1981, 95% of 164 in 1982) than expected from the area occupied by gaps (adjusting for sampling effort) (χ^2 = 120, 1,223, 426 respectively, all $P \leq 0.001$). Insect foraging was also significantly concentrated in gaps (adjusted as above; $\chi^2 = 30.1$, $P < 0.001$; $\chi^2 = 11.7$, $P < 0.001$; $\chi^2 = 8.0$, $P < 0.01$ respectively), but much less strongly than fruit foraging (45% of 60 in gaps in 1980, 88% of 16 in 1981, 41% of 61 in 1982).

Foraging strata (all years pooled) shifted significantly between gap and interior sites. Although subcanopy foragers seldom descended to the understory (17% of bouts), they did so more often than expected in interior sites (contingency table, $\chi^2_1 = 86.47$, $P \leq 0.001$). Understory foragers were not often found in the subcanopy (22% of bouts), but were found more often than expected in interior sites (contingency table, $\chi^2 = 10.36$, $P \leq 0.005$). Thus, the tendency to shift strata was site-dependent. The shift was not due to a differential frequency of occurrence of fruit crops in the two strata in gap and interior, inasmuch as the stratal distribution of fruit crops was virtually identical (64 to 65% in understory) in the two microhabitats (χ^2 contingency table).

Some species (*C. ustulatus, C. guttatus, H. mustelina*) foraged significantly more often for fruits in gaps and for insects in forest interior both overall (3 years combined) and in all testable years separately (Table 5). Other species of frugivores fed on fruits to the same degree (100%) in both treefall gaps and forest interior (*T. migratorius, Q. quiscula*). The six remaining species foraged almost exclusively in treefall gaps and almost exclusively on fruits (except for *D. coronata* in 1982). Thus, certain species apparently shifted their choices of food items with microhabitat, but others did not.

Bird species showed significantly different overall levels of preference for clumped or isolated displays, relative to the frequency of occurrence of these two display categories (46% clumped, irrespective of fruit species) in the study area (χ^2 test of homogeneity), with some annual variation (Table 6). Overall, *T. migratorius* and *C. minimus* used each display type in proportion to its frequency, while *C. ustulatus* ($\chi^2 = 178$) and *C. guttatus* ($\chi^2 = 105$) favored clumped displays and *S. vulgaris* ($\chi^2 = 200$), *D. coronata* ($\chi^2 = 86$), and *C. auratus* ($\chi^2 = 134$) favored isolated displays in general (all $P \leq 0.001$).

Overall, subcanopy birds favored clumped displays significantly less often than understory birds (38% vs. 57%; $\chi^2 = 22.6$, $P \leq 0.001$; see Table 6). Significant differences were found among understory foragers ($\chi^2_4 = 12.7$, $P < 0.02$); by inspection, *D. carolinensis* and *H. mustelina* foraged in clumped displays less often, and *C. ustulatus* more often, than the others.

These data can also be examined from the perspective of the plants whose fruits were eaten and seeds dispersed. For a particular fruiting species, is spatial distribution associated with differences in the composition of the avian fruit-eaters and seed dispersers? All birds, collectively, foraged much more often than expected on isolated *Vitis* and *Parthenocissus* and on clumped *Menispermum* and *Lindera*, other species contributing <1% of the total χ^2 values (goodness of fit, $\chi^2_{13} = 1{,}078$). However, not all species of birds contributed equally to this overall pattern (χ^2 tests of homogeneity). For *Vitis*, *C. auratus* and *T. migratorius* were by far the greatest con-

TABLE 6. Annual percentage of foraging bouts on clumped fruiting displays ($n \geq 10$). The χ^2 test was done on the numbers of bouts, but for comparative purposes, percentages appear in the table; * marks significant differences among years. *Sturnus vulgaris* (11% of 27 total observations) and *Dendroica coronata* (18% of 28) had too few observations in most years to warrant entry in the table.

	All years	1980	1981	1982
All birds (including those not analyzed separately)*	48	67 (52)	43 (422)	55 (164)
Subcanopy species (all):*	38	—	28 (262)	67 (85)
*Colaptes auratus**	32	—	7 (31)	62 (26)
*Turdus migratorius**	40	—	31 (168)	69 (52)
Understory species (all):*	57	72 (47)	71 (123)	31 (90)
*Catharus ustulatus**	68	—	78 (90)	41 (41)
C. minimus	52	55 (11)	—	46 (13)
C. guttatus	57	83 (12)	48 (21)	45 (11)
Hylocichla mustelina	39	53 (15)	—	25 (12)
Dumetella carolinensis	38	—	—	31 (13)

tributors to a significant χ^2 value ($\chi_{\text{diff}}^2 = 15.0$, $P \leq 0.05$), both species strongly favoring isolated *Vitis* displays. For *Lindera,* there was a significant departure from homogeneity among avian foragers, with *C. ustulatus* strongly favoring clumped displays ($\chi_{\text{diff}}^2 = 7.1$, $P < 0.05$). Thus, for *Vitis* and *Lindera,* clumped and isolated displays were visited by different arrays of frugivores. There was no significant difference among bird species in their usage of clumped vs. isolated displays of *Menispermum* and *Parthenocissus*—all species preferred isolated displays of *Parthenocissus* and clumped displays of *Menispermum.*

POSTFORAGING BEHAVIOR

The relative frequency of departure from the foraging site after a feeding bout gives an index of vagility of the consumers and of the ingested seeds. Departure is often so rapid (within 2 min, Hoppes 1985) that virtually all seeds are carried off to some minimum distance. However, as long as departure behavior is consistent among foraging bouts, high departure frequencies in this sample indicate an increased likelihood of seeds being carried more than the minimal distance from the source.

Birds left the site significantly more often on

TABLE 7. Estimates of relative value of the avian frugivores as dispersal agents for certain fruit species. Average relative frequency of an avian forager leaving the foraging site after a fruit-foraging bout is in the second column all years combined. (a) Average number of fruits/bout; (b) estimated efficacy of carrying ingested seeds from foraging site (a × average probability of bird leaving site); (c) the proportion of all fruits of that species eaten by the indicated bird species (derived from Table 3); (d) index of the relative importance (numerically) of the indicated bird species in dispersing seeds of each plant species (b × c).

		Fruit species							
		Lindera				*Vitis*			
Bird species	Frequency of leaving	a	b	c	d	a	b	c	d
Dendroica coronata	100%					1.5	1.5	0.01	0.02
Catharus ustulatus	76	1.9	1.4	0.51	0.71	3.1	2.4	0.05	0.12
C. guttatus	78					2.9	2.3	0.03	0.07
C. minimus	79	1.0	0.8	0.03	0.02	4.0	3.2	0.04	0.13
C. fuscescens	81	1.9	1.7	0.17	0.29				
Dumetella carolinensis	46					3.7	1.7	0.04	0.07
Hylocichla mustelina	82	1.6	1.3	0.16	0.21				
Sturnus vulgaris	56					3.2	3.1	0.03	0.09
Turdus migratorius	82					5.8	4.8	0.66	3.30
Quiscalus quiscula	100								
Colaptes auratus	87					4.7	4.0	0.13	0.52

average after fruit-feeding bouts (81%) than after insect-feeding bouts (32%) ($\chi^2_{10} = 196, P \leq 0.001$). Departure frequencies after fruit foraging differed significantly among bird species (contingency table, $\chi^2_{10} = 23.5, P \leq 0.01$). By inspection of the χ^2 table from the combined data for 3 years, *D. coronata* and *C. ustulatus* departed considerably more often than expected, while *D. carolinensis* tended to stay in a foraging site more often than expected. (The other species differed relatively little from expected.) None of the differences among bird species was associated consistently with body size, degree of frugivory, stratum, or phenology (by partitioning of χ^2), and there were no significant annual differences in departure frequencies. Thus, there was a rather high probability that a seed would be carried away from the parent plant, with some differences among frugivores.

Postforaging behavior of frugivores (all species combined) varied significantly (contingency table, $\chi^2_5 = 32.8, P \leq 0.001$) with the fruit consumed: departures from the site followed consumption of *Parthenocissus* more often than expected and of *Vitis* and *Lindera* less often than expected; the other species differed little from expected. Although *Turdus* left *Parthenocissus* sites significantly more often than *Vitis* sites ($\chi^2_1 = 11.45, P \leq 0.001$), four other species (*C. ustulatus, C. minimus, C. guttatus, C. auratus*) did not change their tendency to leave a foraging site depending on the fruit consumed (χ^2) (the remaining species could not be tested because of small sample sizes).

CONSEQUENCES FOR SEED DISPERSAL

There were marked differences among bird species in the estimated numbers of seeds carried away after an average foraging bout (Table 7). *Catharus ustulatus* carried more *Lindera* seeds away (per bout) than *C. minimus. Colaptes auratus* and *T. migratorius* carried off more *Vitis* seeds, per bout, than *D. carolinensis* or *D. coronata. Quiscalus quiscula* carried away many more *Parthenocissus* seeds per bout than *D. coronata.* Thus, for each plant species, a foraging visit by some bird species was more useful in dispersing seeds than a visit by other bird species.

However, the numerical abundances and fruit-foraging preferences of the bird species also affect the total numbers of seeds transported. The numbers of fruits eaten reflect both foraging preferences and numerical abundances of the bird species. For *Lindera, C. ustulatus* was far more important (in terms of total numbers of seeds transported) as a potential dispersal agent, compared to three other species (Table 7), than postforaging behavior alone would indicate. Similarly, *T. migratorius* was by far the most important potential disperser of *Vitis* and, to a lesser degree, *Parthenocissus,* by virtue of the relatively large quantities eaten. Annual differences in population sizes would mean that the

TABLE 7. Extended.

Fruit species															
Parthenocissus				*Toxicodendron*				*Menispermum*				*Smilax*			
a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
1.3	1.3	0.01	0.01	3.2	3.2	0.71	2.3								
4.4	3.3	0.05	0.17												
								2.3	1.8	0.84	1.5	2.1	1.6	0.70	1.10
												1.4	1.4	0.30	0.42
3.7	3.6	0.11	0.40												
5.3	4.3	0.46	2.00												
9.1	9.1	0.08	0.73												
6.8	5.9	0.14	0.83												

relative value of different birds will vary greatly from year to year.

There was little correspondence between the relative amount of pulp ingested by a bird and the estimated vagility of the bird or its possible efficacy as a disperser for seeds of that fruit species. For example, *T. migratorius* would seem to be an effective disperser of ingested *Vitis* seeds but had only average pulp-ingestion rates, and *C. minimus* obtained relatively more pulp from *Lindera* than *C. ustulatus* but probably was a poorer dispersal agent.

DISCUSSION

Subcanopy and understory frugivores differed consistently in average body size, occurrence in years of low fruit abundance, frequency of foraging on clumped fruiting displays, tendency to void seeds by regurgitation (Johnson et al. 1985), and speed of movement away from a fruit source (Hoppes 1985). To this degree these groups constitute two guilds of frugivore, from the perspective of the plants whose seeds are dispersed.

One of the five subcanopy frugivores is an introduced species (*S. vulgaris*) without a long history of interaction with native North American plants. Two of the five subcanopy foragers (*T. migratorius, Q. quiscula*) are now more abundant than they were before European settlement of this continent (Graber and Graber 1963). Thus, the plants dispersed chiefly by these bird species may be subject to a dispersal regime quite different from that prevailing in previous times. Plant distribution and abundance must also differ, and so present-day relationships between fruit-eating birds and fruiting species are likely to be somewhat different from those of earlier days.

DIET COMPOSITION

The degree of frugivory and the species of fruits consumed varied from year to year for most bird species. Bird species that were similar in fruit diets were not particularly similar in bill or body size. We found no positive correlations of fruit or seed sizes with bill or body sizes or with diversity of consumers. All of these observations reinforce the interpretation of this mutualism as a diffuse one (Thompson 1982; Wheelwright and Orians 1982; Herrera 1984a, 1984b; Moermond and Denslow 1985). McKey (1975) discussed the possibility that large-seeded fruits would be consumed by fewer kinds of avian frugivores (perhaps more specialized to a diet of fruits) than are small-seeded fruits. We found no such tendency in this study, perhaps in part because the gape widths of all birds in this study, except *D. coronata,* exceeded 10 mm, and thus exceeded the dimensions of our largest fruit (*Lindera*). The relatively small size of our largest fruits and seeds (i.e., ≤ 1 cm) may also explain why we found no correlations of gape width of consumers with the sizes of diversities of fruits or seeds consumed, in contrast to Wheelwright's (1985) tropical system, which had a wider range of fruit and gape sizes.

Herrera (1984a) reported some evidence of reciprocal plant-bird dependency for certain plant-bird species pairs, especially at his highland site. We found four such pairs in our system, using a somewhat different, but correlated, measure. However, the interpretation is not entirely straightforward, and use of average values may obscure some realities of the interactions. In 1982, *C. guttatus* was present but ate no *Menispermum*; in 1980, *T. migratorius* was virtually absent, despite the presence of at least some *Vitis*; and in 1980 and 1982, *D. coronata* was very rare, despite the presence of some *Toxicodendron* crops. Although the low numbers of *Turdus* and *Dendroica* might have been linked to possibly low numbers of *Vitis* and *Toxicodendron* fruits in those years, thus emphasizing a dependency of the birds on the plants, this kind of explanation cannot work for *C. guttatus/Menispermum,* because the birds were present but ate other fruits and insects. This dietary switch of *C. guttatus* could, perhaps, have exacted a metabolic or behavioral cost related to the absence of *Menispermum* in the diet, but we lack any grounds for assuming there was one. The great majority of our observations suggests a lack of mutual dependency, as was also true in Herrera's study.

FEEDING RATES

The average number of fruits consumed per feeding bout was less than three for all birds eating *Smilax, Menispermum,* and *Lindera* and ranged up to six for *Vitis* and nine for *Parthenocissus* (which were eaten by the largest frugivores). Most small frugivorous birds typically consume only a few fruits at a time (Holthuijzen and Adkisson 1984, and references following below). Several factors might explain the low numbers of fruits consumed at a sitting, including avoidance of too large a dose of secondary chemicals (Janzen 1983), minimizing exposure to predators (Howe 1979), seed size (Levey 1987), and in some cases simply the capacity of the birds to handle the bulk of pulp and seeds. The number of fruits consumed per feeding bout is only sometimes related to frugivore body size (Holthuijzen and Sharik 1985, this study).

The relative profitability (pulp intake : metabolic body mass of bird) of fruits varied several fold. The birds did not concentrate their foraging principally on the fruits that provided the greatest rate of yield of pulp, presumably because other factors, including fruit abundance, influenced their choices (see also Sorensen 1981, Martin 1985). Despite the low profitability of *Toxicodendron* fruits for *D. coronata,* this fruit is an important winter food for this species (references in Skeate 1985, Willson and Hoppes 1986).

Our index of profitability should be adjusted for differing digestibilities of various fruits by each of the bird species (Johnson et al. 1985), but data are not available for each of the bird-fruit combinations for which we have field data. However, the values for digestive efficiency generally varied by a factor of 2 or less (Johnson et al. 1985), so the larger differences in profitability (up to 7 or, in one case, 50 fold) observed in this study would not be obliterated even if the more profitable fruit were less digestible.

Differences in numbers of fruits consumed per bout may have consequences for seed/seedling ecology of the plant species being dispersed. If the seeds consumed in a single meal tend to be voided simultaneously (at least more often so than seeds from different meals), *Parthenocissus* seeds would be deposited in larger clusters, on average, than the seeds of *Smilax* and *Vitis,* which in turn would be deposited in bigger groups than *Toxicodendron, Menispermum,* and *Lindera.* This trend would be exacerbated by the single-seededness of the last three fruit types, in contrast to the tendency of the first three fruit types to have more than one seed/fruit (Johnson et al. 1985). Deposition of seeds in groups might affect seed/seedling mortality from density-responsive factors such as predation, disease, or competition (e.g., Davidar 1983). An increase in meal size among bird species eating a particular fruit species would mean that, while the total number of seeds carried per meal would also increase, the tendency to deposit those seeds in larger clusters might bring some attendant disadvantages. Because the consequences of seed and seedling density vary enormously with ecological circumstances and density effects are not always apparent (Connell et al. 1984; Willson et al., unpubl.), such potential disadvantages cannot be assumed. If the clustered seeds are siblings, there may even be some advantages to growing in a group (Willson et al. 1987; D. A. Goldman, unpubl.).

SPATIAL PATTERNS

Gap vs. interior. Most of the frugivores in this study foraged for fruit preferentially in treefall gaps, and forest frugivores in central Illinois generally are more abundant in gaps than in forest interior in autumn (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986). *Catharus guttatus* in our study was the least frugivorous of the frugivores, on average, and was the only species to favor foraging in forest interior. However, its degree of frugivory varied annually (this study), and so did its use of treefall gaps (Martin and Karr 1986). Foraging for insects by the frugivores in our study was also concentrated in gaps, but less so than fruit foraging, except in the high fruit year (1982). Both fruits and insects (or at least foliage on which to hunt for insects) are often concentrated in treefall gaps (Blake and Hoppes 1986, Martin and Karr 1986). Fruit removal rates are commonly higher in gaps than in the interior, presumably as a result of these avian activity patterns (Thompson and Willson 1978, Moore and Willson 1982, Willson and Melampy 1983, Denslow 1987).

If the apparent preference of most frugivorous species for foraging in and around treefall gaps means that they spend more time, altogether, in such sites than in the forest interior, then seeds carried by those species may have a higher probability of being deposited in or near a gap (see also Hoppes 1985). The possible effect of this concentration of seeds will obviously vary with the germination and establishment requirements of the plant species, as well as density-related processes that affect establishment and growth. If the plants growing from gap-deposited seeds can mature and bear fruit crops within the life span of the gap, to some extent there may be a positive feedback between foraging-site preferences of avian frugivores and the distribution of their food plants (Herrera 1985; but see also Canham and Marks 1985). Patterns of avian use of treefall gaps seems to vary geographically (Schemske and Brokaw 1981, Willson et al. 1982, Herrera 1985), but the possible consequences for plant recruitment patterns have not been explored.

Clumped vs. isolated displays. The avian foragers differed in their relative use of clumped and isolated displays, and display-type preferences often varied with the fruit species eaten. From the perspective of the parent plant whose seeds are dispersed, the potential advantage of growing alone or in a group of conspecifics (or as single vs. multistemmed individuals) varied, with some species (*Vitis, Parthenocissus*) being favored when isolated, and *Lindera* and *Menispermum* when clumped. Because *T. migratorius* was probably the most important disperser of *Parthenocissus* and *Vitis* (Table 7), its preference for isolated displays of these species should enhance the advantage of isolation. Similarly, the most important disperser of *Lindera* was probably *C. ustulatus,* which favored clumped displays of this species more than other birds and thus enhanced the potential advantage obtained by clumped *Lindera.* Such preferences thus may contribute to differential success of fruiting individuals that vary in number of stems or that grow in different dispersion densities. If plants have no way to determine whether they grow alone or in a group, the differential success provides a source of variation in fitness that, taken alone, cannot be altered by selection. But if the plants can control their dispersion (e.g., by allelopathy), there is the potential for selection to increase (*Lindera*) or decrease (*Vitis, Parthenocissus*) conspecific association. Such conjectures depend, however, on consistency of foraging preferences and, at least for *Lindera,* earlier results suggested a slight preference for isolated bushes (Moore and Willson 1982), in contrast to the results of this study. The apparent idiosyncratic nature of the interactions of avian foraging and fruit-crop spacing, or the complexity of the relationships between spatial context and fruit removal (Denslow 1987), suggest a need for further study.

POST FORAGING BEHAVIOR

All frugivores usually left the site after consuming a variable but small number of fruits, so most seeds consumed were carried some minimum distance away from the parent plant (see also Holthuijzen and Sharik 1985, Levey 1986). Certain bird species were more likely to leave a foraging site than others, as was true in other studies (Cruz 1981, Sorensen 1981) and departures were more frequent from certain kinds of fruiting plants. As a result, some bird species are probably more efficacious transporters of seeds for particular plant species than others. The seed shadow produced by a frugivorous bird species reflects both the efficacy of transport after each feeding bout and the sheer number of fruits consumed (see also Herrera and Jordano 1981, Herrera 1984a, and others). However, the most efficacious dispersers are not necessarily the most common (Table 7). We can expect regional and annual variation in the numerical importance of different frugivores (e.g., compare Baird 1980, in which *D. coronata* was a less important consumer of *Toxicodendron* and *T. migratorius* was a less important consumer of *Vitis* than in our study).

Differences among frugivores in the speed and distance moved after feeding (Hoppes 1985) will contribute to the variation among seed shadows generated by different bird species. Subcanopy foragers moved much more rapidly to a distance of ≥20 m from a fruit crop than did understory foragers (Hoppes 1985). If differences in vagility are characteristic of these two groups of birds, subcanopy foragers would thus be likely to generate a longer seed shadow than understory foragers. Thus, although both *D. coronata* and *D. carolinensis* carried off about the same number of *Vitis* seeds per bout, *D. coronata* was likely to carry the seeds to a considerably greater distance than *D. carolinensis. Dendroica coronata* carried fewer *Parthenocissus* seeds per bout than *C. ustulatus,* so (given an equal number of birds) the density of the seed shadow generated by *D. coronata* would be lower, but its far-flying tendency could increase the length of the seed shadow. The relative advantages of dense and long seed shadows depend on the distribution of safe sites for the seeds in both space and time (given seed dormancy) (see Murray 1986) and are unmeasured.

Bird species differ in the frequency distribution of habitats/microhabitats visited and therefore they differ in sites of seed deposition. For instance, *C. guttatus* is much less likely to visit a treefall gap than *C. ustulatus* and *C. minimus,* so the shape of seed shadow generated by *C. guttatus* would be quite different from that of the other, similar-sized, thrushes. The consequences for the plants have not been assessed but would depend, in part, on the ability of recruits to use existing gaps as opposed to waiting for a new one to form. Sites of seed deposition are of obvious importance to dispersal success (Sorensen 1981, Herrera 1984c, Murray 1986), but for our system we have not quantified this for different frugivores (but see Hoppes 1985 for a beginning). In general, however, there is a tendency for high levels of seed deposition to occur around the edges of treefall gaps and for frugivores to move toward other gaps with good fruit crops (Hoppes 1985). Whether quantity of seeds transported can compensate to any degree for decreases in dispersal distance or changes in site of deposition is not known. A very important next step in dispersal studies is the detailed examination of the consequences of variation in length and density of seed shadows.

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