Patterns of Fruit Presentation and Seed Dispersal in Bird-Disseminated Woody Plants in the Eastern Deciduous Forest

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PATTERNS OF FRUIT PRESENTATION AND SEED DISPERSAL IN BIRD-DISSEMINATED WOODY PLANTS IN THE EASTERN DECIDUOUS FOREST

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Reviews of the types of seeds carried by birds (Ridley 1930; McAtee 1947; Martin et al. 1951; Van der Pijl 1972) as well as more recent quantitative studies (Snow 1962, 1965; Snow and Snow 1971; Snow 1970; Smith 1975; Howe 1977; McDiarmid et al. 1977) demonstrate the importance of birds as dispersal agents. Coevolutionary relationships between fruits and frugivorous birds have been studied primarily in tropical systems and theoretical treatment of tropical fruiting patterns provide a basis for testing prediction in areas with low seasonal climatic fluctuation (Janzen 1969, 1970, 1971; Snow 1971; Morton 1973; McKey 1975; Howe and Estabrook 1977).

Fruit dispersal patterns in the temperate zone are less clear (Regal 1977). Snow (1971) has provided the clearest interpretation of possible temperate fruiting patterns, although he restricts this interpretation to Europe and considers it "provisional and partly speculative" (p. 199). Morton (1973) briefly considered patterns of fruiting in the temperate zone, suggesting that temporal patterning in fruit presentation is influenced by the abundance of insects in spring. He hypothesized that birds would feed selectively on insects at this time, reducing potential for seed dispersal by birds.

Several hypotheses may be tested concerning patterns of fruit abundance, time of maturation, nutrient quality, persistence, and seed-predator avoidance for bird-disseminated fruits in the temperate zone.

1. The number of bird-disseminated plant species and their densities may be greater in geographic locations where larger numbers of frugivorous birds are found.
2. The timing of fruit maturation is a trade-off between presenting fruit when maximum quality and quantity of dispersal agents are available (leading to a single time for fruit maturation for all species) and competition among species for attracting dispersal agents (leading to a temporal spread in fruit maturation times).
3. Higher nutrient reward and palatability in fruits will attract bird dispersal agents more rapidly and will result in more rapid seed dissemination.
4. Higher nutrient reward will result in more rapid attack by microbial agents.

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Microbial attack may make fruits unacceptable to birds, and fruits with lower nutrient reward may remain acceptable to birds for longer periods of time.

5. Fruits which encounter lower probabilities of dispersal by birds may attract mammalian dispersers as well. In these species we should find adaptations to avoid mammalian seed predation.

Here I suggest that fruitless periods are a consequence of natural selection for fruit presentation at times when the probability for dispersal is maximal. I examine timing of presentation of bird-disseminated fruits in the eastern deciduous forest of North America to test the above hypothesis, and I show that the large numbers of frugivorous birds during fall migration and the higher probability of dispersal at this time of year affect timing of fruiting, nutrient quality of fruits, and latitudinal patterns of fruit availability in the temperate zone. The components of this interaction are first examined separately to illustrate the temporal changes in abundance of both birds and bird-disseminated fruits.

FRUITING SPECIES

The eastern deciduous forest extends eastward from 98°W and southward from 49°N in North America (Braun 1950). Within this region over 125 species of woody trees, shrubs, and vines present fruits, the seeds of which are dispersed primarily by birds (U.S. Dep. of Agriculture, Forest Service 1974; table 1). I have chosen species subjectively to include native woody species with fleshy fruits having maximum dimension less than 2.5 cm, and for which information on fruiting times is available. Many nonwoody plants also present bird-disseminated fruits, but fruiting patterns of these species, with some exceptions, are not available in the literature and are not considered here. The patterns presented below, however, should apply to most if not all species of bird-disseminated fruits, and do in cases where data are available.

LATITUDINAL PATTERNS OF FRUITING

Plants which have bird-disseminated fruits are not equally represented in the floras of different parts of the eastern deciduous forest. The best quantitative data (Braun 1950) presents information on canopy tree species composition from all parts of this region.

I divided the eastern United States into nine zones of 1.5 degrees of latitude (table 2). From the 341 forests recorded by Braun I determined the average percentage of bird-disseminated canopy trees as a function of latitude (table 2). Percentage representation of bird-disseminated trees decreases with increasing latitude; both the number of species and the percentage representation of individual species decreases. For example, individual southern forests had as many as eight of the 14 tree species with bird-disseminated fruits (Braun 1950).

TEMPERATE FRUGIVOROUS BIRDS

Many bird species in the eastern deciduous forest eat fruits (Martin et al. 1951). A smaller number of these species consume fruit as a major portion of their diet at

TABLE 1

APPROXIMATE FRUIT DISPERSAL TIMES (FOR 40° N), SEED WEIGHTS, AND FRUIT TYPES FOR BIRD-DISSEMINATED WOODY PLANTS OF THE EASTERN DECIDUOUS FOREST

Species	Fruit Dispersal	Seeds/kg ÷ 1,000*	% Crude Fat	Fruit Type
Amelanchier alnifolia (Nutt.) Nutt.	July → Aug.	180.8		SS
Amelanchier arborea (Michx. f.) Fern	June → Aug.	176.4		SS
Amelanchier canadensis (L.) Medic.	May → June	...	4.45†	SS
Amelanchier laevis Wreg	June → Aug.	...		SS
Amelanchier sanguinea (Pursh) DC.	July → Sept.	185.2		SS
Aralia hispida Vent.	Aug. → Sept.	202.8		?
Aralia nudicaulis L.	Aug. → ?	218.3		?
Aralia spinosa L.	Sept. → Oct.	288.8		?
Arctostaphylos uva-ursi (L.) Spreng	Aug. → Mar.	90.2		FL
Aronia arbutifolia (L.) Elliott	Sept. → Spring	564.4	3.80†	FL
Aronia melanocarpa (Michx.) Elliott	Sept. → Winter	608.5	3.44†	FL
Aronia prunifolia (Marsh.) Rehd.	Sept. → Winter	...		FL
Bumelia languinosa (Michx.) Pers.	Oct. → Winter	12.6	19.7	?
Celastrus scandens L.	Sept. → Winter	57.3		FL
Celtis laevigata Willd.	Oct. → Winter	13.2	6.9	FL
Celtis occidentalis L.	Oct. → Winter	9.5	4.37†	FL
Chionanthus virginicus L.	Sept. → ?	...		?
Cornus alterniflora L.	July → Sept.	17.6		FH
Cornus amomum Mill.	Aug. → Sept.	26.9		FH
Cornus canadensis L.	Aug. → Oct.	147.7		?
Cornus drummondii C.A. Meyer	Aug. → Winter	34.6		FL
Cornus florida L.	Sept. → Nov.	9.9	16.7	FH
Cornus racemosa Lam.	Sept. → Oct.	28.7	26.73†	FH
Cornus rugosa Lam.	Sept. → ?	41.9		?
Cornus stolonifera Michx.	Sept. → Winter	40.8		FL
Cotinus obovatus Raf.	July → ?	111.1		?
Crataegus arnoldiana Sarg.	Sept. → Winter	...		FL
Crataegus chrysocarpa Ashe.	Sept. → ?	23.6		?
Crataegus crus-galli L.	Oct. → Winter	...	3.29†	FL
Crataegus douglasii Lindl.	Sept. → Fall	49.8		?
Crataegus mollis Scheele	Sept. → Fall	...		?
Crataegus marshallii Eggl.	Sept. → ?	...	8.6	FL
Crataegus phaenopyrum (L.f.) Med.	Oct. → ?	65.7		?
Crataegus punctata Jacq.	Sept. → Fall	10.4		?
Crataegus succulenta Schrad.	Sept. → ?	45.4		?
Elaegnus commutata Bernh.	Sept. → ?	8.4		FL
Euonymus americanus L.	Sept. → ?	77.4	33.7	?
Euonymus atropurpurens Jacq.	Sept. → Oct.	37.3		FH
Euonymous obovatus Nutt.	Aug. → Oct.	56.2		FH
Gaultheria hispidula (L.) Bigel	Aug. → Winter	6,818.9		FL
Gaultheria procumbens L.	Sept. → Winter	8,498.8		FL
Gaylussacia baccata (Wangh.) K. Koch	July → Aug.	780.4		SS
Ilex glabra (L.) A. Gray	Fall → Spring	63.9		FL
Ilex montana Torr. and Gray	Sept. → Spring	77.2		FL
Ilex opaca Ait.	Sept. → Mar.	62.6	7.9	FL
Ilex verticillata (L.) A. Gray	Sept. → Winter	202.8	5.10†	FL
Ilex vomitoria Ait.	Sept. → Winter	83.3	7.7	FL
Juniperus ashei Buchholz	Sept. → Winter	22.3		FL
Juniperus communis L.	Aug. → 2 years	80.5		FL
Juniperus silicicola (Small) Bailey	Oct. → Winter	...		FL
Juniperus virginiana L.	Sept. → Mar.	96.1		FL
Lindera benzoin L. Blume	Sept. → Oct.	9.9	50.73† 47.82 56.21‡	FH

(continued)

TABLE 1 (*Continued*)

Species	Fruit Dispersal	Seeds/kg ÷ 1,000*	% Crude Fat	Fruit Type
Lonicera canadensis Marsh.	July → Sept.	. . .		SS
Lonicera dioica L.	June → Oct.	. . .		SS
Lonicera glaucescens Rydb.	Aug. → Sept.	. . .		SS
Lonicera hirsuta Eat.	July → Oct.	. . .		SS
Lonicera oblongifolia (Goldie)	Aug. → ?	520.3		SS
Magnolia acuminata L.	Aug. → ?	11.9	21.99†	?
Magnolia fraseri Wlat.	Aug. → ?	9.9		?
Magnolia grandiflora L.	Aug. → ?	14.1		?
Magnolia macrophylla Michx.	Aug. → ?	. . .		?
Magnolia tripetala L.	Aug. → ?	. . .		?
Magnolia virginiana L.	Aug. → ?	16.5		?
Menispermum canadense L.	Sept. → ?	16.8		?
Mitchella repens L.	July → Winter	427.7	7.4	FL
Morus rubra L.	June → Aug.	793.7		SS
Myrica cerifera L.	Aug. → Winter	185.2	23.2	FL
Myrica gale L.	July → Winter	. . .		FL
Myrica pennsylvanica Loisel.	Sept. → Winter	121.2		FL
Nemopanthus mucronatus (L.) Trel.	Aug. → (Somewhat persistent)	99.2	7.71†	FL
Nyssa aquatica L.	Sept. → Nov.	1.1		?
Nyssa ogeche Bartr.	July → Aug.	2.7		?
Nyssa sylvatica Marsh.	Sept. → Dec.	7.3	14.4	?
Parthenocissus quinquefolia (L.) Planch.	Sept. → Feb.	34.4		FL
Prunus alleghaniensis Porter	Aug. → ?	6.4		SL
Prunus angustifolia Marsh.	May → July	2.2		SL
Prunus munsoniana Weight	Aug. → Sept.	3.7		?
Prunus pennsylvanica L.f.	Aug. → Sept.	31.3		SL
Prunus pumilia L.	Aug. → Sept.	6.4		?
Prunus serotina Ehrh.	Aug. → Sept.	9.3		SL
Prunus virginiana L.	Aug. → Oct.	10.6	6.26† 3.89 5.70‡	SL
Rhamnus alnifolius L'Her.	Aug. → rapidly dispersed	144.4		FH
Rhus aromatica Ait.	Aug. → following summer	. . .		FL
Rhus copallina L.	Sept. → following summer	125.7	26.1	FL
Rhus glabra L.	Sept. → following summer	108.0	11.23† 22.4	FL
Rhus trilobata Nutt.	Aug. → following summer	44.7		FL
Rhus typhina L.	July → following summer	117.5	14.54†	FL
Ribes americanum Mill.	June → Sept.	690.0		SS
Ribes cynosbata L.	July → Sept.	451.9		SS
Ribes lacustre (Pers.) Poir	Aug. → ?	1,135.4		SS
Ribes missouriense Nutt.	June → Sept.	357.1		SS
Ribes rotundifolium Michx.	July → Sept.	. . .		SS
Rosa blanda Ait.	Sept. → Winter	. . .		FL
Rosa setigera Michx.	Aug. → Winter	110.2		FL
Rubus allegheniensis Porter	Aug. → Sept.	577.6		SS
Rubus canadensis L.	July → Sept.	477.3		SS
Rubus flagellaris Willd.	June → Sept.	288.8		SS
Rubus hispidus L.	Aug. → Oct.	409.0		SS

(*continued*)

TABLE 1 (*Continued*)

Species	Fruit Dispersal	Seeds/kg ÷ 1,000*	% Crude Fat	Fruit Type
Rubus idaeus L.	July → Oct.	723.1		SS
Rubus occidentalis L.	June → Aug.	736.3	7.58†	SS
Rubus odoratus L.	July → Sept.	1,086.9		SS
Sabal palmetto (Walt.) Lodd.	Oct. → ?	2.9		?
Sabal etonia Swingle	Oct. → ?	3.7		?
Sambucus canadensis L.	Aug. → Oct.	511.5	12.94† 16.0	?
Sambucus glauca Nutt.	Aug. → Oct.	451.9		?
Sambucus pubens Michx.	June → Nov.	630.5		?
Sapindus drummondii Hook and Arn.	Sept. → Winter	1.1		FL
Sassafras albidum (L.) Roxb.	Aug. → Sept.	12.8		FH
Serenoa repens (Bartr.) Small	Sept. → ?	2.4		?
Shepherdia canadensis (L.) Nutt	July → Sept.	90.4		?
Solanum dulcamara L.	Aug. → ?	771.6	28.77†	?
Sorbus americana Marsh.	Aug. → Mar.	352.7	4.66†	FL
Sorbus decora (Sarg.) Schneid.	Aug. → Mar.	280.0		FL
Symphoricarpos albus Blake	Sept. → Winter	167.5		FL
Symphoricarpos cocidentalia Hook	Sept. → Winter	164.0		FL
Taxus canadensis Marsh.	Aug. → ?	19.4		?
Vaccinium angustifolium Ait.	July → Aug.	4,348.0	3.80†	SS
Vaccinium caespitosum Michx.	July → Sept.	11,708.7		SS
Vaccinium croymbosum L.	June → Aug.	2,150.6		SS
Viburnum acerifolium L.	Aug. → Spring	28.9		FL
Viburnum alnifolium Marsh.	Aug. → Fall	25.3		FL
Viburnum cassinoides L.	Sept. → Nov.	60.8		FL
Viburnum dentatum L.	Sept. → Dec.	45.0		FL
Viburnum lentago L.	Sept. → May	13.0		FL
Viburnum prunifolium L.	Sept. → Mar.	10.6		FL
Viburnum rafinesquianum Schultes	Sept. → ?	...		FL
Viburnum recognitum Fern	Aug. → Dec.	...		FL
Vitis labrusca L.	Aug. → Dec.	33.3		FL

SUMMARY

	FRUIT CHARACTERISTICS				
FRUIT TYPE	No. of Species	Seed Size	Lipids	Sugars	Retention on Plant
Summer small-seeded (SS)	27	small	low	high	low
Summer large-seeded (SL)	5	large	low	variable	low
Fall high-quality (FH)	9	large	high	variable	variable
Fall low-quality (FL)	51	variable	low	low	high
Unknown	36				

NOTE.—SS = summer small-seeded, SL = summer large-seeded, FL = fall low-quality, FH = fall high-quality.

* Original source used "seeds per pound."

† Fleshy fruits and seeds.

‡ Seeds only.

TABLE 2

LATITUDINAL PATTERN OF BIRD-DISSEMINATED CANOPY TREES

Degrees Latitude °N	No. of Forests	No. of Tree Species	Mean % Bird-Disseminated Trees	SD
<35°	2	3	25.00	14.3
35°–36.5°	48	8	4.89	4.4
36.5°–38°	89	12	4.04	3.8
38°–39.5°	38	6	2.00	2.8
39.5°–41°	10	3	1.96	2.7
41°–42.5°	46	4	1.63	3.5
42.5°–44°	23	1	.06	.2
44°–45.5°	28	0	.00	.0
45.5°–47°	57	2	.04	.2

	Latitudinal Division								
Tree Species	<35°	35°–36.5°	36.5°–38°	38°–39.5°	39.5°–41°	41°–42.5°	42.5°–44°	44°–45.5°	45.5°–47°
Amelanchier laevis		x							
Celtis occidentalis		x	x	x		x			
Cornus florida			x						
Ilex opaca	x	x	x						
Magnolia acuminata		x	x	x	x	x			
Magnolia fraseri		x	x						
Magnolia grandiflora	x								
Magnolia macrophylla			x						
Magnolia tripetala			x						
Morus rubra	x	x	x	x					
Nyssa sylvatica		x	x	x	x	x			
Prunus serotina			x	x	x	x	x		x
Sassafras albidum		x	x	x					
Sorbus americana									x

some time during the year (table 3). The major frugivores (table 3) include members of three families, the mimic-thrushes (Mimidae), the thrushes (Turdidae), and the waxwings (Bombycillidae; Martin et al. 1951). With the possible exception of the cedar waxwing, even the major frugivorous species eat insects and feed insects to their young during the breeding season. All but the northern mockingbird are migratory, and all but the northern mockingbird and the brown thrasher feed primarily in forests.

To compare latitudinal patterns of bird density with bird-disseminated canopy trees I used the nine forest-feeding frugivores (table 3). Starlings may also be frugivores in the forest, but since they are introduced species and have not coevolved with the plant species they are not considered here. Data compiled from the Breeding Bird Survey (Van Velzen and Robbins 1971) show that these nine species as a group, breed in increasing numbers with increasing latitude in the eastern deciduous forest (fig. 1). Several of these species, especially the gray-cheeked thrush, have the center of their beeeding distributions located even farther north than the extent of the Breeding Bird Survey and all migrate south

TABLE 3

NATIVE FRUGIVOROUS BIRDS IN THE EASTERN DECIDUOUS FOREST
(data from Martin et al. 1951).

- Nonmigratory
  - Melagrididae
    - Turkey (*Meleagris gallopavo*)
  - Tetraonidae
    - Ruffed grouse (*Bonasa umbellus*)
  - Phasianidae
    - Bobwhite (*Colinus virginianus*)
  - Picidae
    - Pileated woodpecker (*Dryocopus pileatus*)
    - Red-bellied woodpecker (*Centurus carolinus*)
    - Downy woodpecker (*Dendrocopos pubescens*)
  - Corvidae
    - Common crow (*Corvus brachyrhynchos*)
  - Mimidae
    - Northern mockingbird (*Mimus polyglottos*)
- Migratory
  - Picidae
    - Common flicker (*Colaptes auratus*)
  - Hirundinidae
    - Tree swallow (*Iridoprocne bicolor*)
  - Mimidae
    - Brown thrasher (*Toxostoma rufum*)
    - *Gray catbird (*Dumetella carolinensis*)
  - Turididae
    - *American robin (*Turdus migratorius*)
    - *Wood thrush (*Hylochichla mustelina*)
    - *Hermit thrush (*Catharus guttatus*)
    - *Swainson's thrush (*Catharus ustulatus*)
    - *Gray-cheeked thrush (*Catharus minimus*)
    - *Veery (*Catharus fuscescens*)
    - *Eastern bluebird (*Sialia sialis*)
  - Bombycillidae
    - *Cedar waxwing (*Bombycilla cedrorum*)
  - Vireonidae
    - Warbling vireo (*Vireo gilvus*)
  - Parulidae
    - Yellow-rumped warbler (*Dendroica coronata*)
    - Yellow-breasted chat (*Icteria virens*)
  - Icteridae
    - Orchard oriole (*Icterus spurius*)
    - Northern oriole (*Icterus galbula*)
  - Thraupidae
    - Summer tanager (*Piranga rubra*)
  - Fringillidae
    - Cardinal (*Richmondena cardinalis*)
    - Rose-breasted grosbeak (*Pheucticus ludovicianus*)
    - Evening grosbeak (*Hesperiphona vespertina*)
    - Purple finch (*Carpodacus purpureus*)
    - Pine grosbeak (*Pinicola enucleator*)
    - Rufous-sided towhee (*Pipilo erythrophthalmus*)

* Major frugivores within forests.

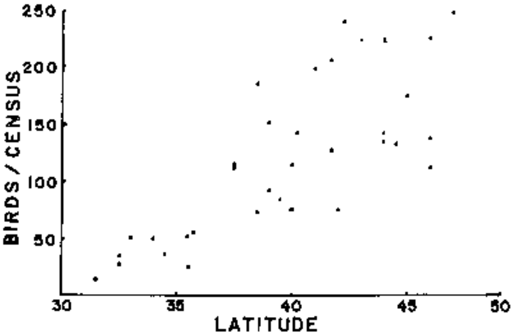

FIG. 1.—Major, frugivorous, breeding birds (table 3) at different latitudes in the eastern deciduous forest. Data points are average number of birds recorded from 50 stops along 25-mile routes in states and provinces in the eastern deciduous forest. Data are from 1,731 of these routes censused early in the breeding season in 1968 and 1969. The number of routes contributing to each point range from 3 (Rhode Island) to 175 (New York). The points below the mean for any latitude are generally the central states while those above the mean are the eastern states.

spending the winter in either the southern United States (American robin, cedar waxwing, hermit thrush, eastern bluebird) or in Central and South America (others).

BIRD MIGRATION

The flux of migratory frugivores over a latitude in the eastern deciduous forest varies inversely with latitude, and is a function of the number of breeding frugivores north of that latitude. As one moves south in this region there is an increasing probability that a point in the forest will be visited by a frugivorous bird. These species also migrate north in spring, but during the fall the number of individuals migrating is greater. Substantial mortality occurs both during migration and on the wintering grounds resulting in fewer birds available to eat fruits in the spring. Frugivores begin moving south in August, with peak migrant numbers passing in mid-September in the central portion of the eastern deciduous forest.

Mist-net captures (table 4) illustrate the relatively rapid movement of individuals. Densities are difficult to estimate from mist-net captures because some species are more readily captured than others, but maximum densities during migration can be high (table 5). Wood thrushes migrate earlier than the four species in table 4, but the dates are within the migratory period for the other species of primary frugivores (Baird et al. 1957, 1958).

TIMING OF FRUIT PRESENTATION

This peak migration of frugivorous birds coincides with the peak presentation of bird-disseminated fruits for woody plants in the central, eastern deciduous forest

TABLE 4

TEN-YR SUMMARY OF BANDING DATA FROM ISLAND BEACH STATE PARK, NEW JERSEY, FOR FOUR SPECIES OF FALL MIGRANT THRUSHES*

	DATE OF CAPTURE		
SPECIES	First 5% of Total No.	First 50% of Total No.	First 95% of Total No.
Veery	Aug. 28	Sept. 11	Sept. 27
Swainson's thrush	Sept. 7	Sept. 24	Oct. 8
Gray-cheeked thrush	Sept. 15	Sept. 28	Oct. 11
Hermit thrush	Oct. 4	Oct. 20	Oct. 31

* Bertram G. Murray, Jr., personal communication.

(fig. 2). The majority of bird-disseminated fruits ripen and become available for dispersal in August or September. These ripening times vary with latitude, and within species ripening generally occurs earlier at higher latitudes (U.S. Dep. of Agriculture, Forest Service 1974). I have estimated times of maturation at 40°N for this analysis. Many of these fruits remain attached to the plant until they are dispersed or dry up, but fruits of some species fall soon after ripening if they are not taken by birds.

Seeds of fruits eaten by birds are either disgorged or voided a relatively short time following ingestion. Walsberg (1975) found that passage through the digestive tract of *Phainopeplas nitens* took from 12 to 45 min for seeds of the desert mistletoe (*Phoradendron californicum*). Seeds which are disgorged probably are deposited even sooner. Gut passage time for blueberries in a hermit thrush was about 30 min (Bent 1949). Although there is a potential for long-term retention of seeds in the digestive tract, most seeds are moved relatively short distances. Birds' movements across different habitat types, increasing the diversity of seed deposition sites, may increase the probability for seed deposition in an earlier stage in the successional sere in which the plant can compete successfully. The quality of dispersal afforded seeds by dispersal agents is beyond the scope of this paper. Quality of dispersal involves aspects of seed treatment (McKey 1975) and the nature of the seed shadow generated by the dispersal agent (Janzen 1970). For later successional plants short distance movement within suitable habitat may

TABLE 5

FRUGIVORE DENSITIES ILLUSTRATED BY MIST-NET CAPTURES

Species	No. of Individuals	Net-hr	Birds/ Net-hr	Date	Location
Swainson's thrush	78	463	.168	Sept. 29, 1961	1
Swainson's thrush	111	568	.195	Sept. 24, 1964	1
Hermit thrush	93	353	.260	Oct. 24, 1964	1
Gray catbird	55	258	.258	Oct. 1, 1960	2

NOTE.—Location 1, Ocean City, Maryland; Location 2, Cape May, New Jersey.

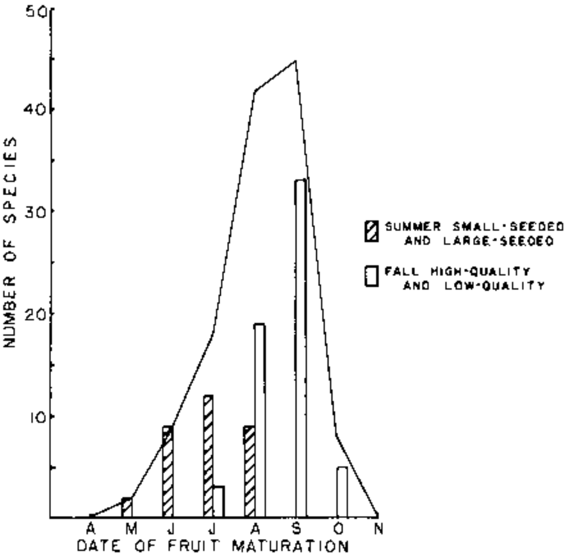

FIG. 2.—Timing of fruit presentation. Best estimate for the first month fruit is available for dispersal at 40°N. Species not occurring at this latitude are recorded on the month of first presentation nearest this latitude. Histogram: Dates of first presentation for summer small-seeded and summer large-seeded fruits (combined) and fall high-quality and fall low-quality fruits (combined).

provide better opportunities for success than larger distance dispersal. The minimum criteria for dispersal agent quality are that the seed is moved beyond the canopy of the parent and that the seed is not killed. During migration birds move through a greater diversity of habitats than when the birds are on their breeding territories. The quantity, or flux, of migrating frugivores increases as one moves south in the north temperate zone, and the quality of these birds as dispersal agents increases during migration because they are eating more fruits to supply the energy (lipids and carbohydrates) used for migration, and they are moving outside fairly uniform habitats.

NUTRIENTS IN FRUITS

Nutrients in fruits are in the form of carbohydrates, lipids, and proteins. Determinations of values for these nutrients in fruits in eastern deciduous forest are few (Wainio and Forbes 1941; Lay 1961; Short and Epps 1976, 1977). A range of percentage dry weight allocation to different nutrients is found in the species which have been measured. Lipid content varies from as low as 0.8% in *Vitis vulpina* L. (the value may be too high as the entire fruit, with seeds, was analyzed) to 47.82% for only the pericarp in *Lindera benzoin* (L.) Blume (Wainio and Forbes 1941; table 1). Lipids are high energy compounds, yielding twice the energy per gram upon catabolism as carbohydrates (Klieber 1961). The values of lipid content measured for *L. benzoin* are as high as any found for fruits fed upon by the oilbird

(*Steatornis caripensis*), a specialist frugivore, in Trinidad (Snow 1962), but not as high as some values obtained from *Stemmadenia donnell-smithii* (Apocynaceae) arils in Costa Rica (McDiarmid et al. 1977). The variation in lipid content and the differences in amounts packaged per fruit provide very different energy packets for birds.

Protein content of both temperate and tropical fruits is less variable than lipid content and is usually between 3% and 13% dry weight, making fruits poor protein sources compared with insects, which are usually above 70% dry weight (Snow 1971; Morton 1973). After young birds have attained adult size, protein requirements are lower and requirements for lipids and carbohydrates to develop subcutaneous fat deposits needed for migration increase.

Carbohydrates are the primary constituents of fruits, but analyses of the composition of these carbohydrates and interpretation of which ones can be used metabolically by birds are rarely available (McDiarmid et al. 1977), but one pattern can be determined. Some fruits contain higher concentrations of mono- and disaccharides than others and are sweet; these include the blueberries (*Vaccinium*), huckleberries (*Gaylussacia*), blackberries (*Rubus*), gooseberries (*Ribes*), strawberries (*Fragaria*), mulberries (*Morus*), and some others. Sweetness, and consequent use as cultivars, for these species sets them apart from the majority of bird-disseminated fruits. Their attractiveness to humans suggests that sweetness and other components of palatability may have evolved to attract mammals.

FRUITING PATTERNS

Removal from the vicinity of the parent plant has positive selective value by increasing probabilities of seed and seedling survival both by removal from direct competition with the parent (Harper et al. 1970) and by removal from potential predation (Janzen 1971; Smith 1975). I believe that competition for dispersal agents has molded the abundance of species in an area and the timing of fruit presentation for eastern deciduous forest species of bird-disseminated fruits.

I examined four variable characteristics of fruits for species in the eastern deciduous forest. These characteristics were seed size, amount of lipid, presence of sugars, and the length of time fruits are retained on the plants following ripening. Four fruiting patterns are apparent which exploit disperser availability. These four patterns fall, independently, at different times of year; two patterns fruit in summer and two in the fall (table 1, summary).

Summer small-seeded fruits.—These are characterized by fruiting early in summer (fig. 2), before the fall migration of frugivorous birds begins. They have small seeds (mean = 1,386,705/kg, range = 180,781–11,684,502/kg; table 1) with tough seed coats (Heit 1967) and fruits are usually borne within 2 m of the ground. These fruits are sweet. For some species in this group, like *Morus* and *Amelanchier*, which are larger trees or shrubs, the fruits fall soon after ripening. Resident mammals and birds feed on these fruits, and both groups serve as potential dispersal agents. The sweetness and odor in some instances serve as additional mammal attractants, characters which are absent from most bird-disseminated fruits (Van der Pijl 1972). Seed predation by mammals may be reduced by reducing energy gained per effort (Schoener 1971; Smith 1970), which is accomplished in summer small-seeded fruits through small seed size. Small seeds are easily passed through the digestive tracts of mammals and have been found in large numbers in intestinal tracts and fecal material of white-footed mouse (*Peromyscus leucopus*), red fox (*Vulpes fulva*), fox squirrel (*Sciurus niger*), black bear (*Ursus americana*), and many others (Martin et al. 1951; Gill and Healy 1974; U.S. Dep. of Agriculture, Forest Service 1974). *Peromyscus* and other species of smaller rodents, which are major seed predators on larger-seeded species (Abbott and Quink 1970; Smith 1975), ingest small seeds with the pericarp, passing them through the digestive tract in viable condition (Krefting and Roe 1949). They may also separate the seeds, consuming the pericarp but not the seeds. Seeds of these fruits are also dispersed by resident and breeding birds, especially ruffed grouse, gray catbird, American robin, and eastern bluebird.

Summer small-seeded species present fruit after the first broods of most frugivorous species have fledged, avoiding the more intense competition for dispersers encountered in the spring when insect protein is important for developing eggs and young (Morton 1973). They also fruit prior to the main migratory period. Although the early fledglings increase the number of available dispersers, and these birds are moving around more than their parents, they do not provide the quantity and quality dispersal of migrants. The fruits have evolved to attract resident birds and mammals as dispersal agents for their seeds.

Summer large-seeded fruits.—These are characterized by fruiting prior to fall bird migration, but in contrast to summer small-seeded fruits, they have large seeds (mean = 9,920/kg, range = 2,260–30,863/kg; table 1). These species are all in the genus *Prunus*, and differ from summer small-seeded fruits by the size of the seeds, which changes the functional relationship with small rodents from seed-disseminators to seed-predators. They differ also in the presentation height of the fruits, which is usually over 2 m. Those species of *Prunus* which have been analyzed have high percentage dry weight carbohydrates and low percentage dry weight lipids, similar to summer small-seeded fruits (Wainio and Forbes 1941; Short and Epps 1977).

Summer fruiting species, small- and large-seeded, have geographic distributions which extend farther north than many fall fruiting species. Comparing species which have ranges extending north of 45°N latitude with those which do not (table 6), a significantly greater number of summer fruiting species' ranges extend north of 45°N ($\chi^2 = 9.1$, df = 1, $P < .005$). Early fruit presentation in these species attracts resident frugivores, which are more abundant in the north, as well as early migrants. Large mammals, raccoons, opossums, foxes, skunks, etc., which eat fallen *Prunus* may have a significant effect on successful seed dissemination (Martin et al. 1951).

Fall high-quality fruits.—These fruits are characterized by presentation at the peak of fall bird migration. They have relatively large seeds (mean = 38,139/kg, range = 9,920–143,303/kg) and the pericarps are rich in lipids. *Cornus florida* with 16.17% lipid (Lay 1961) and *Lindera benzoin* with 47.82% lipid are two species in this group. *Rhamnus alnifolia* with 26.3% lipid is also a high-quality fruit (Short and Epps 1976, 1977). Fruit quality must be judged in terms of nutrients per fruit,

TABLE 6

DISTRIBUTION OF PLANTS WITH BIRD-DISSEMINATED FRUITS, NORTH AND SOUTH OF 45°N LATITUDE IN EASTERN NORTH AMERICA

	NO. OF SPECIES			
	Range Extending North of 45°N		Range not Extending North of 45°N	
Summer small-seeded	21	24	6	8
Summer large-seeded	3		2	
Fall high-quality	3	29	6	31
Fall low-quality	26		25	

NOTE.—For 2 × 2 contingency: $\chi^2 = 5.03$, df = 1, $P < .05$. Using distribution of fall-fruiting species for calculation of expected values: $\chi^2 = 9.10$, df = 1, $P < .005$.

number of fruits eaten in any period of foraging time, and the ratio of pericarp to seeds which must be carried in the digestive tract (McKey 1975). Values for these components are not available, but in some cases good guesses may be made concerning relative value for birds. *Rhus copallina* with 26.1% lipid, *Rhus glabra* with 22.4% lipid, and *Myrica cerifera* with 23.2% lipid, which were also measured by Short and Epps, have thin pericarps and are not classified as high-quality as the energy gain per fruit would be low.

Birds remove high-quality fruits rapidly after ripening. For *L. benzoin* in New Jersey 77.2% of the fruits in 1977 and 90.4% in 1978 had been dispersed by birds by October 31 after the fruit had ripened during the first 2 wk of September (Stiles, MS; table 7). However, for *Viburnum acerifolium,* which ripens during the last week in August in New Jersey, only 2.9% of the fruits had been dispersed by birds by October 31 (table 7). Smith (1975) measured temporal patterns of dispersal for several species from July 1 to November 15 in Illinois. His analysis was concerned primarily with species which are dispersed or drop rapidly in the summer and fall including *Prunus serotina, Cornus racemosa, Vitis labrusca, Rubus occidentalis, Rubus allegheniensis* and *Solanum dulcamara.* Species which fall or are dispersed so rapidly, however, are in the minority.

Fall low-quality fruits.—These include the majority of bird-disseminated fruits in the eastern deciduous forest. *Viburnum acerifolium* is representative of this group which is characterized by presentation at the beginning or at the peak of fall bird migration and by containing relatively low percentage dry weight lipids. Fruits of this group remain on the plant for long periods (table 1), and low rates of seed dispersal by birds continue well into winter. In a study of maple leaf viburnum (*Viburnum acerifolium*) in New Jersey, of 1,183 fruits in 1976–1977 and 2,260 in 1977–1978 on 25 shrubs, 79% and 72% of the fruits, respectively, remained on the shrubs on January 1 following ripening in late August. Of the missing fruits 20% (1976) and 19% (1977) had abscised and 10% (1976) and 9% (1977) had been disseminated by birds (Stiles and Meffe, in prep.). An additional example, not included in the woody plants, is the genus *Smilax.* Short and Epps (1977) measured nutrient content in five species of this genus of fall-fruiting,

TABLE 7

FATES OF FRUITS OF TWO SPECIES OF COMMON UNDERSTORY SHRUBS IN HUTCHESON MEMORIAL FOREST, NEW JERSEY

Species	No. of Fruits Prior to Ripening Date*	% Fruits Remaining on Oct. 31	% Fruits Abscised by Oct. 31	% Fruits Dispersed by Birds by Oct. 31	Total
Lindera (fall high-quality)					
1977	535	6.2	16.5	77.2	99.9
1978	1089	2.0 (0.5) †	7.6	90.4	100.0
Viburnum (fall low-quality)	2162	89.9	7.1	2.9	99.9

NOTE.—Data for 23 *Viburnum acerifolium* and 8 *Lindera benzoin* shrubs.

* Census date in wk prior to ripening for *Viburnum*, August 22; for *Lindera*, August 26.

† Of the 2.0% remaining, 1.5% were rotten.

long-persisting fruits. Mean crude fat content was 6.28% with a range of 4.1% to 8.2%.

These fruits become available when migrant frugivores are moving south, but the fruits are lower in nutrient reward and are less attractive to birds than the high-quality fruits (table 1). Flowering times and fruiting times of these plants are not related in any consistent fashion, as different selective pressures are operating on timing of flowering and fruit presentation. Fruit maturation may begin immediately following flowering as in *Vaccinium*, *Amelanchier*, and *Rubus* or may be delayed for several months as in *Viburnum*, *Lindera*, *Cornus*, and *Juniperus*. The diversity of the interval between flowering and fruiting has also been noted by Snow (1971) for deciduous forests in Europe.

I tested the null hypothesis that fruiting time is a consequence of flowering time, and that the diversity of fruiting times is a consequence of selection for diversity in flowering time. If this is correct the mean flowering to fruiting interval should not be different for summer- and fall-fruiting species. There is, however, a significant difference in mean flowering to fruiting interval ($t = 5.76$, df $= 87$, $P < 0.001$). Mean flowering to fruiting intervals were 2.25 mo ($N = 32$) for summer-fruiting species and 3.91 mo ($N = 57$) for fall-fruiting species.

DISCUSSION

The fruiting patterns discussed above may be under disruptive selection in two different ways. First, summer large-seeded fruits have seeds over two orders of magnitude larger than summer small-seeded fruits. Intermediate-sized seeds may be at a selective disadvantage under predation pressure from small rodents. This could lead to the dichotomy found in seed size of summer fruits.

High levels of predation by mammals, primarily *Peromyscus* and *Tamias*, on large seeds of fall-ripening fruits greatly reduce the probability of seed survival if the fruits fall from the plant (Janzen 1970, 1971; Smith 1975). Stiles and Meffe (in prep.) found for *Viburnum acerifolium* that the probability of seed being found by

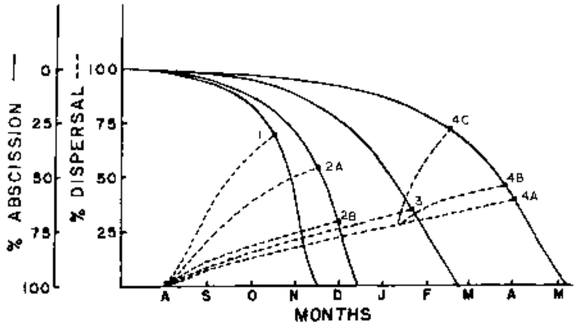

FIG. 3.—Abscission rates (solid lines) and dispersal rates (dashed lines) for 4 hypothetical bird disseminated plants. Points on the curves represent the point in time when no fruits remain on the plants. 1 = fall high-quality fruit; 2A = fall high-quality fruit (lower quality than 1) when fruit species 1 is scarce; 2B = fall high-quality fruit when fruit from species 1 is abundant; 3 = intermediate quality fruit; 4A = fall low-quality fruit during mild winter conditions; 4B = fall low-quality fruit with a short period of time when other resources for frugivores are unavailable; 4C = fall low-quality fruit during very severe winter weather conditions, when other resources for frugivores are unavailable.

Peromyscus increased, on a per seed basis, as seed density increased. Similar results were found for *Prunus serotina* and *Vitis riparia* (Smith 1975). Mice and chipmunks are potential dispersal agents for seeds but even if seeds are not eaten immediately most of the cached seeds are found later and consumed (Abbott and Quink 1970). Therefore, for fall-fruiting species, selection to remain attached to the plant and available for bird dissemination would be high, so long as fruit rotting does not occur.

Second, why don't all plants produce high-quality fruits if percentage dispersal for them is so high? In addition to being attractive to dispersal agents, fruits with high nutrient levels may also be attractive to various microbes (Janzen 1977). The length of time a fruit can remain on a plant, without being rendered unacceptable to birds through attack by microbes and subsequent change in the physical or chemical nature of the fruit, may be inversely proportional to nutrient content (fig. 3). If the nutrient content of a fruit is intermediate and if percentage dispersal is lower during the migratory period than for high-quality fruits, then the more rapid rotting (microbial invasion of these intermediate fruits coupled with the decreased dispersal rates following the migratory period) may result in lower total dispersal of intermediate fruits than of fruits with low nutrient content. Selection for this pattern would be strengthened by increased dispersal rates in midwinter when other food sources become scarce (fig. 3). This would be especially true during periods of snow cover when many other food types are not available (Ridley 1930). Data from *Viburnum acerifolium* in New Jersey support this hypothesis, as in both winters 1976–1977 and 1977–1978 when snow cover was correlated with marked increases in dispersal by birds (Stiles and Meffe, in prep.).

It is more realistic to consider reproductive output, rather than seed number, as constant, in which case plants producing low-quality fruits could produce more

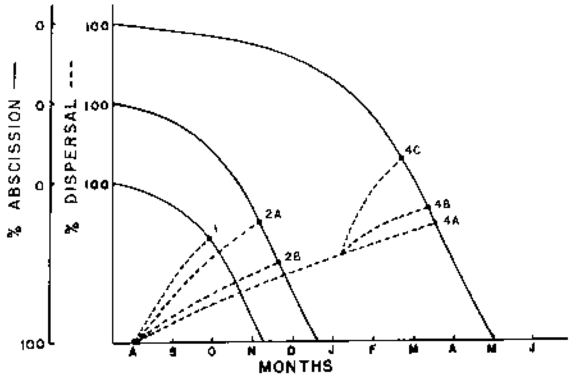

FIG. 4.—Abscission rates (solid lines) and dispersal rates (dashed lines) for 3 hypothetical bird-disseminated plants. Points defined as in fig. 3. Curves drawn on three different different scales to illustrate the numerical differences in numbers of seeds dispersed (see text).

fruits (fig. 4). Even lower percentage dispersal in low-quality fruits would result in similar numbers of seeds disseminated in both low- and high-quality fruits.

The summer small-seeded fruits which provide high sugar content are also open to rapid microbial invasion. With high sugar content and high temperatures, fruits are invaded by fungi and yeasts which convert sugar to ethanol, reducing the acceptability to dispersal agents (Janzen 1977, 1979). High sugar content may be a necessary trade-off to attract both mammals and birds during a period of relatively high food availability, but may lower the length of time the fruits remain acceptable to dispersers.

One mechanism available to plants to increase the time a fruit will remain acceptable for birds is the evolution of toxins which reduce or prevent microbial attack. Most of these are lost during the process of maturation (Eckert and Sommer 1967) as they may also deter dispersal agents, but differential spoilage rates are apparent in different species of fruits. Some species, including *Rubus*, *Prunus*, and *Sassafras* appear to spoil rapidly, whereas *Lindera*, with evident volatile secondary compounds may remain on the plant longer without spoiling (personal observation).

There are many selective pressures influencing seed size other than predation. Microsite availability for seed germination and early competitive ability under different environmental conditions exert selective pressures on seed size. Patterns for fleshy fruits considered here, however, suggest that rodent seed-predators may be important selective agents. Fall low-quality fruits which are presented near the ground, like *Gaultheria procumbens*, *G. hispidula*, and *Mitchella repens*, have small seeds (table 1). *Cornus canadensis*, the only dogwood which presents fruit close to the ground, has seeds about 0.28 times the weight of the next largest seeds of *C. rugosa* and 0.07 times the weight of *C. florida*. Smaller seeds in these, as well as in summer-generalist fruits, may be an evolutionary response to both mouse predation and the importance of mice as seed dispersal agents. Larger-seeded fruits, especially those which are retained on the plant for long periods, are often placed on slender pedicels, in locations with poor accessibility to climbing rodents.

All species do not fall neatly into the patterns presented above. For example, species of *Sambucus* are intermediate between two patterns; they have fall presentation, small seeds, are not retained on the plant for long periods, and the one species which has been measured, *Sambucus canadensis,* has lipid content of 16.0% (Short and Epps 1977). This may be interpreted in the context of the above model as higher energy fruits produced to attract fall migrants, and small seeds to lower mouse predation or increase mouse dispersal of seeds when the fruits fall. Early fruit drop may be adaptive, as the higher nutrient fruits of *Sambucus* would rot more rapidly, becoming unacceptable to birds. Other species may also have temporally separate dispersal agents, such as *Vitis labrusca,* some of the fruits of which fall soon after ripening. Large numbers of *Vitis* are eaten by birds during migration (Smith 1975) and those that fall are consumed and seeds are dispersed by larger mammals (Van Dersal 1938; Martin et al. 1951).

SUMMARY

I have examined presentation and dispersal of bird-disseminated fruits of woody plants in the eastern deciduous forest in terms of available dispersal agents. Timing of fruit presentation and latitudinal patterns in fruit abundance are correlated with fall migration of frugivorous birds.

I have divided bird-disseminated fruits into four patterns based on characteristics of nutrient content, seed size, and persistence on the plant. Summer small-seeded and large-seeded fruits employ a mixed group of bird and mammal dispersers outside the migratory period, avoiding mammalian seed predation through either very small or very large seed size. Fall high-quality fruits are presented during fall bird migration. They are taken by birds in high numbers but are subject to rapid invasion by microorganisms. Fall low-quality fruits are presented during fall bird migration, but in competition with high-quality fruits and insects they achieve only low levels of dispersal at this time. This is coupled with long persistence on the plants and low rates of dispersal over winter which is allowed by low invasion rates by microorganisms. Dispersal of these species may increase sharply if other resources become scarce. A graphical model for disruptive selection in high- and low-quality fruits is presented and intermediate fruit types are discussed in terms of the postulated selective pressures.

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