

THE SELECTION AND USE OF FRUIT BY BIRDS IN AN EASTERN FOREST

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The fruit crops of a number of temperate forest plants that are eaten by birds ripen in the late summer or early fall and become available just before the main southbound migrations of many facultatively frugivorous birds. The fruit that remains at the end of the migratory period constitutes a major food resource for wintering bird populations. Few studies quantify differential use of fruit (Pulliam and Enders 1971). The research reported here was motivated by many questions. Are all types of fruit harvested simultaneously, or do some types disappear before others? What fraction of the original standing crop remains into the winter for harvest by resident populations? Do the food habits of resident species change as the relative abundances of different fruits vary through the winter?

STUDY AREA AND METHODS

In order to gain insight into the above questions, I studied the feeding habits of birds in a 600 ha tract of woods belonging to the Institute for Advanced Studies in Princeton, Mercer Co., New Jersey in the fall and winter of 1974-75. I found 23 species of fruit-bearing plants in the woods and along its margins. The species composition varied in different successional stages and with different moisture and soil conditions. To take into account the variety of stand types represented in the forest, I chose study sites in 3 different, relatively homogenous areas.

The first study area comprised 235 m² in an area grown in young red maple (*Acer rubrum*) and white oak (*Quercus alba*) with American beech (*Fagus grandifolia*) and some flowering dogwoods (*Cornus florida*); the diverse understory included mapleleaf viburnum (*Viburnum acerifolium*), false Solomon's seal (*Smilacina racemosa*), spicebush (*Lindera bensoin*) and Virginia creeper (*Parthenocissus quinquefolia*). In this plot, only the mapleleaf viburnum and false Solomon's seal produced fruit.

The second plot was 470 m² of white oak, tuliptree (*Liriodendron tulipifera*) and shagbark hickory (*Carva ovata*), with subcanopy of flowering dogwood, blackgum (*Nyssa sylvatica*) and American beech. Understory included mapleleaf viburnum, New York fern (*Thelypteris noveboracensis*), greenbrier (*Smilax rotundifolia*), false Solomon's seal and spicebush. The dogwood and blackgum trees produced fruit, but most of the blackgum berries had already dropped when the study began. The viburnum, false Solomon's seal and spicebush had fruit.

The third plot was 470 m² of floodplain forest near the Stony Brook River. An open canopy of 2 large white oaks with box elders (*Acer negundo*) beneath allowed much sunlight to pass through. Understory was mostly tall, woody spicebush and vine poison ivy (*Rhus radicans*) densely entwined the trunks of the oaks. Both the spicebush and poison ivy produced large crops of berries.

All fruit on each plant in the 3 plots was counted at the outset of the study, as were the berries on 8 spicebushes in different parts of the floodplain study area (Table 1). Fruits (usually 30/species) were dried in an oven to constant weight, and then seeds were removed to give dry weight.

TABLE 1
FRUIT AVAILABLE IN THE STUDY PLOTS

Plants	Study plots					
	Red maple		Oak-Hickory		Floodplain	
	fruits/ha	g/ha	fruits/ha	g/ha	fruits/ha	g/ha
<i>Smilacina</i>	6300	190	320	9.6	—	—
<i>Viburnum</i>	10000	110	7800	78	—	—
<i>Lindera</i>	0	0	620	31	74000	3700
<i>Cornus</i>	0	0	3500	350	—	—
			68000 ^a	6800 ^a		

^a *Cornus* in a 36 m² area under a gap in the canopy in the study plot.

I continued counting all fruits in the red maple and oak hickory plots until almost all of the fruit had been eaten, or had dropped from the plants. Because of the large crop in the floodplain, subsequent counts were made of berries on 8 spicebushes in different parts of the study area. Counts were also made of a patch of false Solomon's seal berries in a clearing near a path, and of Dogwood berries in another section of the oak-hickory forest, to compare with results from the study plots (Table 2). Poison ivy fruit was too small to count. The fraction of the original crop remaining was estimated by visual inspection and by comparison of photographs of the same patches taken on different days.

Other abundant fruits eaten by birds growing in woodland edge and riparian situations outside the study plots included Asiatic bittersweet (*Celastrus orbiculatus*), Japanese honeysuckle (*Lonicera japonica*), 4 species of grapes (*Vitis* spp.) and greenbrier. Productivity of these plants was difficult to measure because of their patchy distribution, difference in the productivity of different patches, and because many of the fruits were high above the ground. I searched for patches of these species at the outset of the study, and estimated the fractions of the original crops remaining on subsequent dates.

From 25 September 1974, until 28 March 1975, I made 2 or more trips to the woods per week to record feeding observations. On 23 November, at the end of fall migration, I began weekly counts of birds along a 2100 m census route through oak-hickory and red maple forest near the study areas, then through the floodplain forest, and back to my starting point, along an open field at the edge of the woods. All birds heard and seen within 30 m on either side of my route were counted. The total area included in the census was approximately 10 ha. Each bird seen eating 1 or more fruits constituted 1 observation (see Appendix).

RESULTS

Fruit productivity in the forest.—The greatest fruit production occurred in the most open parts of the forest (Table 1). The counts from the study plots and estimates of other crops are incorporated in Fig. 1. Differences in the amount of dropped fruit which was subsequently eaten by birds varied with different species and different habitats, and was exceedingly difficult to quantify. Of fruits dropped mid- to late November, I saw no birds eating the fruit of false Solomon's seal, and only once that of ma-leleaf viburnum. Dropped spicebush berries were eaten sparingly, except

TABLE 2
NUMBERS OF BERRIES REMAINING IN STUDY PLOTS ON SUBSEQUENT DATES

<i>Red maple study plot</i>					
Date	<i>Viburnum</i>	<i>Smilacina</i> (in plot)	<i>Smilacina</i> (in clearing)		
29 Sept.	259	145	—		
7 Oct.	259	126	274		
19 Oct.	—	65	208		
29 Oct.	256	59	156		
6 Nov.	225	55	148		
22 Nov.	22	40	*		
<i>Oak-Hickory study plot</i>					
Date	<i>Viburnum</i>	<i>Smilacina</i>	<i>Cornus</i>	<i>Cornus</i> (second patch)	<i>Lindera</i>
9 Oct.	392	16	398	—	31
17 Oct.	—	12	375	—	12
29 Oct.	339	12	66	273	8
6 Nov.	—	*	36	101	7
14 Nov.	210	—	24	70	—
22 Nov.	—	—	21	51	—
3 Dec.	112	—	—	—	—
<i>Floodplain study plot</i>					
Date	<i>Lindera</i> (8 selected bushes)				
22 Oct.	573				
31 Oct.	503				
6 Nov.	408				
15 Nov.	289				
22 Nov.	75				

* *Smilacina* stalks were covered by fallen leaves.

by a flock of White-throated Sparrows (*Zonotrichia albicollis*) on 12 December. Although grapes and dogwood berries fell steadily beginning in late September, these plants usually grew in open areas where fallen fruits were visible, and eaten by birds until crops were nearly exhausted.

The use of fruit by fall and winter birds.—Twelve of the 13 commonest migratory species and 11 of the 19 resident species seen between 25 September and 14 November were observed eating fruit, and many of these species were almost wholly frugivorous during this period. Dogwood was the largest and most widely used crop. Large flocks of migratory American Robins (*Turdus migratorius*) and Common Grackles (*Quiscalus quiscula*) fed on dogwood in woodland edge, where fruit production was heaviest. As the berries began dropping, 10 species of birds ate them from the

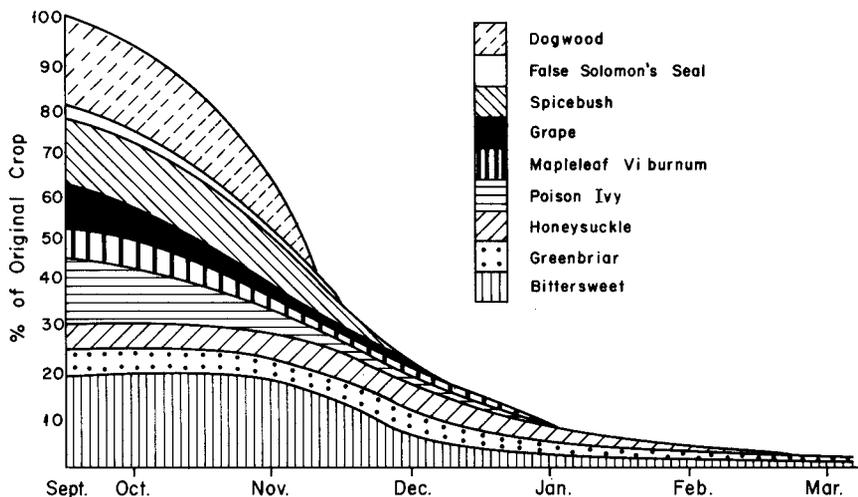


FIG. 1. The times at which different fruits dropped or were consumed by birds. The total height of the curve represents the fraction of the original crop remaining; the widths of the individual sectors show how much of the total is composed of each species. The curve is steepest in late September, October and early November, when bird density in the woods was highest. By the time the last migrants left in mid-November, the crop had been reduced to approximately 30% of the original total.

ground. By mid-October, most of the berries along the woodland margins had been eaten, and the flocks moved into the forest, congregating in small patches and eating all available dogwood berries. The disappearance of patches of dogwood fruit was so abrupt that only 1 dropped berry could be found in the study plot on 6 November (Table 2). By this time, most of the migrants had gone and no more than 10% of the original dogwood crop remained on the branches and the ground to be eaten by winter residents.

Grapes were used extensively by 8 species. Robins and grackles fed on grapes from vines, limbs of nearby trees and the ground in September and October. An estimated 90% of the crop had fallen by 23 November. Cardinals (*Cardinalis cardinalis*) fed on remaining partly-dried grapes until mid-December. Poison ivy berries were eaten by 10 bird species. This fruit grows in conspicuous clusters, is slow to fall, and may have been the most fully used of any of the fruits in the forest.

Bittersweet, a major crop along the forest paths and margins, was the last fruit to ripen (late September to early October), and lasted to late March. The berries began dropping in early November, and were eaten both from the vine and the ground by all frugivorous winter residents. The persistent fruits of Japanese honeysuckle and greenbrier were important

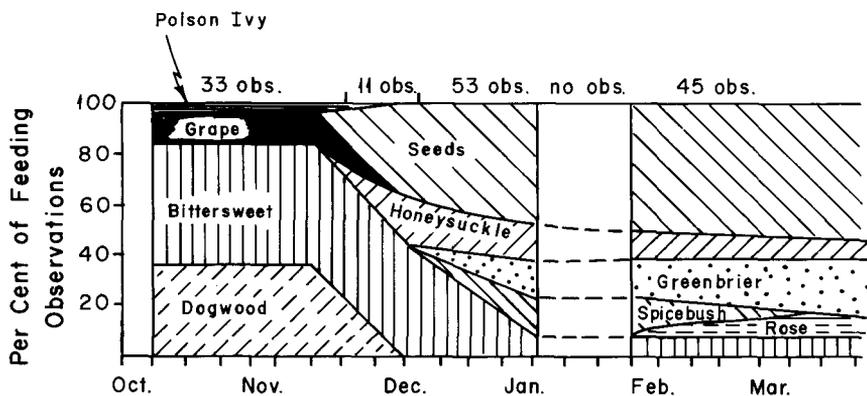


FIG. 2. The foods of the White-throated Sparrow.

late winter and early spring foods for Cardinals and White-throated Sparrows (Fig. 2). Honeysuckle berries lasted until late February, while the firm greenbrier fruits were retained through the winter, until most of them had been eaten.

Feeding ecology of wintering birds.—The depletion of dogwood berries and grapes in late October coincided with the departure of many of the migratory birds. Perhaps a causal relationship exists here. Further study over a period of several years would be required to test this idea.

Later migrants, including robins, Hermit Thrushes (*Catharus guttata*), Rusty Blackbirds (*Euphagus carolinus*) and Yellow-rumped Warblers (*Dendroica coronata*), fed on bittersweet and poison ivy fruits. The last migrant to leave, in mid-November, was the Yellow-rumped Warbler. Between the third week of November and the end of February, the bird species composition and abundances fluctuated very little. During this period the forest interior was inhabited almost exclusively by bark and twig feeding birds—Black-capped Chickadees (*Parus atricapillus*— Fig. 3), Tufted Titmice (*Parus bicolor*), Downy (*Picoides pubescens*) and Hairy (*P. villosus*) woodpeckers, White-breasted Nuthatches (*Sitta carolinensis*), Brown Creepers (*Certhia familiaris*) and Golden-crowned Kinglets (*Regulus satrapa*). The only other birds observed in this part of the forest during these months were a robin, 2 Hermit Thrushes and an occasional Blue Jay (*Cyanocitta cristata*), or Winter Wren (*Troglodytes troglodytes*).

Frugivorous winter residents.—The frugivorous winter birds foraged almost exclusively along margins and in clearings in the forest, showing marked seasonal changes in their diets and a high degree of overlap in foods eaten (Figs. 2, 3). The most common of these species were White-throated Sparrows, Cardinals and Dark-eyed Juncos (*Junco hyemalis*).

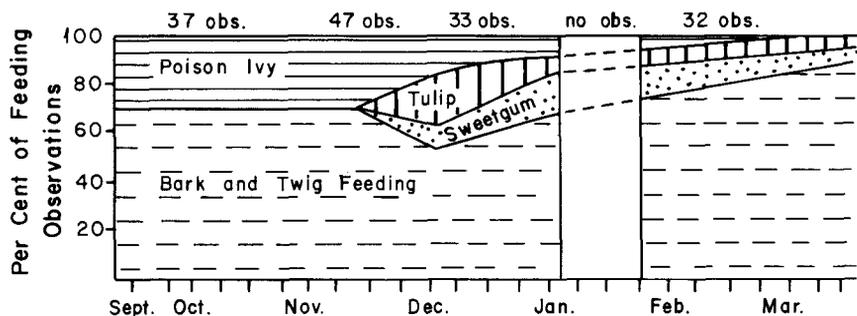


FIG. 3. The foods of the Black-capped Chickadee.

The use of fruit by these species has been noted previously (Martin, Zim and Nelson 1951).

White-throated Sparrows (Fig. 2) arrived for the winter in mid October. They almost always foraged in groups; often in mixed-species flocks. In late March they commonly fed on surficial seeds along edges of fields and in grass and shrubs around a marsh, in association with juncos, Song Sparrows (*Melospiza melodia*) and Mourning Doves (*Zenaidura macroura*). From September until early November, Cardinals were frequently seen and heard in thickets and vines along the banks of streams on the floodplain. Grapes were their primary food during the fall. As the supply of grapes was depleted, Cardinals switched to bittersweet fruit from vines along the fields, dried blackberries (*Rubus allegheniensis*) and seeds of bur-marigold (*Bidens cernua*) and ailanthus (*A. glandulosa*) from around the marsh. From December until February, Cardinals frequently fed in greenbrier and honeysuckle thickets and foraged on the ground with White-throated Sparrows and juncos. In March they began feeding in fields and on lawns, and on the growing buds of the trees around the marsh. Juncos usually foraged on the ground in small flocks. In the fall they ate fallen berries on the paths, insects from fallen logs and branches, and the seeds of weeds and grasses. During the winter they relied more heavily on seeds, usually feeding in the grass along the edges of the woods.

Relationships among species.—During the fall and winter, birds of different species often used the same foods (see Appendix). Differences in macrohabitat choices minimized competition for food. For example, in early fall, flocks of robins fed on dogwood berries in the margins and clearings, while Hermit and Wood thrushes (*Hylocichla mustelina*) remained deeper in the woods. White-throated Sparrows and juncos arrived later in the fall, and they joined the robins in eating dogwood fruit on the edges of the woods and in the paths. As that was used up, the robins

moved deeper into the forest to eat dogwood, but the sparrows and juncos switched to other foods.

Different species were also observed dividing a common resource by using different feeding stations within a habitat. Robins and grackles ate dogwood berries from perches in the larger branches of trees and from the ground, while sparrows fed on smaller branches and thin vines. Juncos were seen eating berries only on the ground. Among the species that ate poison ivy berries, Yellow-rumped Warblers fed on the extreme tips of branches, while Downy, Hairy and Red-bellied (*Melanerpes carolinensis*) woodpeckers, and Common Flickers (*Colaptes auratus auratus*) foraged from larger branches near the trunk.

Mixed species flocking.—Mixed flocks of chickadees, titmice, Downy Woodpeckers and Golden-crowned Kinglets formed during the winter. White-throated Sparrows, Dark-eyed Juncos and Cardinals often foraged in groups on the ground and in low shrubbery. While there was some overlap in the foods eaten, divergent foraging methods and differences in microhabitat use were observed. The frequency of observation of interspecific flocking was greatest from early December until the second week in February, and declined as spring approached.

Mixed flocks of wintering birds have been noted by a number of observers (Short 1961, Morse 1970, Kear 1972). Two main explanations have been hypothesized: (1) flocking enhances feeding efficiency by minimizing duplication of effort in foraging (Cody 1971); (2) flocks aid in predator avoidance (Murton 1971, Lazarus 1972, Morse 1977). Powell (1974) demonstrated that individuals in flocks spend more time searching for food and less time in surveillance than lone individuals (see also Sabine 1949, Turner 1965). Flocking seems particularly advantageous in exploiting foods that are stationary, non-renewing, with patchy distribution, as were the apparent principal winter food resources available in the area studied.

DISCUSSION AND CONCLUSIONS

Basis of food preferences.—In temperate forests, many fruits become ripe in autumn, when arthropods are harder to find and bird populations are largest due to the influx of migrants. The conspicuous colors and high nutritional values of fruits have probably evolved to attract birds to disperse seeds (McAtee 1947, Snow 1971). In this study, birds preferred some fruits over others found in the same parts of the forest. Dry weights of 10 of the most common fruits in the forest were compared. Dogwood and grape, 2 of the most preferred fruits in early fall, also had the heaviest dry pulps.

Differences in the nutritional values of fruits may influence feeding preferences (Morton 1973, Pulliam 1975); they may also be outweighed by

other factors. With the exception of spicebush, the most abundant fruits were also the most heavily used (see predictions made in Emlen 1966 and Pulliam 1974). Eugene S. Morton (pers. comm.) noted the relationship between bird species that occur in large, monospecific flocks (e.g., robins and grackles) and their use of abundant concentrated fruit, such as dogwood, and suggested that social behavior, rather than nutrition, may restrict these species to certain foods. Jerome Jackson (pers. comm.) noted that the relative accessibility of fruits may also be a factor (e.g., false Solomon's seal and mapleleaf viburnum, which have berries on stalks that will not support a bird, were rarely used). During the late fall and winter, when food was scarce, the most valuable foods were those retained longest by the plants.

I have shown that the available fruit crops are subject to uneven harvest. Preferred species, such as dogwood, grapes and poison ivy, are avidly consumed by a wide variety of migrant and resident birds. The crops of these fruits were virtually exhausted before the end of the migratory period. Other species, including the less accessible fruits noted above, are eaten infrequently, if at all. Other species, including bittersweet, greenbrier and honeysuckle are persistent and provide a major resource for wintering populations. The total amount of fruit remaining on 7 December was estimated to be 20% of the initial standing crop of all species noted on 25 September.

The diets of the resident species change through the season. As the preferred foods are exhausted or become depleted, new items are added to their diets, including fruits that had previously been ignored. Winter resident frugivores tend to be dietary generalists, although several species consume the available foods in different proportions.

SUMMARY

I estimated the standing fruit crop in a mixed deciduous forest in Princeton, New Jersey at the beginning of fall migration in September 1974 and at frequent intervals until mid-March 1975. I made weekly counts of birds and recorded feeding observations throughout the fall and winter to determine how the fruit crop was used by migratory and resident species. Abundant, concentrated fruits, such as dogwood berries and grapes, were consumed by many bird species and were heavily depleted by the end of the migratory period. Other fruits found in the same parts of the forest fell to the ground uneaten. I estimated that only 20% of the original fruit crop remained on 7 December.

As the preferred fruits were exhausted, the wintering birds added new items to their diets. These included the persistent fruits of several species which had previously been ignored. Mixed-species flocking was common among frugivorous birds during the winter months.

ACKNOWLEDGMENTS

I am grateful to John Terborgh for his guidance and assistance during the study. I thank E. S. Morton, J. A. Jackson and J. C. Barlow for their advice on earlier drafts of the manuscript.

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APPENDIX
CONTINUED

Species	Spicebush		Greenbrier		Japanese Honeysuckle		
	No. of obs.	Date of obs. 1st last	No. of obs.	Date of obs. 1st last	No. of obs.	Date of obs. 1st last	
Rusty Blackbird	1	12/12	6	12/12	2	21/12	5/3
Cardinal							
Black-capped Chickadee							
Mourning Dove	1	25/9					
Purple Finch							
(<i>Carpodacus purpureus</i>)							
Yellow-shafted Flicker							
Common Grackle					1	26/2	
Dark-eyed Junco							
Mockingbird							
(<i>Mimus polyglottos</i>)			1	12/12			
American Robin	21	25/9					
Starling							
(<i>Sturnus vulgaris</i>)							
White-throated Sparrow	20	12/12					
Hermit Thrush	1	26/11			24	22/11	21/2
Wood Thrush							
Tufted Titmouse							
Rufous-sided Towhee							
(<i>Pipilo erythrophthalmus</i>)							
Yellow-rumped Warbler							
Cedar Waxwing							
(<i>Bombicilla cedrorum</i>)							
Downy Woodpecker							
Hairy Woodpecker							
Red-bellied Woodpecker							
Red-eyed Vireo	1	25/9					
(<i>Vireo olivaceus</i>)							