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Spatial and temporal variation in fruit use by wildlife in a forested landscape

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Abstract

We monitored production and removal rates of fruit from 22 common plant species over 2 years in five habitats of a managed landscape in South Carolina (USA). Our long-term goal is to determine the importance of fruit as a resource for vertebrates and to provide recommendations for management of key species and habitats. This study lays the foundation for that goal by documenting fruit production and availability, variation in use by wildlife, and how these factors vary by plant species, habitat, and season. Six species produced >1 kg dry mass of pulp per hectare per year. Vertebrates consumed $\geq 50\%$ of fruits in 17 of the 22 plant species. Fruit loss to insects and microbes was generally small and varied significantly among seasons, being lowest in fall and winter. The length of time ripe fruit survived on plants varied among species from 3 to 165 days. Survival time of fruits did not vary significantly among habitats but was significantly shorter in the summer than in fall or winter. Approximately, half the species produced fruit in the fall and winter and these fruits were primarily consumed by over-wintering wildlife. This pattern is inconsistent with the general belief that fruit production in the eastern United States is timed to correspond with periods of high bird abundance during fall migration. Production and consumption of winter fruits deserves further attention from forest managers, as relatively little other food is available in winter, energy demands of over-wintering birds are high, and current management practices often reduce fruit availability of key species (e.g., *Myrica cerifera*). We suggest that fruit is more important than generally realized in maintaining vertebrate diversity in temperate forests and that the focus of managers on hard mast production should be broadened to include fruiting plants.

Keywords: Migratory birds; Frugivory; Fruit consumption; Fruit phenology; Fruit production; Managed forests; Savannah River Site

1. Introduction

Terrestrial habitats in eastern North America produce abundant quantities of fleshy fruits, yet relatively little is known about how much of this fruit is consumed by wildlife or how long fruit remains available after it is produced. The availability and use of this resource is a prerequisite for understanding how important fruit is in maintaining healthy and diverse communities of fruit-eating animals, especially migratory birds and other non-game wildlife. The importance of fruit as a food resource has received relatively little attention in North America where even the most frugivorous species, Cedar Waxwings (*Bombycilla cedrorum*), American Robins (*Turdus migratorius*) and Yellow-rumped Warblers (*Dendroica coronata*),

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are only seasonally so, supplementing their diets with insects and other invertebrates for most of the year (Martin et al., 1951; Wheelwright, 1986; Witmer, 1996). This is in marked contrast to the diverse communities of more strictly frugivorous birds found in tropical habitats (Moermond and Denslow, 1985; Terborgh, 1986; Fleming et al., 1987; Karr et al., 1990; Levey et al., 1994). The reliance of tropical frugivores on fruiting plants throughout the year clearly demonstrates the importance of fruit as a food resource in the tropics, but the lack of an equivalent obligate frugivore guild in North America makes it difficult to assess the importance of fruit as a food source for North American birds.

Despite the lack of a strictly frugivorous guild, many species in eastern North America do include fruit in their diet on a seasonal basis (Martin et al., 1951). Included among these are many migratory and game species of interest to resource managers (Wright, 1941; Willson, 1986; Skeate, 1987; Parrish, 1997). Fruit may be more important than previously realized in maintaining diverse communities of wildlife, especially birds, the majority of which include at least some fruit in their diets (Martin et al., 1951; Willson, 1986; Parrish, 1997). From the perspective of wildlife management, fruit has many advantages as food source. Compared to many other food sources, fruits are easy to find and capture, and are high in energy (i.e., sugars and/or lipids: Snow, 1971; Morton, 1973; Stiles, 1980, 1993; Borowicz and Stephenson, 1985; Johnson et al., 1985; Willson, 1986; Borowicz, 1988; White, 1989; Bairlein, 1990). In addition, many fruits are available during autumn and winter, when energy demands of wildlife are high and other food sources, such as insects, are generally less abundant (Morton, 1973; Thompson and Willson, 1979).

We offer a community-based study of fruit production and consumption. Our work is placed in the context of managed forests. We believe that it is especially important to understand the role of fruit as food for wildlife in managed forests because these lands occupy large areas and because they are managed for multiple purposes, including conservation of non-game wildlife. Yet, management activities may have conflicting goals. Of particular interest, in this context is the fact that current management practices in the southeastern United States often directly suppress fruiting plants through mechanical removal, prescribed burning, and chemical herbicides to remove under- and mid-story plants (e.g. Kalmbacher et al., 1993; Boyer, 2000; Haywood et al., 2000; Shelton and Cain, 2000). Although these activities are often intended to benefit some wildlife species, the importance of lost fruit resources needs to be evaluated. While the impacts of various management practices on habitat use by wildlife in the southeastern United States has received attention (Hamel et al., 1982; Hunter et al., 1993; Kilgo et al., 1998, 1999), how these practices impact food supplies important to different groups of species is not adequately understood (Thill, 1990; Greenberg and McGrane, 1996; Perry et al., 1999). A more detailed understanding of how wildlife use fruiting plants will eventually help managers design approaches to improve habitat for species that require open habitats, such as red-cockaded woodpeckers, while minimizing the negative impacts on other species of wildlife (Wilson et al., 1995).

We quantified fruit abundance and fates of individual fruits in five habitat types in a managed landscape in South Carolina. We examined the interplay between four factors that reflect the importance of fruit to birds. The first factor is fruit biomass per hectare. All else being equal, species that produce more biomass are likely to be more important in sustaining populations of frugivores. Our analyses focus on the 22 species that produce the most fruit biomass in our study sites. Sheer production of fruit, however, is irrelevant if fruits are not eaten. Thus, the second factor, fruit fate, examines what happens to fruit. We distinguished between fruit consumed by vertebrates, consumed by invertebrates (insect damage and microbial rot), and destroyed by abiotic conditions (desiccation). Those species that have a higher percentage of their fruits consumed by vertebrates are likely to be more important than species with lower consumption by vertebrates. The third factor, how long individual ripe fruits persist (hereafter "survival") provides an index of availability. We used survival analysis to determine and compare rates of fruit removal (i.e., consumption by wildlife) among species and habitats. The fourth factor, seasonality, provides context for the other three factors. In particular, it is unlikely that the importance of fruits to birds is temporally constant. By examining fruit production, fate, and removal rates among seasons, we can gain insight into when fruit use is greatest and, presumably, most important.

Specifically, we determined: (1) the dry mass of fruit pulp produced per unit area for each species, (2) the proportion of each species' total fruit crop removed by vertebrates, (3) the rate at which ripe fruit disappeared from plants, and (4) the influence of fruit abundance, season, habitat, and plant species on the proportion of fruits removed by vertebrates and on the rate of fruit disappearance. These data provide the first step in determining the relative importance of different species of fruit for frugivores.

2. Methods

This study was conducted at the Savannah River National Environmental Research Park in South Carolina, USA (33°20′N, 81°40′W) from July 1996 through May 1998. This 780 km^2 site, located along the Savannah River in the sand-hills habitat between the Piedmont and Coastal Plain, consists of a mixture of second growth hardwood forest and pine plantations. Detailed descriptions of the site, its history and management are provided by Odum (1991) and White and Gaines (2000).

Fifty-six 0.1 ha study plots were established across the five different habitat types that in sum comprise 83% of the site (Workman and McLeod, 1990). Hardwood forest sites included (1) 10 plots in upland hardwood forests, with a canopy consisting of several species of oaks and hickories (*Quercus* and *Carya*), and (2) 10 plots in mesic riparian hardwood forests (hereafter called Bottomlands) located along small tributaries of the Savannah River and composed of oaks, tupelo (*Nyssa sylvatica*), redbay (*Persea borbonia*) and *Magnolia*. The hardwood sites are not actively managed but were disturbed by agriculture prior to the establishment of the Savannah River Site in the early 1950s. In general, wet Bottomlands were not cleared for agriculture and have since been designated protected research areas by the US Department of Energy. These two hardwood habitat types cover 4 and 15% of the site, respectively. Managed pine plantations cover 64% of the Savannah River Site, and the understory in these habitats is burned on a 4–5 years cycle. Pine plantation study plots included (3) 13 plots in longleaf pine (*Pinus palustris*) stands, and (4) 13 plots in loblolly pine (*Pinus taeda*) stands. All pine plantation sites were dominated by trees planted in the mid-1950s and pine stands burned during the course of our study were not included. Finally (5) 10 plots were located in areas where pine plantations were clear-cut prior to beginning this project in 1994. These plots, which we refer to as clear-cuts, were planted in either loblolly or longleaf pine in the winters of 1993 and 1994 and were undergoing rapid changes in species composition and physical structure during the time of this study (between 1996 and 1998).

In each plot, every individual fruit-producing plant was identified and permanently marked. The numbers of ripe and unripe fruit on these plants have been counted each month since August 1994. From a total pool of approximately 60 fruiting species recorded on our plots, we chose the 22 species that were the most prolific fruit producers. This subset of species accounts for approximately 90% of the total fruit biomass produced in the Savannah River Site landscape (K. Greenberg, D. Levey, J. McCarty, S. Pearson, S. Sargent, unpublished data). With the exception of a few larger-fruited species consumed primarily by mammals, such as Prickly-pear (*Opuntia compressa*), Chickasaw Plum (*Prunus angustifolia*), and Hog Plum (*Prunus umbellata*), birds are the primary vertebrate consumers of the fruits we followed (Martin et al., 1951). Thus, we emphasize bird, rather than mammal, consumption of fruit in this study.

2.1. Fruit fate

To determine what proportion of the available fruit was consumed, we marked and then repeatedly censused individual fruits from the 22 species with highest fruit biomass production in our study plots. We monitored fruit fate in the habitat type(s) where each species occurred: six species in upland hardwoods, three species in bottomland hardwoods, eight species in longleaf pine, six species in loblolly pine and seven species in clear-cuts (Table 1). Eight species were monitored in more than one habitat type. All species were studied during their peak fruiting seasons between July 1996 and May 1998.

For each species, we selected 3–49 (average = 19; S.D. = 15) individual plants, distributed as equally as possible among our study plots. Our goal was to

Table 1
Plant species monitored for fruit fate and disappearance rate (fruit survival)[a]

	Plots (*n*)	Plants (*n*)	Fruits (*n*)	Habitat	Season available	Biomass produced (g/ha)
Callicarpa americana (beautyberry)	8	18	290	Loblolly	Fall	15
Celtis occidentalis (American Hackberry)	2	4	40	Longleaf	Winter	20
Cornus florida (flowering dogwood)	9	26	260	Upland	Fall	6313
Crataegus flava (hawthorne)	6	12	120	Longleaf and loblolly	Summer	644
Ilex opaca (American holly)	8	19	190	Upland and bottomland	Winter	2391
Mitchella repens (partridgeberry)	4	49	100	Upland and bottomland	Fall	45
Myrica cerifera (waxmyrtle)	3	9	319	Longleaf	Winter	58
Opuntia compressa (Prickly-pear)	7	39	364	Clear-cut	Winter	1230
Phytolacca americana (pokeweed)	3	9	85	Clear-cut	Summer	260
Prunus angustifolia (Chickasaw Plum)	4	5	50	Upland	Summer	12
Prunus serotina (black cherry)	9	45	525	Clear-cut and loblolly	Summer	498
Prunus umbellata (Hog Plum)	3	3	30	Loblolly	Summer	45
Rhus copallina (winged sumac)	6	14	4230	Clear-cut	Winter	3693
Rhus toxicodendron (poison oak)	10	46	598	Longleaf and loblolly	Fall	217
Rubus cuneifolius (blackberry)	6	17	249	Clear-cut	Summer	2113
Sassafras albidum (sassafras)	3	3	30	Clear-cut	Summer	49
Smilax bona-nox (bullbrier)	3	4	38	Upland and longleaf	Winter	8
Vaccinius arboreum (farkleberry)	10	22	300	Upland	Fall	506
V. corymbosum (highbush blueberry)	2	6	40	Bottomland	Summer	232
V. stamineum (tall deerberry)	10	33	675	Longleaf and clear-cut	Summer	14869
Vitis aestivalis (summer grape)	3	3	30	Longleaf	Summer	167
Vitis rotundifolia (muscadine grape)	14	40	523	Longleaf and loblolly	Summer	790

[a] The number of plots where plants were monitored, number of plants monitored, and number of fruits followed, are given for each species. The habitat(s) where each species was monitored, and the season where most fruit disappeared are also provided. The average biomass of fruit produced is given as grams dry mass per hectare for each species based on the habitat in which it was monitored (unpublished data).

maximize spatial replication because fruit removal can be highly variable among sites (e.g., Willson and Whelan, 1993). On each plant we marked at least 10 fully formed fruits (average = 12; S.D. = 4) widely distributed across the plant, followed the rate at which they were removed, and recorded their eventual fate. This approach was not feasible for species with fewer than 10 fruit per plant such as *Mitchella repens*. For these species, additional plants were included in each plot. In most cases, fruits were marked with a small dot of paint (<1 mm diameter) placed inconspicuously near the pedicel (Levey, 1987). The attachment of the pedicel to the branch was marked with a second dot, indicating the original location of each fruit. In species with multiple fruits borne in a single cluster, such as *Cornus florida* and *Ilex opaca*, only one fruit per cluster was marked. Small, clustered fruits such as on *Myrica cerifera* and *Rhus copallina* were not individually marked. Instead, clusters were marked and the number of fruit remaining in each cluster recorded. Plants with fruit were initially monitored at intervals of 2–7 days. Visits were more frequent immediately after marking and for plants whose fruits were removed rapidly. The interval between visits lengthened for species whose fruits remained on the plant for >30 days.

On each visit, the presence or absence of each fruit was noted and any damage due to insects or microbes was recorded. When a fruit was missing from a branch, we searched the ground below its former location for fallen fruit. Previously, undamaged fruits that disappeared and were not found under the plant were considered to have been consumed by vertebrates. We note that frugivorous birds and mammals often eat fallen fruit (Corlett, 1996) and that studies emphasizing the importance of validating the fate of fallen fruits have primarily focused on fitness consequences for fruiting plants (Willson and Whelan, 1993; Laska and Stiles, 1994). In the context of our study's focus on fruit use by wildlife, it makes little difference whether fruit is eaten from the plant or from the ground. Our study is from the animal perspective, and as long as fruit is eventually consumed, it makes little difference whether fruit is eaten from the plant or from the ground.

With the exception of winged sumac (*R. copallina*), fruit were followed until all had disappeared or were damaged. Ripe sumac fruit remained on the plant for many months and, in fact, many of the previous year's fruit remained when flowering began in the summer. Sumac fruits not eaten by May (when new fruit species start to appear) were thus considered to be unused.

2.2. Statistical analyses

We classified fruit fate as "consumed" if a fruit appeared to be removed by vertebrates or "unconsumed" if it was destroyed by insects or microbes, or if it fell from the plant and eventually desiccated. Admittedly, this classification scheme is vertebrate-biased, as all fruits are eventually "consumed" in one way or another (e.g. by microbes or invertebrates).

The proportions of fruit eaten by vertebrates (consumed) or damaged by insects and/or microbes (unconsumed) were calculated. Fruit fates were compared among habitats and among species using non-parametric Kruskal–Wallis tests. The rate at which ripe fruit disappeared was estimated using Kaplan–Meier survival estimates (Willson and Whelan, 1993; Sall and Lehman, 1996). Survival analysis yields the time for an event to occur, allowing inclusion of individuals lost before the end of a study (right-censored data). Rates of disappearance included fruits removed by vertebrates, consumed by other organisms, and desiccated fruit that fell from the plant. For species that occurred in more than one habitat, we used a non-parametric Wilcoxon sign rank test to determine if fruits survived longer in one habitat than another. These comparisons focus on the most prolific species in these habitats, together accounting for about 90% of the total fruit production, because these are most likely to be of interest to managers. Therefore, one caveat of our comparisons between habitats and among species is that they may not be truly representative of community-wide patterns because the community also contains rare species that we did not sample.

For all tests, alpha was set at 0.05. We corrected for Type I error with sequential Bonferroni tests (Rice, 1989). We did not correct for phylogeny; species in the same genus or family were treated identically to those not in the same genus or family. In a strict sense, this approach violates the assumption of independence among samples (Harvey and Pagel, 1991). Note that most of our species (73%) belong to different genera and most of our genera belong to different families (22 species and 16 genera in 14 families). More important, our study is ecological, not evolutionary. We are not interested in evolutionary inferences, which necessitate phylogenetic independence. Instead, we are interested in the amount of fruit produced and consumed.

3. Results

3.1. Fruit fates

Of the 22 species, 17 species had $\geq 50\%$ of their fruits consumed by vertebrates (Table 2). Losses to insects were small and varied significantly among seasons ($H = 6.71$, $P = 0.03$, Kruskal–Wallis). Species fruiting in the fall had the lowest loss of fruits to insects ($0.1 \pm 0.1\%$, $n = 5$), those fruiting in summer had the highest ($6.4 \pm 3.2\%$, $n = 11$) and those retaining fruit in the winter were intermediate in their levels of insect damage ($1.3 \pm 1.3\%$, $n = 6$).

Species tended to have most of their fruit crop consumed by vertebrates and no species had less than 30% of its crop consumed, resulting in a highly skewed distribution among species, with a median of 73% of the fruit crop being consumed (range = $30-99\%$). Eight species had >90% of their crop eaten by vertebrates and 14 species had >70% eaten, including many of the species producing the largest fruit biomass, such as *C. florida* and *Rubus cuneifolius*. Finally, five species had <50% of their crop consumed. These included species with high production of fruit biomass, most notably *Vaccinium stamineum* and *R. copallina* (Table 2).

There was no correlation between the biomass of fruit a species produced and the percent of its fruit crop consumed ($r = -0.22$, $P = 0.31$; Fig. 1a). Species with a high proportion of their fruit used by vertebrates included both species with low biomass production (e.g., *Callicarpa americana* and *M. repens*) and high biomass production (e.g., *R. cuneifolius* and *C. florida*). In contrast, some of the most prolific species had less than half their fruit removed by vertebrates (e.g., *R. copallina*).

Table 2
Variation in the percent of the fruit crop consumed by vertebrates and the length of time fruit remained available (survival in days) for species monitored at the Savannah River Site[a]

	Percent consumed		Survival (days)		
	Mean ± S.E.	P_{plot}	Mean ± S.E.	P_{plant}	P_{plot}
C. americana	95.6 ± 2.3	0.060	020.1 ± 1.1	<0.001*	0.014*
C. occidentalis	95.0 ± 5.0		060.5 ± 3.2	0.002*	<0.001*
C. florida	78.1 ± 3.5	0.092	075.4 ± 1.5	<0.001*	<0.001*
C. flava	30.0 ± 8.7	0.300	013.9 ± 1.0	<0.001*	<0.001*
I. opaca	51.1 ± 8.0	0.088	110.1 ± 5.2	<0.001*	<0.001*
M. repens	66.6 ± 4.5	0.392	130.3 ± 8.1		0.067
M. cerifera	98.0 ± 1.2	0.486	102.5 ± 1.1	<0.001*	
O. compressa	91.9 ± 3.7	0.035	092.6 ± 3.1	<0.001*	<0.001*
P. americana	71.1 ± 9.5	0.159	017.0 ± 1.5	<0.001*	0.001*
P. angustifolia	84.0 ± 6.0	0.375	002.7 ± 0.2	<0.001*	
P. serotina	71.7 ± 4.6	0.016	038.2 ± 0.8	<0.001*	<0.001*
P. umbellata	43.3 ± 20.3	0.368	012.3 ± 1.7	0.007*	0.007*
R. copallina	32.3 ± 8.5	0.422	152.4 ± 0.5	<0.001*	<0.001*
R. toxicodendron	99.1 ± 0.7	0.568	047.5 ± 1.5	<0.001*	<0.001*
R. cuneifolius	92.8 ± 2.3	0.256	030.1 ± 1.1	<0.001*	
S. albidum	50.0 ± 26.5	0.368	012.1 ± 1.5	<0.001*	
S. bona-nox	43.8 ± 17.7	0.861	088.6 ± 10.0	0.593	0.566
V. arboreum	93.1 ± 2.0	0.223	089.3 ± 2.9	<0.001*	<0.001*
V. corymbosum	95.0 ± 3.4		034.1 ± 2.3	0.104	
V. stamineum	40.2 ± 5.1	0.012	008.9 ± 0.3	<0.001*	<0.001*
V. aestivalis	73.3 ± 26.7		020.5 ± 2.9	<0.001*	
V. rotundifolia	88.4 ± 2.4	0.286	016.5 ± 0.6	<0.001*	<0.001*

[a] Survival: Kaplan–Meier survival estimate in days. Variation among plants and plots was evaluated with Kruskal–Wallis (percent consumed) or Wilcoxon tests (survival). *P*-values are given for the differences among individual plants for survival (P_{plant}) and for difference among plots in percent used and survival (P_{plot}). *P*-values that are significant after correcting for multiple comparisons are indicated by "*". Missing values indicate that insufficient data were available to test for effects of plants or plots.

Only three species, *O. compressa*, *P. serotina*, and *V. stamineum*, showed variation in percent consumption among plots of the same habitat type and these differences were not significant after the correction for multiple comparisons was applied (Rice, 1989). In general, percent consumption held constant within species from one plot to another within the same habitat (Table 2). Among species, percent consumption was not influenced by season ($F_{2,19} = 1.52$; $P = 0.24$; Fig. 2a) or habitat ($F_{4,25} = 0.02$; $P = 0.99$; Fig. 2c). In two of the eight species that we monitored in two different habitats, percent consumption varied significantly between habitats (*P. serotina* and *V. stamineum*; Table 3). The absolute size of between habitat differences in fruit fate were generally small. In short and considering all species, one habitat type did not have a consistently higher percent of fruit removed by wildlife.

3.2. Rates of fruit disappearance

The length of time ripe fruits survived on plants varied dramatically among species, from as short as 3 days (*P. angustifolia*) to >165 days (*R. copallina*; Table 2). Biomass of fruit pulp produced (g/ha) was a poor predictor of how long ripe fruit persisted on a species ($r = 0.17$, $P = 0.43$; Fig. 1b). Likewise, habitat differences failed to explain significant variation among species in fruit survival ($F_{4,25} = 2.3$, $P = 0.08$), although there was a strong trend towards longer survival of fruit produced in upland and bottomland hardwoods relative to the other habitat types (Fig. 2d). In contrast, season had a strong impact on fruit persistence ($F_{2,19} = 19.4$, $P < 0.001$); species fruiting in summer had their fruits disappear significantly faster than those species bearing ripe fruit in fall or winter (Fig. 2b).

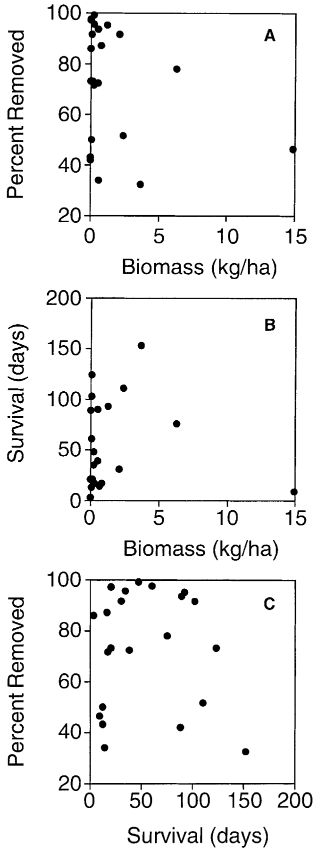

Fig. 1. The relationship between fruit biomass produced and use of fruit by vertebrates. The total biomass of fruit produced by a species did not influence the proportion of its fruit crop removed by vertebrates ((A) Spearman rank correlation, $r = -0.22$, $z = 1.01$, $n = 22$, $P = 0.31$); even when the outlier with highest production (*V. stamineum*) is removed ($r = -0.12$, $z = 0.51$, $n = 21$, $P = 0.61$). Biomass produced was not correlated with the average survival time of fruits ((B) $r = 0.17$, $z = 0.79$, $n = 22$, $P = 0.43$; excluding *V. stamineum* $r = 0.32$, $z = 1.45$, $P = 0.15$). The length of time fruit persisted on a plant was not related to the proportion of the fruit crop taken by vertebrates ((C) $r = 0.17$, $z = 0.79$, $n = 22$, $P = 0.43$).

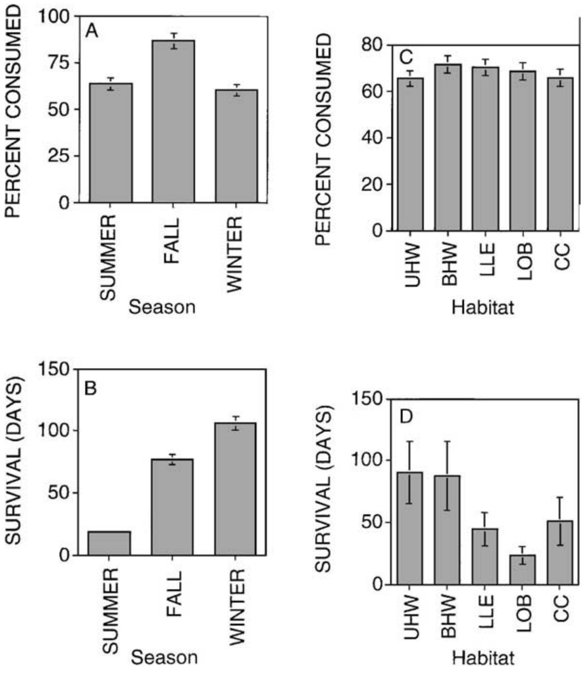

Fig. 2. The effect of season and habitat on the percent of the fruit crop consumed by vertebrates and average survival time of fruits. Species fruiting in different seasons did not differ in percent consumed ((A) ANOVA, $F_{2,19} = 1.52$, $P = 0.24$). Season of fruiting did have an effect on average survival time of fruits ((B) $F_{2,19} = 19.4$, $P < 0.001$); species fruiting in summer had their fruits disappear significantly faster than species fruiting in fall or winter (Scheffe's post hoc tests). Species from different habitats did not differ in percent consumed ((C) $F_{4,25} = 0.02$, $P = 0.99$) or average survival time of fruits ((D) $F_{4,25} = 2.32$, $P = 0.08$). Error bars = 1 S.E. UHW: upland hardwood forests, BHW: bottomland hardwood forests, LLW: longleaf pine stands, LOB: loblolly pine stands, and CC: clear-cuts.

Within species, there was also considerable variation in fruit survival. Eighty-seven percent of species with sufficient sample size displayed significant variation in fruit survival among plots and 90% displayed significant variation among individual plants, regardless of plot (P's < 0.05; Wilcoxon tests; Table 2). Underlying this variation in at least five species were differences in survival among habitats; five of the eight species monitored in each of two habitats showed significant differences between habitats (P's < 0.05; Wilcoxon tests; Table 3).

Species with fruit that remained on the plant for longer periods were no more or less likely to be consumed by vertebrates. In particular, there was no significant correlation between the percent of the fruit crop eaten by vertebrates and the average survival time ($r = 0.17$, $P = 0.43$; Fig. 1c).

3.3. Timing of removal

We focus here on the 12 species regularly consumed by birds that produced the most dry mass of fruit pulp per hectare in each season (Table 1). The six species

Table 3
Effect of habitat type on the percent of total fruit crop consumed by vertebrates and on the length of fruit survival[a]

	Habitat	Percent consumed		Survival (days)	
		Mean ± S.E.	P_{habitat}	Mean ± S.E.	P_{habitat}
C. flava	Loblolly pine	033.3 ± 12.0	0.718	011.2 ± 0.9	0.82
	Longleaf pine	026.7 ± 13.3		016.6 ± 1.8	
I. opaca	Upland hardwood	054.0 ± 18.9	0.833	146.7 ± 8.4	<0.001*
	Bottomland hardwood	050.0 ± 9.0		098.3 ± 5.7	
M. repens	Upland hardwood	77.4	0.157	128.1 ± 13.1	0.88
	Bottomland hardwood	063.0 ± 3.7		128.2 ± 9.8	
P. serotina	Loblolly pine	053.5 ± 8.4	0.001*	028.0 ± 1.3	<0.001*
	Clear-cut	082.8 ± 4.1		039.4 ± 0.9	
R. toxicodendron	Loblolly pine	098.2 ± 1.4	0.135	054.4 ± 2.5	<0.001*
	Longleaf pine	100.0		042.1 ± 1.8	
S. bona-nox	Upland hardwood	050.0 ± 20.0	0.800	085.5 ± 13.7	0.57
	Longleaf pine	037.5 ± 37.5		088.5 ± 7.6	
V. stamineum	Clear-cut	058.5 ± 9.5	0.003*	008.2 ± 0.4	0.001*
	Longleaf pine	028.3 ± 4.1		009.5 ± 0.4	
V. rotundifolia	Loblolly pine	089.4 ± 2.7	0.743	015.2 ± 1.0	<0.001*
	Longleaf pine	087.7 ± 3.5		017.3 ± 0.6	

[a] Survival: Kaplan–Meier survival estimate in days. Differences between habitat types were tested using Wilcoxon tests. Significant effects that are significant after correcting for multiple comparisons (overall $P < 0.05$) are indicated by "*".

producing the most fruit in summer tended to have steep survival curves (Fig. 3). Three species, *Prunus serotina*, *R. cuneifolius*, and *Vaccinium corymbosum* were the first species to produce fruit in the late spring and all were eaten at approximately the same time (June and early July). *V. stamineum* and *Crataegus flava* disappeared rapidly in mid-July and August, but the majority of the fruit was eaten by insects or fell off the plant and then dried up (Table 2). In late summer fruit was once again eaten in large quantities by birds and mammals when *Vitis rotundifolia* was produced (Fig. 3). Other late summer fruits produced in significant quantities included *Vitis aestivalis* and *Phytolacca americana*, both of which are primarily consumed by vertebrates.

In the fall and winter, seven species had large quantities of available fruit (Table 1). Of these, *O. compressa* is seldom eaten by birds (pers. obs.). The remaining six species have fruits that are eaten by a wide range of both birds and mammals. Fruit from these species became available at approximately the same time, yet varied dramatically in how quickly their fruit crops were depleted (Fig. 4). *Rhus toxicodendron* was the first of these species to disappear in large numbers; >80% of its fruit crop was gone before the remaining species were similarly depleted (Fig. 4). In early November, *C. florida*, *Vaccinium arboreum*, and *I. opaca* fruits began to be consumed. Finally, after approximately half of these species' fruit crops

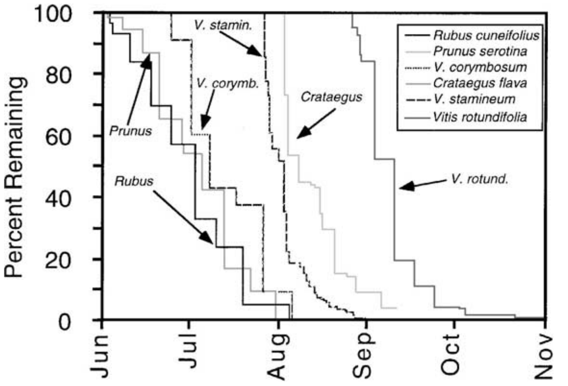

Fig. 3. Fruit survival of species producing in summer and eaten by birds. Fruit survival (based on Kaplan–Meier survival estimates) was significantly different among species (Wilcoxon, $P < 0.001$).

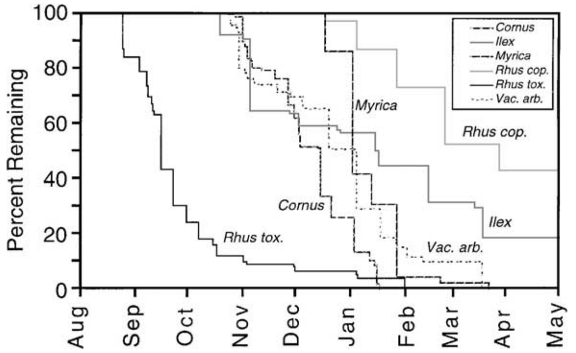

Fig. 4. Fruit survival of the six common fall and winter fruit species widely eaten by birds. Fruit survival (based on Kaplan–Meier survival estimates) was significantly different among species (Wilcoxon, $P < 0.001$).

were consumed, fruits of the two remaining species, *M. cerifera* and *R. copallina* began to disappear (Fig. 4).

4. Discussion

Our goal was to document community-wide patterns of fruit production and consumption in five habitats of a managed forest. Considering only the 22 species that produced the most fruit biomass during our study, average production of pulp per species averaged $1.6 \pm 3.3\,\mathrm{kg\,ha^{-1}}$ per year (dry mass; Table 1). Six species produced >1 $\mathrm{kg\,ha^{-1}}$ per year (Table 1). All habitats except loblolly pine contained at least one of these species and, likewise, fruit was available from at least one of these species every season.

To put these fruit production values into perspective, consider that some of most common avian frugivores in the eastern United States consume 4–9 g per day of fruit pulp (dry mass), when on an all fruit diet ($n = 6$ spp. of birds, 7 spp. of fruits; Levey and Karasov, 1989; Witmer and Van Soest, 1998). In a very crude sense, overall fruit production by 22 species at our site can thus provide enough food per hectare for 733–1649 bird-days (one bird-day = the quantity of *fruit required to meet the entire energetic demands of one bird for one day*; assuming equal proportion of each habitat type). However, most frugivorous species eat a mixed diet of fruit and insects (Martin et al., 1951; Willson, 1986). Thus, the consumption rate necessary to support most birds in most circumstances is likely lower than the above estimate and, consequently, the number of bird-days supported by fruit production is likely higher. The distribution of these bird-days across species and seasons will help to determine the importance of fruit as a resource. For example, if fruit is eaten by a diverse suite of species during relatively short periods of time when other foods are scarce, its importance may be further increased. The data on the timing of consumption of fall and winter fruits presented here suggests that consumption is greatest during the winter season when other foods are most likely to be scarce.

An important caveat to the discussion that follows is that our study period spanned approximately 2 years and our results may not be representative of longer-term patterns. Two previous studies in the eastern United States found little inter-year variation in timing of fruit production (Skeate, 1987; Willson and Whelan, 1993). These studies were limited to 2 and 4 years, however. In other temperate areas, annual variation in both timing and production of fruit crops can be substantial (Herrera, 1998; Herrera et al., 1998).

4.1. Fruit fates

Not only was production generally high in most habitats, but most fruits of most species were consumed by vertebrates. Although, it remains uncertain what would happen if fruit supplies were reduced, the thorough and wide-spread use of fruits at our site suggests fruit is an important resource for wildlife, especially for over-wintering birds.

Fruit use by vertebrates at other temperate sites appears similarly high. Most fruiting species have most of their fruit crop removed by vertebrates (Herrera and Jordano, 1981; Sorensen, 1981; Jordano, 1982, 1989; Courtney and Manzur, 1985; Burger, 1987). The proportion of the fruit crop removed, however, can be extremely variable and much lower than 50% (Murray, 1987; French and Westoby, 1992; Sallabanks, 1992; Thebaud and Debussche, 1992; Laska and Stiles, 1994; Masaki et al., 1994). In many cases, fruits are not consumed by vertebrates because they are first damaged by insects or microbes (Jordano, 1987; Buchholz and Levey, 1990; Traveset et al., 1995; Garcia et al., 1999). Vertebrates are thus in competition with smaller, invertebrate frugivores

(Janzen, 1977). From this perspective, it makes sense for resource managers to pay special attention to species that bear fruit in the fall and winter. Fruits of these species are less likely to be lost to invertebrate frugivores (Table 2). In addition, birds' dependence on fruits typically peaks during fall and winter because availability of the major alternative food source, insects, is low and because birds' energetic demands are high due to migration and cold temperatures (Janzen, 1977; Bairlein, 1990; Bairlein and Gwinner, 1994; Parrish, 1997).

4.2. *Rates of fruit disappearance*

The survival curves of fruit species formed a continuum from species whose fruit rapidly disappeared to highly persistent species whose fruit remained available for months (Table 2 and Figs. 3 and 4). These differences are a function of both the rate at which vertebrates used fruit and the rate at which other organisms consumed or destroyed fruit. Fruit removal rate alone does not indicate the importance of particular species but does indicate the length of time its fruits are available for wildlife. For example, both *V. stamineum* and *V. rotundifolia* are Summer-fruiting species with relatively short survival times, yet *V. rotundifolia* is twice as likely to be eaten by a vertebrate (Table 2).

In addition to differences among species, disappearance rates were often characterized by significant variation among individual plants, among plants in different plots, and among habitat types within a species. High variability in removal rates within and among species is commonly reported; attempts to document and explain it drive many studies (Denslow, 1987; Sargent, 1990; French and Westoby, 1992; Sallabanks, 1992; Englund, 1993; Willson and Whelan, 1993; Laska and Stiles, 1994). Fruit nutrient content likely plays a role in determining why some fruits are taken more quickly than others (Martínez del Rio and Stevens, 1989; Martínez del Rio and Restrepo, 1993; Stiles, 1993; Fuentes, 1994; Witmer and Van Soest, 1998). But studies that have focused on this relationship in temperate systems have revealed few generalities (Sorensen, 1984; Johnson et al., 1985; Herrera, 1987; Borowicz, 1988; Debussche and Isenmann, 1989; Jordano, 1992; Martínez del Rio and Restrepo, 1993; Willson and Whelan, 1993). Studies of captive birds have revealed large variation in fruit preferences among individual birds (Jung, 1992; Willson and Comet, 1993; Willson, 1994). Furthermore, widely varying extrinsic factors such as habitat, fruit density, and neighborhood effects influence probability of fruit removal (Levey et al., 1984; Moermond and Denslow, 1985; Howe, 1986; Sargent, 1990; Jordano, 1992; Whelan et al., 1998). Taken together, these studies emphasize that fruit removal is highly unpredictable.

Indeed, fruit removal rates at our site were highly variable and difficult to explain. The overall abundance of fruit had little impact on removal rate, as prolific fruiters did not have longer survivorship of fruit than other, less prolific species (Fig. 1b). Likewise, differences in fruit survival among habitats were not predictable within or among species (Table 3 and Fig. 2).

Summer-fruiting species were significantly less persistent than those available in fall and winter (Fig. 2), a pattern that seems typical in eastern North America (Gargiullo and Stiles, 1991; Cipollini and Stiles, 1992; Cipollini and Levey, 1997a). In general, summer fruits tend to be highly nutritious (high carbohydrate content), palatable (low in secondary metabolites), and quickly removed, whereas winter fruits tend to be less nutritious, less palatable, and slowly removed (Cipollini and Levey, 1997a). Indeed, experiments with captive frugivores have confirmed that summer fruits are preferred over winter fruits (Gargiullo and Stiles, 1991; Cipollini and Stiles, 1993; Cipollini and Levey, 1997b). The interpretation of these relationships is that summer-fruiting species have rapid removal rates because they are highly nutritious. High removal rates minimize the chance of microbial attack and hence lessen the need for defensive secondary metabolites. Because of their persistence, winter-fruiting species, on the other hand, require much protection from microbial attack and therefore have reduced palatability due to high concentrations of secondary metabolites. Despite this well-supported view of summer fruits being higher quality than winter fruits (Stiles, 1980), our results clearly demonstrate the importance of winter fruits—they are consistently available for a long periods, undeniably provide calories, and are eventually consumed.

Given that both the percent of fruit eaten by vertebrates and the rate at which fruit was removed varied greatly among species, one might have expected a correlation between percent eaten and the removal rate. This was not the case; species that were heavily fed upon by vertebrates did not disappear more rapidly. This pattern suggests that whatever characteristics of fruit are important in determining differences in use, these characters do not affect disappearance rate and relative use by vertebrates in the same way.

4.3. Timing of removal

It has been widely suggested that fruit is especially important for birds during fall migration (Jordano, 1988; Bairlein, 1990; Moore and Yong, 1991; Bairlein and Gwinner, 1994). Likewise, it has also been hypothesized that the seasonal pulse of migrants is the most important selective force influencing the timing of fruit production in eastern North America (Thompson and Willson, 1979). This hypothesis is based on the observation that fruit abundance and migrant abundance peak simultaneously, occurring later in the fall at sites farther south. While the forested habitats we studied showed an autumn peak in fruit production, patterns of fruit removal were not consistent with the hypothesis that most fruit was consumed by migrating birds. Available information on the phenology of autumn bird migration at our site suggests that the abundance of migrants likely peaks in early October (Kilgo et al., 1999, J. McCarty, pers. obs.), after its peak in Illinois (Thompson and Willson, 1979) and before its peak in Florida (Skeate, 1987). When we look at the species of fruit that were available early in the fall (Fig. 3), only one common species, poison oak (*R. toxicodendron*), was removed in significant numbers during migration. However, approximately 80% of its fruits were removed in September and the highest removal rate was in the first half of the month—well before the probable peak in migrant abundance. Most fruit available at our site during fall migration was not eaten until late autumn, when it was most likely consumed by over-wintering birds or resident mammals, not by migrating birds.

At least two factors make our study site different from many other areas where frugivory in migrating birds has been emphasized. First, fruit is known to be important for migrants at stopover sites (Jordano, 1988; Parrish, 1997), where large numbers of migrants must rapidly build up energy reserves before continuing migration. Our inland site is not directly comparable to such coastal sites. Second, other studies of frugivory have focused on more northern areas, where cold temperatures in migration may limit the availability of insects and other alternative foods. In contrast, our site in the southern United States had generally mild temperatures during migration and insects were presumably available. Later in the season, when temperatures in South Carolina are cooler, more fruit was removed.

A similar pattern of fruit use by wintering birds was found in north-central Florida, where 24 of the 36 species had ripe fruit available in the winter. Many of these species also bore fruit in the fall, during the peak of migration (Skeate, 1987). However, the number of species in fruit peaked in December, long after migration. Frugivorous birds were also common at this time and consisted of over-wintering migrants from north temperate habitats. A parallel situation occurs in southern Spain (Herrera, 1984, 1995).

5. Conclusions

Resource managers in eastern North America have typically focused their attention on hard mast production and game species (Downs, 1944; Goodrum et al., 1971; Nixon et al., 1980, 1987; Kaminski et al., 1993; Johnson et al., 1995; Masters et al., 1996). As this perspective broadens to include a diversity of non-game species, attention should be devoted to fruit and frugivores (Perry et al., 1999). We emphasize that more vertebrate species in eastern North America consume fruit than consume hard mast (Martin et al., 1951) and more plant species produce fruit than produce hard mast. More generally, an average of 42% of woody plant species produce fruit in temperate coniferous forests and 35% in temperate deciduous forests (Jordano, 1992). Among bird communities, an average of 35% of species in temperate coniferous forests are frugivorous and 39% in temperate deciduous forests are frugivorous (Willson, 1986; data from Table VI; regions and seasons combined; note that many additional species occasionally consume fruit). Thus, a substantial portion of the plant community relies on animals for seed dispersal and a substantial portion of the animal community relies on plants for food. Although it is uncertain what would happen to frugivore populations if management practices increased fruit supplies, numerous studies documenting positive correlations between fruit and frugivore abundance suggest potential of such practices to increase frugivore density and diversity (Blake and Hoppes, 1986; Jordano, 1992; Levey and Stiles, 1992; Rey, 1995; but see Willson and Whelan, 1993; Herrera, 1998).

Variation in patterns of fruit use and rate of removal provides insights into the role of fruit as a resource for vertebrates. Relatively low rate of fruit use during fall bird migration is followed by a period of rapid removal of many fruit species by over-wintering birds. This illustrates the importance of fruit as a resource for over-wintering birds—a group of birds whose needs are often overlooked in temperate zone management practices (Martin and Finch, 1995). Likewise, differences among habitats in both fruit availability and use emphasizes the need for management to focus not just on individual fruiting species but on fruit communities and habitat patterns across the landscape.

A broader approach to wildlife resources in managed forests is necessary for another reason: fruit resources may prove important for sustaining frugivore populations during brief but critical periods. We provide two examples, both of which warrant more study. First, birds immediately after fledging have not acquired the skills to find and capture insects efficiently (Wunderle, 1991; VanderWerf, 1994). During this period they may be temporarily dependent on fruit to fulfil their energetic requirements. Recent evidence suggests that, indeed, young birds key in on areas of high fruit abundance (Vega Rivera et al., 1998). Second, during periods of especially harsh winter weather, species that would otherwise consume seeds or insects may switch to fruit because foraging for their typical diet under these conditions would be impossible or too energetically expensive. In contrast, foraging for fruit is relatively easy because fruits are not cryptic, not physically protected, and not difficult to capture. Because harsh weather is often of short duration, even one or two of meals of fruit might provide enough calories for a small bird to survive until weather conditions improve.

With respect to management for winter fruits in the southeastern United States that can sustain birds during periods of bad weather, we recommend attention to *M. cerifera*. Although, *M. cerifera* may be a keystone species for fruit-eating birds in the southeastern United States (McClanahan and Wolfe, 1993), many current management practices are aimed at reducing its abundance (Kalmbacher et al., 1993; Haywood et al., 2000). At our site and throughout the Coastal Plain, controlled burns and cutting of mid-story plants (‘‘mid-story removal’’) is common in managed pine forests (Waldrop et al., 1992), practices that clearly reduce fruit production by *Myrica* (Kalmbacher et al., 1993). These practices impact most fruiting understory species but *Myrica* is often specially targeted because it has traditionally been considered an ‘‘inferior’’ food for game species (Haywood et al., 2000). Yet, *Myrica* fruits are available when few other food sources are abundant and in our study, 98% of its crop was consumed by vertebrates; little went to waste. Even bird species that are typically considered insectivorous readily consume *Myrica* fruit in some situations (Martin et al., 1951; Parrish, 1997; J. McCarty, pers. obs.). Prescribed burns are an important component of ecosystem management in this region, especially for long-leaf pine forests, and benefit a wide range of native plant and animal species (Farrar, 1998; Barnett, 1999). Our observations suggest that *Myrica* can rebound quickly after fire and its management may prove to be compatible with many of the aims of prescribed burning.

Forest management practices that remove fruiting plants are common in other regions as well. Management activities such as prescribed burns or mechanical treatments that remove understory fruiting shrubs are often needed to reduce fuel loads or to maintain selected species and communities, including grasslands and savannas. Practices intended to restore and maintain these communities are a necessary part of the over-all goal of conserving diversity. However, loss of fruit-producing plants necessitates a loss of food and other resources for wildlife. This trade-off needs to be recognized when making decisions about the mix of management activities across a landscape. Patterns of fruit production and consumption at our site suggest that fruit is a common and important resource for wildlife, especially over-wintering birds. Management practices that take fruit production and consumption into account will likely be more effective at maintaining biodiversity than those that do not.

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