Pattern, adaptation, and constraint in fruiting synchrony within vertebrate-dispersed woody plants

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Patterns of within-plant fruit ripening synchrony were examined for 12 woody species in southeastern Michigan, USA. Flowering was more synchronous than fruiting in all individuals tested, suggesting that flowering may constrain fruiting synchrony. However, flowering and fruiting synchrony were not positively correlated among individuals of *Amelanchier arborea* or *Prunus virginiana* and only weakly correlated among nine species, indicating that selection may act independently on the two phenological events. Contrary to the frugivore availability hypothesis, summer fruiting species were not less synchronous than autumn fruiters. Species in which fruits undergo a dual color change during ripening tended to have more asynchronous ripening, but this pattern was confounded by a phylogenetic pattern. Two species in the Ericaceae had the most asynchronous flowering and fruiting; among the remaining species the strongest pattern was that trees were more asynchronous than shrubs.

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Introduction

The degree of within-plant synchrony in fruit ripening varies widely among plant species; this variation has been addressed by several adaptive hypotheses. Synchronous fruit ripening may satiate seed predators (Janzen 1971) or attract opportunistic seed-dispersing animals (McKey 1975, Howe and Estabrook 1977). Asynchronous ripening of fruit may maximize reproduction when the end of the growing season is unpredictable, avoid satiation of specialist dispersers (McKey 1975, Howe and Estabrook 1977), reduce loss of ripe fruit to insects and microbes (Herrera 1982), or reduce the risk of failure of an entire season's reproduction by spreading seed germination over time (Stapanian 1982). Two other hypotheses have been proposed specifically for the evolution of asynchronous ripening in summer-fruiting bird-dispersed species in mid-latitudes of eastern North America. Thompson and Willson (1979) argued that frugivorous birds were less abundant in summer than autumn and that by ripening fruits asynchronously, both within and among individuals, summer fruiters

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avoid satiating their dispersers and hence decrease the time ripe fruits are exposed to pre-dispersal predators. Stiles (1982) and Willson and Thompson (1982) argued that in some species "preripe fruit flags" (partially ripe fruits colored distinctly from both unripe and fully ripe fruit) combine with asynchronous ripening to produce temporally bicolored fruit displays that enhance dispersal when frugivorous birds are not abundant.

Before evaluating adaptive hypotheses for a phenological pattern, it is necessary to determine whether the pattern is more than a consequence of earlier events which may be determined by a different set of selective forces. It has been shown that the *timing* of a phenological event (e.g. fruit ripening) may be constrained by the timing of an earlier event (e.g. flowering) (Slade et al. 1975, Lacey 1982). Similarly, the *synchrony* of ripening may be constrained by the synchrony of an earlier phenological stage.

Bawa (1983) has summarized advantages of synchronous and asynchronous flowering. Synchronous (mass) flowering may provide visual cues to pollinators, improve ability to compete for pollinators, satiate flower

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Family and species	Growth Fru		color	Filled seeds per	
	IOrm	Part ripe	Ripe	$\frac{1}{1}$	
AQUIFOLIACEAE					
1. Ilex verticillata (L.) A. Gray	S		red	4.1 ± 1.5	
2. Nemopanthus mucronata (L.) Loes	S		red	2.6 ± 1.2	
CORNACEAE					
3. Cornus amomum Miller	S		blue	1.0	
4. C. florida L.	Т		red	1.0	
5. C. foemina Miller ^a	S		white	1.0	
6. C. stolonifera Michaux	S		white	1.0	
ERICACEAE					
7. Gaylussacia baccata (Wang.) K. Koch	S	red	black	10.0	
8. Vaccinium corymbosum L.	S	pink	blue	9.4 ± 6.4	
ROSACEAE					
9. Amelanchier arborea (Michaux f.) Fern.	Т	pink	blue	5.5 ± 5.0	
10. Aronia prunifolia (Marsh.) Rehder ^b	S	red	black	2.5 ± 1.2	
11. Prunus serotina Ehrh.	Т	red	black	1.0	
12. P. virginiana L.	S(T)	red	dark red	1.0	

Table 1. The 12 study species and their growth form (S = shrub, T = tree), fruit color (specific color criteria given in Gorchov (1987a); color of partly ripe fruit listed only if it contrasts with ripe fruit color), and seed number per fruit (sample sizes range from 2 to 5 plants, 65 to 282 fruits, per species).

^aequivalent to C. racemosa Lam.

^bTwo morphs distinguishable, but only the more common, glabrous morph (= A. melanocarpa (Michaux) Ell.) was studied.

predators, or facilitate geitonogamy. Asynchronous (extended) flowering may reduce geitonogamy, increase the diversity of matings, provide better control of relative investment in flowers vs fruits, or reduce the risk of reproductive failure.

Unless flowering and fruiting synchrony are independent, selection on one can affect the other. If all fruits required the same amount of time to develop from fertilization to ripening, then ripening synchrony would be identical to fertilization synchrony. Fertilization synchrony, in turn, reflects flower opening synchrony to the extent that flowers are fertilized an equal time after opening. The last condition is approximately met when flowers are receptive for only brief periods, which is a common situation (Primack 1985a).

While several studies have described the relationship between flowering and fruiting times among species in a community (e.g. Foster 1982, Wheelwright 1985, Primack 1985b) and a few have examined this relationship among conspecific individuals (Slade et al. 1975, Lacey 1982, Marquis 1988), less is known of the relationship between within-plant flowering synchrony and withinplant fruiting synchrony.

In this study I examined whether fruiting synchrony is constrained by flowering synchrony in vertebrate-dispersed woody species in southeastern Michigan. Three approaches were used to evaluate the constraint of flowering synchrony. First I determined whether the variance in ripening date was significantly different from the variance in flowering date for a number of individual plants of several species. Second I tested whether flowering synchrony was correlated with fruiting synchrony in the same season among conspecific individual plants. Third, I tested whether flowering synchrony was correlated with fruiting synchrony among the study species. I also explored whether ripening synchrony is influenced by crop size or removal of ripe fruit.

Results of the above investigations suggested that fruiting synchrony is not subject to strong constraints, so I examined fruiting patterns in light of several adaptive hypotheses. Specifically, I tested whether the autumn-fruiting species in the study area had more synchronous within-plant fruiting than the summer fruiters, a pattern central to the hypotheses of, but not documented by, Thompson and Willson (1979), Stiles (1982), and Willson and Thompson (1982). I also tested whether patterns among species in fruiting synchrony were related to plant growth form, variation in number of seeds per fruit, or phylogeny. I conclude with a discussion of the role of these and other factors in the evolution of fruiting synchrony.

Methods

Study site and species

This study was conducted between 1983 and 1986 at the E. S. George Wildlife Reserve in Livingston County, southeastern Michigan, an area maintained for research by the Museum of Zoology, University of Michigan. The climate and vegetation have been described by Rogers (1942), Cantrall (1943), Evans and Dahl (1955), and Cooper (1958). I studied most of the common woody species with fleshy fruits and insect-pollinated

flowers located in the oak-hickory woods, swamp margins, and old fields (Table 1). All 12 of these species are considered bird-dispersed based on morphology (Stiles 1980). Frugivorous birds present at the study site are listed in Gorchov (1987a). Many of the study species are also mammal-dispersed; their seeds have been found intact in scats of raccoons and/or foxes (Gorchov 1987a).

Flowering phenologies were studied for nine of the species; fruiting for all 12. Individual plants were selected to represent a range of sizes and site conditions for each species. All flowers or fruits were censused on plants where this number was small (<75); otherwise flowers and fruits on selected inflorescences were censused. In most cases selection was random or haphazard; in some cases it was constrained by the accessibility of branches. Flowers and fruits were censused daily or every other day. Inflorescence selection methods and census frequencies are detailed in Gorchov (1987a). Calendar dates were converted to Julian days for statistical analyses.

Criteria for phenological events

A flower was considered "open" when the stigma was visible through the petals, because at this stage it was presumably accessible to pollinators. Flowers were censused in the mid- to late morning or during the early afternoon. Fruits were considered ripe when they reached the final color in the ripening process (Table 1).

Quantification of synchrony

Flowering synchrony was quantified as the standard deviation (SD) of the opening dates for the censused flowers on an individual plant; lower SD signifies greater synchrony. Similarly, ripening synchrony was measured as the SD of ripening dates for censused fruits. SD is highly correlated with a second measure of synchrony: the minimum number of consecutive days that included $\geq 90\%$ of the events (Gorchov 1987a).

Flowering vs fruiting synchrony

Within-plant analyses

In order to test if ripening synchrony differed significantly from flowering synchrony for individual plants, variance (SD^2) in flowering date was compared to variance in ripening date using the F test for Homogeneity of Variances (Sokal and Rohlf 1981). Plants from seven species were used in this analysis. The number of plants of each species with sufficient data (opening dates for \geq 30 flowers and ripening dates for \geq 30 fruits) ranged from 14 for *Amelanchier arborea* to one for several species. On some, but not all, plants the fruits monitored included only those that developed from the monitored flowers (Table 3).

Among-plant analyses

If flowering synchrony constrains fruit ripening synchrony, then plants with more synchronous flowering should have more synchronous ripening. This prediction was tested by measuring the correlation between within-plant flowering synchrony and within-plant ripening synchrony among conspecific individuals. This analysis was done both for a species characterized by synchronous ripening (*Prunus virginiana*) and for an asynchronous ripener (*A. arborea*). For each species both flowering and fruiting phenologies were recorded for the same set of plants in 1984.

Among-species analyses

For a summary measure of within-plant flowering synchrony for each species, I used the unweighted mean of within-plant flowering SD values for all individuals of that species (henceforth: "Mean Flowering SD"). For each species, I calculated "Mean Ripening SD" in an analogous fashion. These measures were used in product-moment and rank-order correlations to test whether there was a significant relationship between flowering and fruiting synchrony among species.

Effects of crop size and removal

Crop size

The relationship among conspecific individuals between ripening synchrony and fruit crop size was explored by product-moment correlation. Rank correlation was used for *A. arborea* because crop size estimates in this species were not precise. Analyses were done for all species X year combinations for which both crop size and within-plant ripening synchrony data were available for \geq six plants.

Fruit removal

To test if the presence of ripe fruit affects the ripening of nearby fruit I compared fruit ripening dates on branches on which fruits were removed as they ripened to those on branches protected from frugivores with exclosures. I chose three plants of a species with synchronous ripening, *P. virginiana*, and three of an asynchronous ripener, *A. arborea*, all growing in moderate shade. On each plant I chose three branches or groups of adjacent branches on different parts of the plant but with similar, large numbers of fruit. Just before ripening began (15 June 1984 for *A. arborea*, 16–18 July 1984 for *P. virginiana*) one branch was randomly assigned to the removal treatment and the other to the retention (exclosure) treatment.

Exclosures were made of Ross Garden Net polypropylene (mesh 1.8 cm) in order to exclude birds and mammals but negligibly affect light, air, or moisture.

Fruits were censused daily (*P. virginiana*) or every 2 d (*A. arborea*). In the removal treatment, fruits were removed when partially ripe. These removal dates were compared with the dates fruits in the retention treat-

Table 2. Grand mean fruit ripen	ing date, ripening season	, ripening synchrony (SD) of fruit ripening	events on a plant; units are
days), and flowering synchrony	(SD of flowering events of	on a plant; units are days	s) for the 12 study	y species.

Species	Mean ripe	Season	Ripe	ening SD	Flowering SD	
	date	date	N ^a	Mean	N	Mean
Ilex verticillata	20 Sep.	Autumn	8	4.66	6	1.64
Nemopanthus mucronatus	8 July	Summer	7	2.87		
Cornus amomum	14 Aug.	Autumn	9	3.74	7	2.17
C. florida	21 Sep.	Autumn	6	5.79		
C. foemina	22 Aug.	Autumn	12	3.53	7	1.17
C. stolonifera	29 June	Summer	10	2.95		
Gavlussacia baccata	31 Julv	Summer	10	8.61	9	4.86
Vaccinium corvmbosum	22 July	Summer	16	10.58	11	3.91
Amelanchier arborea	23 June	Summer	19	7.04	16	1.01
Aronia prunifolia	14 Aug.	Autumn	9	4.54	10	2.19
Prunus serotina	29 Aug.	Autumn	10	6.74	7	1.44
P. virginiana	26 July	Summer	13	2.71	12	1.19

^aNumber of plants

ment reached the same partially ripe color. Frugivorous insects were removed from both treatments as encountered to minimize fruit damage.

For A. arborea ripening date was analyzed by twoway ANOVA with treatment and plant as independent variables. Two-way ANOVA was not appropriate for P. virginiana because the assumption of homogeneity of variance was violated; instead ripening dates on removal and protection branches were compared for each plant by Mann-Whitney U Test. To test the effects of these treatments on ripening synchrony, I compared for each plant the variance in ripening date for a) removal and b) protection branches using the F Test for Homogeneity of Variances.

Patterns among species in ripening synchrony

Season of ripening

For each species I calculated the unweighted mean of all individual plant mean ripening dates. This grand mean was used to assign each species to one of two seasons (Table 2) based on breeding and migration dates of frugivorous birds in southeastern Michigan and adjacent Ontario (summarized in Gorchov 1987a). "Summer" is the period when most bird species are nesting and extends from the earliest fruit ripening (late May) until early August. "Autumn" begins when most resident bird species have completed breeding and the early autumn migrants from further north have arrived (mid-August). These definitions are based on criteria referred to in other investigations of bird-fruit interactions in temperate eastern North America. Thompson and Willson (1979) considered species ripening fruits in late August "fall" fruiters, and Stiles (1980) characterized 19 August-ripening species as "fall" species and only nine August-ripeners as "summer" species.

To explore whether results of comparisons based on this categorization were robust, I 1) repeated each analysis adding each of four earliest "autumn" species sequentially to the "summer" category, and 2) used the grand mean ripening date itself as a continuous measure of ripening period.

Dual color change

Species were considered to have dual color change during ripening if partially ripe fruits had a color that was distinct from both unripe and completely ripe fruit. This was the criterion used by Stiles (1982), who called these "preripe fruit flags" and by Willson and Thompson (1982), who referred to "temporally bicolored" fruit displays. Five of my 12 study species were scored by Willson and Thompson (1982) as having temporally bicolored fruit displays. I added *Gaylussacia baccata* to this group (Table 1) because its fruits pass through a red stage during ripening and eventually turn black. The partially ripe fruits of the other six species are either duller shades of the ripe color or partly green and partly ripe colored.

Seed number

Fruit ripening date is negatively correlated with the number of seeds per fruit within individuals in two of the study species, *A. arborea* and *V. corymbosum* (Gorchov 1985). This finding suggests that ripening may be more asynchronous in those species characterized by a variable number of seeds per fruit. To test this hypothesis the number of developed seeds per fruit was sampled for each species (Table 1). Seed number was constant in the four *Cornus* and two *Prunus* spp. (all one-seeded) and in *G. baccata* (nearly always 10 seeds per fruit) and variable in the other five species.

Growth form

Most species could be unequivocally designated as tree or shrub (Table 1). *P. virginiana* usually grew as a shrub but some individuals were small trees. In overall size and fruit number *P. virginiana* tended to be intermediTable 3. Variances in flower opening and fruit ripening dates for individual plants, ratios of these variances, and F-tests for the homogeneity of these variances. Variances are in days². N = Number of flowers or fruits censused; fruit number followed by ^b indicates that only fruits that developed from sampled flowers were monitored, on other plants additional fruits were also monitored. * P <0.05, ** P <0.01, *** P <0.001.

Family and species	Year	Plant	Flo	wering	Fruit	ripening	Ratio	F-test
		number	N	Variance _F	N	Variance _R	Var _R /Var _F	
AOUIFOLIACEAE								
Ilex verticillata	1983	1	34	1.34	30 ^b	7.8	5.8	* * *
		2	94	1.10	82 ^b	6.4	5.8	* * *
	1985	1	76	2.92	59 ^b	64.2	22.0	* * *
	1700	2	75	8.95	36	56.8	6.34	***
CORNACEAE								
Cornus amomum	1983	3	274	4.84	43	8.2	1.69	*
C. foemina	1983	1	400	1.80	42	4.8	2.67	***
ERICACEAE								
Gaylussacia baccata	1983	6	124	22.84	51 ^b	49.4	2.16	**
, ,		10	117	24.30	70 ^b	55.1	2.27	**
ROSACEAE								
Amelanchier arborea	1984	E3	68	1.04	72	51.3	49.3	***
		E4	51	1.02	58	36.2	35.4	***
		E5	86	1.32	63	24.9	18.8	* * *
		E6	88	2.96	62	45.1	15.3	* * *
		E7	91	1.32	59	71.8	54.3	* * *
		E9	79	0.83	65	38.0	18.3	* * *
		E10	103	1.00	67	79.1	79.1	* * *
		B 8	562	1.44	56 ^b	31.6	21.9	* * *
		B27	79	0.90	70	34.1	37.8	* * *
		B28	85	1.19	60	48.3	40.7	* * *
		B29	94	1.44	66	88.8	61.7	* * *
	1985	E7	87	0.25	45	63.4	254	* * *
		B 8	89	0.24	39	31.8	133	* * *
		B28	587	0.51	180 ^b	47.1	92.4	* * *
Prunus serotina	1983	1	278	2.37	41	62.7	26.5	***
		2	295	2.89	34	53.6	18.5	* * *
		4	306	3.13	129	68.9	22.0	* * *
	1984	4	288	0.72	32	22.4	31.4	* * *
P. virginiana	1984	5	558	0.98	76	9.5	9.7	* * *
0		9	182	1.88	62	6.7	3.6	* * *
		10	236	1.44	88	3.9	2.7	* * *
		30	308	0.98	86	10.1	10.3	* * *
		36	150	0.71	43	12.0	16.8	* * *
	1985	30	141	0.83	69	9.3	11.2	* * *

^aRatio compared to values of F with N_R, N_F degrees of freedom

* p <0.05, ** p <0.01, *** p <0.001,

^bincludes only fruits derived from the sample of flowers monitored, on other plants additional fruits were also monitored.

ate between the tree and shrub species included in the study.

Statistical analyses

One-way analyses of variance (ANOVAs) were used to test for differences in Mean Ripening SD (within-plant ripening synchrony) among categories of species. For each ANOVA, the assumption of equality of variance was found to be valid. Functional dependence of Mean Ripening SD on 1) Mean Flowering SD and 2) grand mean ripening date was explored with linear regressions. Although not all of these variables were normally distributed, the crucial assumption of linear regression – that the residuals show no dependence on the design (independent) variable – was met in each case. The relationship between Mean Flowering and Ripening SD was also analyzed using the non-parametric ordering test (equivalent to Kendall's rank correlation).

These statistical tests all assume independence of the different species, an assumption that may be violated in comparative studies when all study species are not equally related phylogenetically (Felsenstein 1985). To address the possible dependence of related species (i.e. phylogenetic inertia), species were grouped by plant family and Mean Ripening SD was compared among these groups by ANOVA.



Flowering SD (days)

Fig. 1. Within-plant fruiting synchrony (standard deviation of fruiting dates) vs within-plant flowering synchrony for 11 *Amelanchier arborea* plants, 1984.

Results

Flowering vs fruit ripening synchrony

Within plants

All plants studied opened flowers significantly more synchronously than they ripened fruits (Table 3). This was true for individuals of species with relatively synchronous ripening (*P. virginiana, Ilex verticillata, Cornus amomum* and *C. foemina*) as well as for individuals of relatively asynchronously ripening species (*A. arborea, P. serotina, and G. baccata*).

Among plants

Flowering synchrony was not correlated with fruit ripening synchrony among individual plants of A. arborea, a species with asynchronous fruit ripening (Fig. 1, r = -0.08, n = 11). There was a tendency for flowering synchrony to be negatively correlated with fruiting synchrony in P. virginiana, a synchronous ripener, but this was not significant (Fig. 2, r = -0.78, n = 5, P > 0.05). In neither species did plants with more synchronous flowering have more synchronous fruit ripening.

Among species

The regression of Mean Ripening SD on Mean Flowering SD was significant ($r^2 = 0.49$, P <0.05, Fig. 3) among the nine species for which both phenologies were quantified, although the rank correlation was not (Kendall's tau = 0.28, P >0.30). The significance of this regression was attributable to the two species in the family Ericaceae, V. corymbosum and G. baccata, which have very asynchronous flowering and fruiting. When these two species are excluded from the analysis, the rank correlation among the remaining seven species



Fig. 2. Within-plant fruiting synchrony vs within-plant flowering synchrony for five *Prunus virginiana* plants censused in 1984.

was not significant (tau = -0.14, P > 0.70; linear regression inappropriate because residuals dependent on flowering synchrony).

Effects of crop size and removal

Crop size

For none of the seven species with adequate data was there a significant correlation among plants between crop size and ripening synchrony (Table 4). Sample sizes



Mean Flowering SD (days)

Fig. 3. Mean Ripening SD (within-plant ripening synchrony) vs Mean Flowering SD for nine vertebrate-dispersed woody plant species. Numbers refer to species (Tab. 1). The regression line is Y = 1.36 X + 2.85 (r² = 0.49, P <0.05). Symbols refer to plant family: \triangle = Aquifoliaceae, \square = Cornaceae, \diamondsuit = Ericaceae, \bigcirc = Rosaceae. Filled symbols are tree species, open symbols are shrubs.

Table 4. Correlation between fruit crop size and ripening synchrony (SD of ripening dates within plants) among conspecific individuals. Pearson product-moment correlation coefficients are given for all species except A. *arborea*, for which the Spearman's rank-order correlation coefficient was calculated because estimates of crop size were not precise. None of the correlations were significant (P < 0.05).

Species	Year	No. of plants	Fruit crop size (range)	SD of ripening (range)	Correlation
Cornus amomum	1985	8	99–1029	3.0–5.2	0.19
C. stolonifera	1986	6	83-340	2.4-3.9	-0.18
Gavlussacia baccata	1985	8	80-246	5.9-14.8	-0.5
Vaccinium corymbosum	1985	10	76–1000	6.7–16.9	0.10
Amelanchier arborea	1985	7	42-600	5.1-8.5	0.56
Aronia prunifolia	1986	6	75-330	4.2-5.0	0.76
Prunus virginiana	1984	6	67-320	1.7-3.5	0.40
	1985	6	41–1654	1.9-4.9	-0.47

were small, however, so the conclusion that ripening synchrony is unrelated to crop size remains tentative.

Fruit removal

On two of the three *P. virginiana* plants ripening occurred *earlier* on the branch from which fruits were removed as they ripened than on the branch in the exclosure (Table 5: plant #21, U = 79.5 and plant #52, U = 1173.5, each P <0.001). However, on the third plant ripening was later on the removal branch (U = 1751, P <0.01). In each case the difference was small, however, only 0.7 to 2.2 days separated the mean ripening dates for the two treatments on the same plant (Table 5). On the first two plants ripening *synchrony* did not differ between the treatments but on the third plant ripening was more synchronous on the removal branch (Table 5, F = 1.9, df = 67, 68, P < 0.01).

There was no significant effect of fruit removal on ripening *date* in *A. arborea* (Table 5, F = 1.0, df = 1, 326). Ripening dates did differ significantly among the three plants (F = 13.3, df = 2, 326, P < 0.001) but there

Table 5. Effect of removal (R) vs protection (P) of ripe fruit on mean ripening date and ripening synchrony (SD) in *Prunus virginiana* and *Amelanchier arborea*. N = number of fruits on the manipulated branch. Units for x and SD of ripening date are in days; for *P. virginiana* day 1 = 1 July, 1984, for *A. arborea* day 1 = 1 June, 1984.

Species	Plant	int Treatment		Ripening date			
	number		N	x	SD		
P. virginiana	21	R	30	21.3	1.1		
0		Р	23	22.7	0.9		
	52	R	77	26.0	2.1		
		Р	67	28.1	2.1		
	53	R	69	24.1	1.2		
		Р	68	23.4	1.7		
A. arborea	6	R	92	34.6	8.6		
	-	Р	66	34.7	8.5		
	18	R	64	30.7	9.3		
	10	P	41	30.5	10.0		
	34	R	27	30.1	7.5		
	5.	Р	42	26.9	9.1		

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was no significant plant-treatment interaction (F = 0.8, df = 2, 326). For none of the three plants was there a significant difference in ripening *synchrony* between removal and retention branches (Table 5).

Patterns among species in ripening synchrony

No seasonal pattern in within-plant ripening synchrony was evident (Fig. 4). Autumn-fruiters were not more synchronous than summer-fruiters (Tables 2, 6). This lack of a seasonal difference was maintained regardless of whether some or all of the mid- to late August fruiting species are considered summer rather than autumn fruiters; for these other groupings the F values were smaller than that reported in Table 6. The regression between Mean Ripening SD and grand mean ripening date for the twelve study species was not significant ($r^2 = 0.00$).

The six species with fruits that go through a dual color change during ripening had marginally more asynchronous ripening than did the six with only a single color change (Table 6). However, one of the species with dual



Fig. 4. Mean Ripening SD vs grand mean ripening date for 12 vertebrate-dispersed woody plant species. Numbers and symbols are as in Fig. 3.

Table 6.	One-way analyses of variance	(ANOVAs) on Mean	Ripening SD f	or the 12 study spe	cies. $N = Number$ of species i	in
category	. For each category the mean	of the species' "Mean	Ripening SD"	(Tab. 2) values is gi	ven. $N.S. = not significant.$	

Independent Variable	Category	Ν	Mean Ripening SD	df	F	
Season of ripening	Summer Autumn	6 6	5.8 4.9	1,10	0.4	N.S.
Color change during ripening	Single Dual	6 6	3.9 6.7	1,10	5.0	$\mathbf{P}=0.05$
Seed number	Constant Variable	7 5	4.9 6.0	1,10	0.5	N.S.
Growth form	Tree Shrub	3 9	6.5 4.9	1,10	0.9	N.S.
Plant family	Aquifoliaceae Cornaceae Rosaceae Ericaceae	2 4 4 2	3.8 4.0 5.3 9.6	3,8	6.2	P <0.05

color change, *P. virginiana*, showed the most synchronous ripening of all the species.

Species with a constant number of seeds did not differ significantly in Mean Ripening SD from those with variable seed numbers nor did trees differ from shrubs (Table 6).

Plant family accounted for more of the variation in Mean Ripening SD than did any of the other independent variables, accounting for 70% (eta²) of the variance among species (P <0.05, Table 6). Subdividing the Rosaceae into the subfamilies Pomoideae (*A. arborea* and *Aronia prunifolia*) and Prunoideae (*Prunus* spp.) did not improve the amount of the variance explained (F = 4.4, df = 4, 7, P <0.05 eta² = 0.71).

The significance of this ANOVA was attributable to the high mean for the Ericaceae; the two most asynchronous ripening species are members of this family. When the two ericaceous species were omitted, the ANOVA on the remaining families was not significant (F = 0.8, df = 2, 7). Aquifoliaceae and Cornaceae were characterized by synchronous ripening, and ripening was variable but typically synchronous among species in the Rosaceae.

Analysis excluding ericaceous species

Although Mean Ripening SD was found to be significantly related to both plant family and Mean Flowering SD, both relationships were dependent on the inclusion of the two species in the Ericaceae. To test if the asynchronously ripening ericaceous species masked patterns in ripening synchrony among the other species, the above analyses were repeated for the latter group.

Among the 10 non-ericaceous species, season of ripening still did not explain a significant proportion of the variance in Mean Ripening SD (F = 0.9, df = 1, 8). Nor was the regression of Mean Ripening SD on mean ripening date significant ($r^2 = 0.06$, P >0.40). With the exception of the earliest ripening species, A. arborea, there was a trend among the non-ericaceous species for ripening to be less synchronous later in the season (Fig. 4), opposite of the predicted pattern.

There was no tendency among the 10 non-ericaceous species for species with dual color change during ripening to have more asynchronous ripening than those with a single color change or for species with variable seed number to be more asynchronous (F = 1.7 and F = 0.3, respectively, df = 1, 8 for both).

Growth form did account for a significant proportion of the variance in Mean Ripening SD among these 10 species (F = 29.2, df = 1, 8, P <0.001, eta² = 0.78): trees had more asynchronous ripening than shrubs. This relationship remains highly significant if *P. virginiana* is excluded from the analysis, but is only marginally significant (F = 4.3, df = 1, 8, P = 0.07) if *P. virginiana* is classified as a tree.

Discussion

Flowering and fruiting synchrony

Fruit ripening synchrony appears sufficiently uncoupled from flowering synchrony that it can respond independently to selection. Among conspecific individuals of the two species investigated, there was no positive correlation between flowering and fruiting synchrony. Among the nine study species the relationship between Mean Flowering and Ripening SD was not strong and broke down when ericaceous species were excluded.

Flowering does appear to impose one constraint on fruiting synchrony, however: fruiting is always less synchronous than flowering. Not only is Mean Ripening SD greater than Mean Flowering SD for each of the nine species, but within individuals fruiting was always found to be significantly more asynchronous than flowering (7 species, 1 - 14 individuals per species). The

pattern of more asynchronous fruiting than flowering has also been reported for other species (e.g. *Piper arieanum* (Marquis 1988)).

Why is ripening more asynchronous than flowering? Obviously there must be at least some variance in the flower-fruit interval within a plant, but this variance need not necessarily lead to more asynchronous ripening. For instance, if flower-fruit interval were shorter for fruits from later flowers, then ripening would be more synchronous than flowering. Such a negative correlation could result either from delayed allocation of maternal resources to fruits developing from early flowers (Lee and Bazzaz 1982), or a dependence of ripening on an environmental cue. However, negative correlations between flowering date and flower-fruit intervals were not found within individuals of three species (A). arborea, I. verticillata, and V. corymbosum) in which individual flowers were followed through fruit development and ripening (Gorchov 1985, 1987a).

The absence of significant correlations between the flowering date and flower-fruit interval indicates that these phenological variables contribute independently to variance in ripening. This independence, plus the great variability in flower-fruit interval, resulted in ripening phenologies that were much more asynchronous than flowering phenologies.

Thus a proximate explanation for the observed asynchronous ripening in these species lies not in asynchronous flowering but rather in the causes of the variance in the flower-fruit interval. There is a strong correlation between the length of the flower-fruit interval and the number of full seeds in a fruit within individuals of *A*. *arborea* and *V. corymbosum*; in both species, fruits with more seeds developed faster (Gorchov 1985). However, the present study shows that species in which seed number per fruit is variable do not have more asynchronous ripening than species with constant seed number, illustrating that a factor important in explaining a phenological pattern within a species may fail to explain patterns among species.

Seasonal patterns in ripening synchrony

Among the 12 species studied there was no tendency for autumn ripeners to show more synchronous withinplant ripening than summer ripeners, contrary to the pattern described by Thompson and Willson (1979) for their study site in Illinois. Although there may be differences of opinion as to whether a particular species should be considered "summer-" or "autumn-ripening", the absence of a seasonal pattern is a robust result: it is obtained regardless of whether species ripening fruits in August are considered summer- or autumn-ripeners. Exclusion of the two ericaceous species does not change this result. A similar lack of difference in ripening synchrony between summer-fruiting species and species fruiting in other seasons has been demonstrated for bird-dispersed species in northern Florida (Skeate 1987).

Any differences that may exist between regions in seasonal patterns of within-plant ripening synchrony may be due to different selective forces acting on plants due, for example to climate or patterns in seasonal bird abundances. Skeate's (1987) study was done in northern Florida where the growing season is much longer and winter populations of frugivorous birds are greater than in Illinois or Michigan, permitting winter fruiting. However, even at this low latitude, frugivorous birds are more abundant in the autumn than in the summer (Skeate 1987), a key assumption in Thompson and Willson's (1979) model. Climatic constraints would be expected to be similar between Illinois and Michigan, as the two study sites are only 450 km apart. However, selective factors may differ over such relatively short distances: an abundant summer frugivore at the Michigan site, the cedar waxwing, was not important in Illinois (Thompson and Willson 1979).

Despite potential differences among regions in selective factors, within-plant ripening synchrony appears to be a conservative character. Of the three species for which ripening synchrony has been quantified at more than one site, none shows a qualitative difference between sites: Cornus foemina (= C. racemosa) is among the most synchronous species both in Florida and Michigan (Skeate 1987 and this study, Table 2), Phytolacca americana is among the most asynchronous both in Florida and Illinois (Skeate 1987, Thompson and Willson 1979), and Prunus serotina is among the most asynchronous in Michigan and Illinois (Table 2 and Thompson and Willson 1979).

Seasonal timing of fruit ripening may be more variable among regions than is synchrony. While the order in which species fruit is constant from year to year within a site (Gorchov 1987b), this consistency does not hold between regions. For example, in Illinois *P. sero*tina ripens fruits in the summer (Jul-Aug), before *C.* foemina (Aug-Sep) (Willson and Thompson 1982), whereas in Michigan both species ripen fruit in Aug and Sep, with *C. foemina* tending to be somewhat earlier than *P. serotina* (Table 2). Thus in Illinois the more asynchronous species ripens fruits earlier, but in Michigan the more synchronous species is earlier.

Whatever the reason, the lack of support for the summer/autumn dichotomy in fruit ripening synchrony noted by Thompson and Willson (1979) weakens their hypothesis that asynchronous ripening is an adaptation to avoid satiation of frugivorous birds in the summer. However, a more direct test of this hypothesis would involve manipulation of ripening synchrony and testing for effects on frugivore satiation or dispersal success of the plants. This experiment has been done on *A. arborea*, an asynchronous summer fruiter, with the finding that more synchronous ripening does not slow fruit removal (Gorchov 1988).

Dual color change

Species with fruits that go through a dual color change during ripening showed more asynchronous ripening than those species with fruits that pass through only a single color change. This pattern had been noted, but not documented by Stiles (1982) and Willson and Thompson (1982), who argued that dual color change and asynchronous ripening work together to produce a temporally bicolored fruit display which enhances dispersal during the summer, when dispersers are not abundant. (Partially ripe fruits are presumed to be less susceptible to insects and microbes than ripe fruits, but to contribute to the conspicuousness of the display to frugivorous birds). According to this hypothesis, dual color change plus asynchronous ripening allow a plant to maintain a large colorful display of partially ripe fruits to attract dispersers, while ripening few fruits per day, thus reducing the probability of local dispersers becoming satiated. However, field studies of temporally bicolored fruit displays have provided mixed support for the hypothesis that they enhance fruit removal by dispersers (Morden-Moore and Willson 1982, Willson and Melampy 1983, Greig-Smith 1986).

The relationship between ripening synchrony and dual color change found in this study might be due simply to phylogenetic inertia. All six study species with dual color change were in the Ericaceae or Rosaceae, whereas the six species with only a single color change were in the Aquifoliaceae or Cornaceae, and plant family was the best predictor of ripening synchrony (see below). However, Willson and Thompson (1982) argue that dual color change is an evolutionarily plastic trait, present in some but not all species in certain families and genera.

Phylogenetic patterns

Plant family was the single best predictor of ripening synchrony. The two ericaceous shrub species were the most asynchronous species; when they were excluded from the analysis the ANOVA of Mean Ripening SD on the remaining three families was not significant. The asynchronous ripening in the two ericaceous species may be related to their very asynchronous flowering.

A relationship between ripening synchrony and plant family is also apparent in a reanalysis of Skeate's (1987) data for northern Florida. Plant family accounts for 87% (eta²) of the variance in ripening synchrony among the 30 species (16 families) in his study (using means of two years' data; F = 6.5, df = 15, 14, P < 0.001). When the analysis is limited to the nine families with more than one species represented, family accounts for 74% of the variance (F = 5.0, df = 8, 14, P < 0.005, 23 species). The four families represented by my study species are a subset of these nine families. These four families have identical rankings of mean ripening synchrony in the two studies: Aquifoliaceae is the most synchronous, followed by Cornaceae, Rosaceae, and Ericaceae. This concordance is not due the inclusion of the same species; only one species (C. foemina) was included in both studies. Phylogeny has also been shown to be a major factor determining seasonal timing of flowering (Kochmer and Handel 1986).

Growth form

Most of the variation in ripening synchrony among the 10 non-ericaceous species is accounted for by growth form: trees are more asynchronous than shrubs. This tendency for trees to have more asynchronous ripening than shrubs is also apparent in the wet forest of Costa Rica, where 46 of the tree species but only 34% of the treelet and shrub species show "extended fruiting" (duration for individual plants longer than two weeks) (Opler et al. 1980). Growth form is also correlated with seasonal timing of flowering (Kochmer and Handel 1986).

I propose two post hoc hypotheses for the more asynchronous ripening within individual trees, one adaptive and one non-adaptive. The adaptive explanation is a modification of Thompson and Willson's (1979) frugivore satiation model. Because trees are larger than shrubs, they generally have larger fruit crops and hence ripen more fruits per day, given equivalent ripening synchrony. Thus, if dispersers are scarce and territorial, the tree is more likely to satiate dispersers than is the shrub, and it would be more likely to improve its seed dispersal by asynchronous ripening. This model suggests that the frugivore satiation hypothesis may apply to trees but not to shrubs, rather than to species fruiting during any particular season.

The non-adaptive explanation involves two consequences of the greater spatial distribution of fruits on trees versus shrubs. First, fruits on a tree probably experience a greater range of microclimate (light, temperature, humidity) than fruits on a shrub, and if these environmental variables affect the length of the flowerfruit interval (as in some cultivated fruits, Tukey 1952, Rylski 1979), then fruits on a tree should show greater variation in flower-fruit interval, and hence less synchronous ripening. Within a species, larger individuals presumably have greater variation in fruit microclimate and hence would be expected to have less synchronous ripening. I did not investigate the relationship between ripening synchrony and individual size, but I did test for correlations between ripening synchrony and crop size among individuals of each of seven species and found no significant trends (Table 4).

A second consequence of the wider spatial distribution of fruits on a tree vs a shrub is the longer maximum internal distance between fruits. Local changes in internal chemistry (water, photosynthate, nutrients, hormones) due to microclimate, herbivores, or pathogens are likely to affect the development of nearby fruits more than more distant fruits. To the extent that interfruit distances are greater in trees, they should be less physiologically integrated than shrubs. This reduced integration should result in more pronounced local effects, hence greater variation in flower-fruit interval and less synchronous ripening.

Other hypotheses

Asynchronous ripening may be a bet-hedging strategy against uncertainty in establishment opportunity (Bawa 1983, Rathcke and Lacey 1985). Specifically, for temperate, small-seeded, summer-fruiting species, asvnchronous ripening may be adaptive because it results in staggered seed germination in an environment with temporally unpredictable summer rainfall (Stapanian 1982). However, seeds of only one of the 12 species studied here (V. corymbosum) germinate in the same growing season as they disperse (Schopmeyer 1974, data incomplete for N. mucronatus). The remaining species require a cold period for germination and hence germinate during the spring following dispersal or later; for these species germination synchrony is likely to be uncoupled from dispersal synchrony.

Alternatively, asynchronous ripening may be an adaptation to ensure some dispersal if dispersers are temporally unpredictable and ripe fruits cannot persist because they are subject to rapid decay, predation, or drop (Herrera 1982, Gorchov 1988). A tendency for the more synchronous of the study species to have more strongly attached ripe fruit provides preliminary support for this hypothesis (Gorchov 1988).

Another possibility is that plants can adjust their ripening rates in response to fruit removal. In a Neotropical shrub, Hamelia patens, removal of ripening fruits speeds the ripening of other fruits on an infructescence (Levey 1987). However, removal of fruits as they ripened did not have a consistent effect on ripening synchrony in the two species investigated in this study. Similarly, fruit removal does not affect ripening synchrony in a Phytolacca americana, a fleshy-fruited temperate herb (McDonnell et al. 1984). These findings suggest that the dependence of ripening synchrony on fruit removal, as found for Hamelia, is not a general phenomenon among vertebrate-dispersed plants.

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