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SEQUENCE OF FRUIT RIPENING IN BIRD-DISPERSED PLANTS: CONSISTENCY AMONG YEARS¹

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In recent years there has been increased interest in the ecology and evolution of plant phenologies (Rathcke and Lacey 1985). Long-term records are needed to address some recently posed problems, but few long-term records are available. Most of these are limited to flowering records. Here I introduce biologists to a valuable but neglected source of phenological data, and use some of these data to test for consistency in the ripening sequence of plant species that potentially compete for avian seed dispersal agents.

Studies of the possible coevolution of interacting species require a knowledge of the consistency of their interactions over time (Rathcke and Lacey 1985). For example, the potential for competition (or facilitation, *sensu* Rathcke 1983) between two species of plants for the dispersal services of birds depends partly on whether

the plant species ripen their fruits at the same time. Fruit-ripening times of a species at a single location are known to vary from year to year, but most studies of the ripening phenologies of bird-dispersed plants have been limited to a single year (see Thompson and Willson 1979, Baird 1980, and Stapanian 1982, for eastern North America). Plants that fruit coincidentally one year may fruit at different times in other years. Thus any competition for dispersers would occur irregularly and would be unlikely to result in coevolution. Of the few studies that document ripening phenologies over > 1 yr, only Sherburne (1972) and Skeate (1985) (both 2-yr studies) were done in temperate North America.

From 1883 to 1912 phenological and meteorological records were recorded by Thomas Mikesell in Wauseon, Ohio (41°36' N, 84°07' W) (Smith 1915). The meteorological records include daily precipitation and minimum, maximum, and mean temperatures. The phenological observations include dates of flowering of 114 herb species, dates of leafing, flowering, and fruiting of 48 forest species and 16 edible fruit-bearing species, and dates of planting, flowering, and fruiting of 20 field and garden crops. A single date is listed for each phenological event, and I assume this marks the first date the condition was observed, rather than a date of peak activity. The completeness of these data vary among the species; for the forest species they are

TABLE 1. Variation in "fruit ripe" date (presumably the first date ripe fruit were observed) for 15 species of bird-dispersed plants in Wauseon, Ohio. Data from Smith (1915). Nomenclature follows Smith (1915) except where noted.

Species†	Date fruit ripe*		
	\bar{X}	SD (days)	Range
<i>Gaylussacia baccata</i>	21 Jul	5	15–28 Jul
<i>Vaccinium vacillans</i>	21 Jul	5	16–28 Jul
<i>Sambucus canadensis</i>	18 Aug	9	2 Aug–1 Sep
<i>Cornus amomum</i>	26 Aug	10	15 Aug–10 Sep
<i>Sassafras albidum</i> ‡	4 Sep	13	20 Aug–25 Sep
<i>Celastrus scandens</i>	6 Sep	15	15 Aug–25 Sep
<i>Parthenocissus quinquefolia</i>	10 Sep	13	25 Aug–30 Sep
<i>Rhus typhina</i> §	14 Sep	14	25 Aug–8 Oct
<i>Toxicodendron radicans</i> ¶	14 Sep	12	30 Aug–5 Oct
<i>Menispermum canadense</i>	18 Sep	15	20 Aug–5 Oct
<i>Rosa virginiana</i>	19 Sep	14	1 Sep–2 Oct
<i>Crataegus intricata</i> #	22 Sep	6	11–28 Sep
<i>Euonymus atropurpureus</i>	26 Sep	20	28 Aug–20 Oct
<i>Cornus florida</i>	28 Sep	12	12 Sep–15 Oct
<i>Viburnum prunifolium</i>	29 Sep	9	15 Sep–12 Oct
<i>Rosa carolina</i>	7 Oct	14	5 Sep–20 Oct

* For the eight years 1886–1892, 1894 except for *G. baccata* and *V. vacillans*; for these spp. data are for five years: 1887, 1889–1892.

† Names used by Smith (1915): ‡ *S. variifolium* (Salisb.) Kuntze; § *R. hirta* (L.) Sudw.; ¶ Poison Ivy (no Latin name); # *C. coccinea* L.; || Flowering Dogwood (no Latin name).

most complete for 1884–1899. No information is provided on the specific criteria used to score each phenological event, the number of individuals observed for each species, the spatial distribution of the plants, nor the frequency of observations. However, there is no reason to believe that these methods varied among years or that the data are unreliable for any reason. Smith (1915) stresses that Mikesell was "very accurate in all his records and observations."

Of the 48 forest species observed by Mikesell, 16 are bird-dispersed (Baird 1980, Stiles 1980, and congeners to species listed by Stiles 1980) and have both "in blossom" and "fruit ripe" dates listed for at least 5 yr. These 16 species have among-year ranges of fruit ripening dates that vary from 12 d for *Vaccinium vacillans* (SD = 5 d) to 53 d for *Euonymus atropurpureus* (SD = 20 d) (Table 1).

Despite the variability in ripening dates of each species, the ripening order of the 16 species was similar over the 5 yr for which data are available for all species (1887, 1889–1892) (Kendall's coefficient of concordance, $W = 0.79$, $P < .001$). For 14 of these species the data are complete for an additional 3 yr (1886, 1888, 1894); when the analysis is extended to cover all 8 yr this concordance is maintained ($W = 0.61$, $P < .001$). The high degree of consistency in ripening order

from year to year indicates that the same species tend to overlap in fruiting each year. Conclusions about overlap would be stronger if the duration of fruit ripening and persistence were known.

For species that are also associated spatially, this temporal consistency in ripening sequence suggests that any interspecific competition or facilitation for seed dispersers (Snow 1965, Herrera 1981, Denslow and Moermond 1982, Wheelwright 1985) would tend to occur among the same set of bird-dispersed species each year. These interactions are likely to be strongest when fruiting peaks overlap; unfortunately, the dates of peak fruiting are not provided in Smith (1915). My assumption that the "fruit ripe" dates refer to the onset and not the peak of fruiting is supported by the similarity of the listed fruiting dates with the dates ripe fruit are first observed in southeastern Michigan for *G. baccata*, *S. canadensis*, *C. amomum*, *S. albidum*, *C. florida*, and *R. carolina* (D. L. Gorchoff, personal observation) and in eastern Kansas for *S. canadensis*, *P. quinquefolia*, and *M. canadense* (Stapanian 1982).

If interactions between fruiting species are consistent from year to year, as suggested by this analysis, then natural selection can act directionally on plant traits (e.g., size and ripening synchrony of the fruit crop; fruit color, size, nutritional composition) that improve competitive ability, avoid competition (e.g., adapt to a different disperser), or enhance facilitation.

The consistency in ripening sequence demonstrated here may be due to consistency in flowering sequence.

TABLE 2. Correlations of "flower" date and "fruit ripe" date for 15 bird-dispersed plants in Wauseon, Ohio. Dates are presumed to be the first that open flowers and ripe fruits were observed. Data from Smith (1915).

Species	No. years of data	Mean interval between flower and ripe fruit (d)	Correlation (r)
<i>Sambucus canadensis</i>	14	62	0.72**
<i>Gaylussacia baccata</i>	13	65	0.69**
<i>Vaccinium vacillans</i>	12	66	0.73**
<i>Cornus amomum</i>	12	76	0.38
<i>Parthenocissus quinquefolia</i>	14	79	0.25
<i>Rhus typhina</i>	11	81	0.55
<i>Toxicodendron radicans</i>	15	90	0.05
<i>Rosa carolina</i>	12	90	0.33
<i>Celastrus scandens</i>	12	92	-0.13
<i>Rosa virginiana</i>	13	99	0.25
<i>Menispermum canadense</i>	12	99	0.44
<i>Euonymus atropurpureus</i>	12	100	0.02
<i>Sassafras albidum</i>	10	115	0.47
<i>Viburnum prunifolium</i>	13	129	0.16
<i>Crataegus intricata</i>	14	130	0.01
<i>Cornus florida</i>	8	138	0.14

** $P < .01$; other correlations not significant ($P > .05$).

For the 16 species studied, flowering sequence was more concordant among years than fruit ripening sequence ($W = 0.88$, 5 yr, $P < .001$; for 14 species, 8 yr, $W = 0.88$, $P < .001$). Reliance of these species on correlated cues or requirements (e.g., heat sum) for flowering might account proximally for this high degree of concordance. The ultimate cause of this concordance might involve competition for pollinators. All 16 species are entomophilous, and observations of 8 of these in Illinois reveal that they are visited by overlapping sets of insects (Robertson 1928).

Although among these species flowering sequence is more consistent than fruiting sequence, within species year-to-year variation in fruiting date is not attributable to variation in flowering date for 13 of these species (dates of the onset of flowering and fruiting are not correlated among years, Table 2). Only for the three species with the shortest flower–fruit intervals are flowering and fruiting dates correlated. (Because the dates used in these analyses apparently represent the earliest flowering and fruiting events for each species, these correlations do not necessarily apply to the phenological peaks of a population or to individual plants.)

The species for which flowering and fruiting are not correlated among years show a great deal of year-to-year variation in flower–fruit interval; this variation may be due to variation in environmental conditions such as temperature (Fisher 1962). Other investigators wishing to pursue this last point or other phenological analyses will find a wealth of data available in Smith (1915).

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