The Relationship Between Fruit Crop Sizes and Fruit Removal Rates by Birds

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THE RELATIONSHIP BETWEEN FRUIT CROP SIZES AND FRUIT REMOVAL RATES BY BIRDS[1]

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It has been proposed that large fruit crops attract disproportionately more frugivores than smaller fruit crops (Snow 1971, Howe and Estabrook 1977). If this is so, then competition between plants for frugivores could be an important source of selection on fruit crop sizes. Field tests of this hypothesis on tropical trees have produced equivocal results (Howe and Smallwood 1982). In six species of fall-fruiting temperate plants, we asked whether the percentage of the fruit that was removed was related to the size of the fruit crop.

Methods

The study was conducted at the Smithsonian Environmental Research Center near Edgewater, Maryland, in the fall of 1980. Study species included one herb (*Phytolacca americana*), three shrubs (*Lindera benzoin, Viburnum dentatum, Aralia spinosa*), one tree (*Sassafras albidum*), and one vine (*Toxicodendron radicans*).

All fruiting plants of these six species within 5 m of a 900-m transect were tagged. The transect included mature forest, 30-yr-old forest, abandoned field edges, and marsh borders. The number of fruits removed from each plant was estimated from counts of (a) TF, total fruit production (see below), (b) FR, the number of ripe fruits remaining, and (c) FF, the number of fruits that had fallen to the ground beneath the plant. The latter two parameters were measured by counting fruits during seven biweekly censuses from 21 August until 2 December. The ground under the plants was kept cleared of fallen leaves to facilitate counting FF. Fallen fruit was not removed but, since it rotted rapidly, FF data are not cumulative and reflect recently fallen fruit

on each count day. The number of fruits removed by birds was calculated as TF − FR − FF.

The methods used for estimating the total numbers of fruits produced per plant differed among the species studied. At each census we counted the total number of ripe, unripe, and dried fruits on *Viburnum dentatum* and *Lindera benzoin* plants. In *Sassafras albidum, Toxicodendron radicans,* and *Aralia spinosa* we estimated whole plant counts from a subsample including approximately one-fourth of the plant. When approximately three-quarters of the fruits were gone, whole plant counts were made.

The fruits of *Phytolacca americana* ripen sequentially over a raceme. Fruit production was estimated by sampling the number of fruits in six randomly selected racemes on each plant. The numbers of ripe, unripe, and missing fruits (= number of empty peduncles) were counted. The mean number of ripe fruits per raceme was multiplied by the total number of racemes to get an estimate of ripe fruits per plant.

When the study began, *Viburnum dentatum* and *Sassafras albidum* had begun to ripen fruits, but there had been no removal of fruits (no empty peduncles). In the five synchronously ripening species the first census gave the total fruit crop sizes for each plant, whereas in *Phytolacca*, which ripens fruit sequentially, mean crop size over the entire census period was used as the fruit crop size.

An estimate of bird numbers during the study period was taken by slowly walking along the transect between 0700 and 0800 once a week and counting, by individual and species, all birds seen from the transect. Birds designated as frugivorous were those observed to feed on fruit during intensive observations at individual plants.

Results

There was no significant correlation between the size of a fruit crop and the proportion removed from it in any of the species (Table 1), although there was a significant positive correlation between fruit crop size and the number of fruits removed in all plant species (Table 2). In three of the five plant species with synchronously ripening fruit crops, no correlation was apparent be-

TABLE 1. Correlations between fruit crop size and the percentage of fruits removed by frugivores.

Plant species	N	No. fruits on plant ($\bar{X} \pm$ SD)	% of fruits removed by birds ($\bar{X} \pm$ SD)	r	P
Phytolacca americana	10	1117 ± 1035	52 ± 16	0.017	NS
Lindera benzoin	11	164 ± 104	79 ± 10	−0.51	NS
Sassafras albidum	11	417 ± 213	79 ± 15	0.091	NS
Toxicodendron radicans	10	315 ± 283	46 ± 18	0.274	NS
Aralia spinosa	7	1093 ± 359	76 ± 12	−0.455	NS
Viburnum dentatum	11	378 ± 637	74 ± 12	0.011	NS

TABLE 2. Correlations between fruit crop size and the number of fruits removed by frugivores.

Plant species	N	No. fruits on plant ($\bar{X} \pm$ SD)	No. fruits removed by birds ($\bar{X} \pm$ SD)	r	P
Phytolacca americana	10	1117 ± 1035	829 ± 789	0.93	<.001
Lindera benzoin	11	164 ± 104	151 ± 97	0.98	<.001
Sassafras albidum	11	417 ± 213	373 ± 197	0.97	<.001
Toxicodendron radicans	10	315 ± 283	172 ± 194	0.94	<.001
Aralia spinosa	7	1093 ± 359	980 ± 311	0.89	<.01
Viburnum dentatum	11	378 ± 637	343 ± 565	0.99	<.001

TABLE 3. Correlations between initial size of fruit crop and percentage of fruits removed by the time of the first census.

Plant species	N	No. fruits on plant ($\bar{X} \pm$ SD)	% of fruits removed by birds ($\bar{X} \pm$ SD)	r	P
Lindera benzoin	11	164 ± 104	72 ± 15	−0.058	NS
Sassafras albidum	11	417 ± 213	22 ± 11	0.2030	NS
Toxicodendron radicans	10	315 ± 283	23 ± 22	−0.18	NS

TABLE 4. Bird species and fruits they were observed to eat.

Bird species	Plants whose fruits were eaten*										
	M	S	L	T	V	Px	A	N	C	Vb	P
Colaptes auratus	⋯	⋯	⋯	⋯	X	X	⋯	X	X	⋯	⋯
Dryocopus pileatus	⋯	X	⋯	⋯	⋯	⋯	⋯	X	⋯	⋯	⋯
Melanerpes pileatus	⋯	⋯	⋯	⋯	X	⋯	⋯	X	⋯	⋯	⋯
Sphyrapicus varius	⋯	⋯	⋯	⋯	⋯	⋯	X	⋯	⋯	⋯	⋯
Dendrocopos pubescens	⋯	X	⋯	⋯	⋯	⋯	⋯	⋯	⋯	⋯	⋯
Tyrannus tyrannus	⋯	X	⋯	⋯	⋯	⋯	⋯	⋯	⋯	⋯	⋯
Sayornis phoebe	⋯	⋯	⋯	⋯	⋯	⋯	⋯	⋯	⋯	X	⋯
Parus carolinensis	⋯	X	⋯	X	⋯	⋯	X	⋯	⋯	⋯	⋯
Parus bicolor	⋯	X	⋯	⋯	⋯	⋯	⋯	⋯	⋯	X	⋯
Dumetella carolinensis	⋯	⋯	⋯	⋯	⋯	X	⋯	X	⋯	X	X
Toxostoma rufum	⋯	⋯	⋯	⋯	⋯	⋯	⋯	X	⋯	X	⋯
Turdus migratorius	⋯	X	X	⋯	X	⋯	X	X	X	⋯	X
Hylocichla mustelina	⋯	X	X	⋯	X	⋯	⋯	X	⋯	⋯	X
Catharus guttatus	⋯	X	X	⋯	⋯	⋯	X	X	⋯	⋯	⋯
Catharus ustulatus	⋯	⋯	X	⋯	⋯	⋯	⋯	X	⋯	⋯	X
Catharus minimus	⋯	⋯	⋯	⋯	⋯	⋯	⋯	X	⋯	⋯	⋯
Catharus fuscescens	⋯	X	X	⋯	⋯	⋯	⋯	X	⋯	⋯	⋯
Sialia sialis	⋯	⋯	⋯	⋯	⋯	X	⋯	⋯	⋯	⋯	⋯
Bombycilla cedrorum	⋯	⋯	⋯	⋯	X	⋯	X	X	⋯	⋯	⋯
Vireo olivaceus	⋯	X	X	⋯	⋯	X	⋯	X	⋯	X	X
Vireo gilvus	⋯	X	⋯	⋯	⋯	⋯	⋯	⋯	⋯	X	⋯
Dendroica coronata	X	⋯	⋯	X	⋯	⋯	⋯	⋯	⋯	⋯	⋯
Piranga olivacea	⋯	⋯	⋯	⋯	⋯	X	⋯	X	⋯	⋯	⋯
Cardinalis cardinalis	⋯	X	⋯	⋯	X	⋯	X	⋯	⋯	⋯	X
Zonotrichia albicollis	⋯	⋯	⋯	⋯	⋯	⋯	X	X	⋯	⋯	X

* M = Myrica cerifa, S = Sassafras albidum, L = Lindera benzoin, T = Toxicodendron radicans, V = Vitis sp., Px = Parthenocissus sp., A = Aralia spinosa, N = Nyssa sylvatica, C = Cornus florida, Vb = Viburnum dentatum, P = Phytolacca americana.

tween the initial (= largest crop size for that individual plant) ripe fruit crop size and the proportion of fruits missing at the first fruit count following the initial census (Table 3). The data in Fig. 1 indicate that, in species such as *S. albidum, A. spinosa, V. dentatum,* and *T. radicans,* ripe fruits were available on the plants for some period of time before harvesting by birds began and depletion occurred. This may be related to the peak in bird numbers at the study site, which was late October (Fig. 2). Data on bird species observed eating fruit and the species of fruit consumed are presented in Table 4.
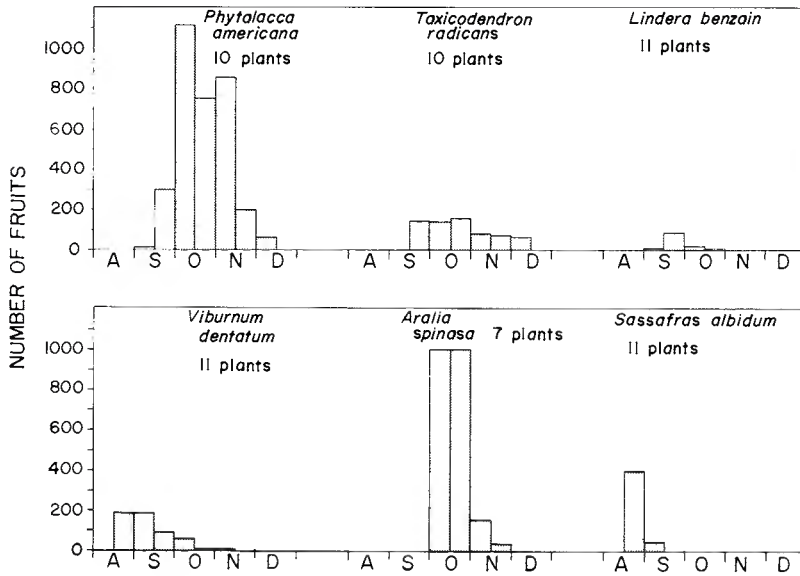
FIG. 1.   Median fruit crop sizes for six species of bird-dispersed plants at Edgewater, Maryland, over the study period from August through December 1980.

Discussion

We found no disproportionate increase in fruit removal for individual plants with large fruit crops compared to individuals with small fruit crops in six fall-fruiting temperate species. These results are similar to data reported in some studies (Howe and De Steven 1979, Howe and Smallwood 1982, Moore and Willson 1982, Stapanian 1982), including some of temperate and some of tropical species, but differ from the results

of others (see Howe and Smallwood 1982). Howe and Vande Kerckhove (1979) found that the number of seeds dispersed per total number of fruits produced was highest for *Casearia* trees with intermediate-sized fruit crops. Howe (1980) found similar results for *Tetragastris panamensis*.

The available data suggest that the hypothesis of an association between dioecy and fleshy fruit evolution (Bawa 1980, Givnish 1980), which postulates that female fitness would increase disproportionately with increasing investment in reproduction, should not rely on the assumption that the proportion of fruits dispersed increases with the size of the fruit crop (Flores and Schemske 1984).

The available data also suggest that more empirical support for the hypothesis of highly coevolved bird dispersal of plant seeds (e.g., McKey 1975) is needed. A linear relationship between fruit crop size and rate of fruit dispersal implies that various types of fruit displays and costs to plants in fruit manufacture might be related primarily to scarcity of dispersers.

FIG. 2.   Results of census of the bird populations at the Edgewater, Maryland, study site.

Literature Cited

Bawa, K. S. 1980. Evolution of dioecy in flowering plants. Annual Review of Ecology and Systematics 11:15–39.

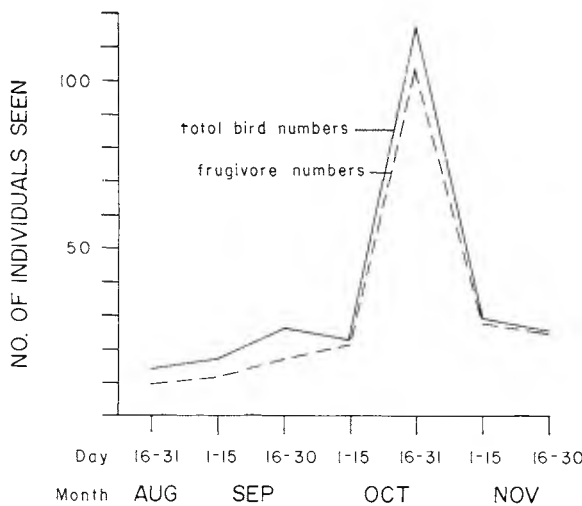Flores, S., and D. W. Schemske. 1984. Dioecy and monecy in the flora of Puerto Rico and the Virgin Islands: ecological correlates. Biotropica **16**:132–139.

Givnish, T. J. 1980. Ecological constraints on the evolution of breeding systems in gymnosperms. Evolution **34**:959–972.

Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. Ecology **61**:944–959.

Howe, H. F., and D. De Steven. 1979. Fruit production, migrant bird visitation and seed dispersal of *Guarea glabra* in Panama. Oecologia (Berlin) **39**:185–196.

Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. American Naturalist **111**:817–832.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13**:201–228.

Howe, H. F., and G. A. Vande Kerckhove. 1981. Fecundity and seed dispersal of a tropical tree. Ecology **60**:180–189.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159–191 *in* L. E. Gilbert and P. H. Raven, editors. Coevolution of animals and plants. University of Texas Press, Austin, Texas, USA.

Moore, L. A., and M. F. Willson. 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. Canadian Journal of Botany **60**:557–560.

Snow, D. 1971. Evolutionary aspects of fruit-eating by birds. Ibis **113**:194–202.

Stapanian, M. A. 1982. A model for fruiting display: seed dispersal by birds for mulberry trees. Ecology **63**:1432–1443.

SIZE BIMODALITY IN PLANT POPULATIONS: AN ALTERNATIVE HYPOTHESIS[1]

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Bimodal size distributions have recently been reported in even-aged populations of freshwater fish (Shelton et al. 1979, Timmons et al. 1980), coniferous and broad-leaved trees (Ford and Newbould 1970, Ford 1975, Mohler et al. 1978), a broad-leaved herb (Ford 1975, Ford and Diggle 1981), and a grass, *Festuca paradoxa* (Rabinowitz 1979). Such bimodality in monospecific plant populations has been thought to result from competition in which large plants preempt resources and suppress the growth of small plants (Ford 1975, Ford and Diggle 1981). This mechanism of dominance and suppression is expected to produce a pattern of increasing bimodality with increasing plant density. However, Rabinowitz (1979) found the opposite density response in *Festuca paradoxa*. I illustrate here an alternative mechanism for producing bimodality, which provides a plausible explanation for the unexpected pattern of increased bimodality at decreased planting density found by Rabinowitz (1979).

Bimodal size distributions can result from initially unimodal size distributions when there is discontinuous variation in exponential growth rates among individuals. Normally distributed variation in exponential growth rates will not produce bimodality. Sources of discontinuous variation may be genetic heterogeneity, environmental heterogeneity, or dominance-and-suppression competition. Such competition may be considered asymmetric because the resulting negative effects are experienced only by the smaller plants. The expected distribution of mass resulting from asymmetric competition becomes more bimodal as increasing plant density increases the number of suppressed plants. Symmetric competition, in which each individual has a negative effect on its competitors proportional to its size, can also produce bimodality, but only in spatially random populations, where variation in the number of neighbors produces variation in exponential growth rates.

In a spatially random scatter of points, the expected number of points within an area of some specified size A can be determined using the Poisson function with the parameter equal to the mean number of points in A. If the points represent plants and A is the area from which one plant draws resources (i.e., the zone of resource depletion), one can predict the number of neighbors within each plant's zone of resource depletion. If a plant's growth rate is inversely proportional to the number of its neighbors, the reduction in the plant's intrinsic growth rate caused by resource depletion can be calculated. Thus, it is possible to use the distribution of the number of neighbors to determine the distribution of reduction in growth rate expected in a randomly spaced plant population of known density (Table 1). The mean reduction in growth rate increases monotonically with increasing density, but the variance is greatest at intermediate densities. The primary difference between spatially random and spatially uni-