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DOES ASYNCHRONOUS FRUIT RIPENING AVOID SATIATION OF SEED DISPERSERS?: A FIELD TEST¹

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Abstract. Asynchronous ripening of fruits within individual, temperate, summer-fruiting, bird-dispersed plants has been proposed to be an adaptation to avoid satiation of dispersers when they are not abundant. I tested a prediction of this hypothesis by manipulating ripening synchrony on individual Amelanchier arborea trees and comparing ripe fruit removal rates from these trees to paired controls. Artificially synchronous ripe fruit displays were created by cutting off unripe fruit and replacing them with ripe fruit. Fruit removal was faster for the manipulated, synchronous tree in three pairs, slower in two pairs, and not significantly different in five other pairs, suggesting that synchronous displays did not satiate dispersers. This unexpected result is attributed to violation of the unstated assumption that dispersers are relatively sedentary in their foraging in the summer and do not concentrate at large fruit displays. In this study the major frugivore of A. arborea, the Cedar Waxwing (Bombycilla cedrorum), foraged widely in flocks of 2-6; other reports reveal that some other frugivorous bird species also forage widely in the summer. This nonterritorial foraging implies that the arrival of dispersers is temporally unpredictable from the perspective of each plant, and it is this temporal unpredictability that may favor asynchronous ripening in plants lacking adaptations for ripe fruit persistence.

Key words: Amelanchier arborea; E. S. George Reserve; frugivory; fruit display; fruit ripening; phenology; seed dispersal; synchrony.

INTRODUCTION

Several hypotheses have been proposed to explain patterns of within-individual fruit ripening synchrony of animal-dispersed plant species. The hypothesis that has received the most attention is that asynchronous ripening improves seed dispersal by avoiding satiation of dispersers when they are limited, either because fruits are taken only by specialists (McKey 1975, Howe and Estabrook 1977) or because ripening occurs when dispersers are not abundant (Thompson and Willson 1979). Thompson and Willson observed that frugivorous birds were less abundant in summer than fall at mid-latitudes in eastern North America and attributed this to two causes. First, there are fewer individual birds in summer than in fall because migrants from farther north have not yet arrived and the young of the year have not yet fledged. Second, fewer bird species specialize on fruit in the summer because insects are more available and are needed to feed the young, while fall migrants seek the energy provided by fruit. They proposed that because of this scarcity of dispersers, summerfruiters should have adaptations that promote the rapid removal of ripe fruit, because ripe fruits remaining on a plant are exposed to predation, desiccation, and decay (Janzen 1977, 1978, Thompson and Willson 1978). Fruits

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² Present address: Department of Biological Sciences, Nelson Biological Laboratory, Rutgers University, Piscataway, New Jersey 08855–1059 USA. of summer species may be more susceptible to predation and decay than those of fall fruiters due to higher sugar and water content and warmer temperatures (Stiles 1980, Stapanian 1982). By reducing the number of fruits ripening per day, i.e., ripening fruits more asynchronously, a summer-fruiting plant may avoid satiating the local avian dispersers and reduce loss to predation and decay.

If asynchronous ripening does avoid satiation of dispersers in the summer, we would predict that more synchronous individuals would have a smaller proportion of their fruits removed. This pattern was expected, but not found, in two neotropical plants: a batdispersed shrub (Fleming 1981) and a bird-dispersed tree (Howe 1983). To date, no tests of this prediction of the frugivore availability hypothesis have been reported for temperate zone plants. I tested this prediction by manipulating fruit displays on individual trees of a summer-fruiting, vertebrate-dispersed species, comparing subsequent natural removal of fruits from these trees to matched controls. Thus this experiment tested whether dispersal is more or less complete for a few synchronous trees in a population of asynchronous individuals. The results indicate that synchronous ripening does not satiate summer frugivores and suggest that these frugivores are not as sedentary in their foraging as has been assumed.

This study compared rates of fruit removal between manipulated and control trees, not the total proportion eventually removed. Because a fruit is less likely to be removed the longer it remains on the parent, due to drop, rot, or consumption by nondispersers (Thompson and Willson 1978), promptness of removal is likely to correlate with the total proportion of fruits removed by dispersers. Fruit removal should be considered a component of dispersal success. Murray (1987) discusses the relative merits of proportion of fruits removed vs. total number removed as estimates of fitness, but for comparisons between plants of similar crop sizes, as in this study, the two measures are equivalent.

METHODS

Downy serviceberry, Amelanchier arborea (Michaux f.) Fern. (Rosaceae: Maloideae) is a large shrub to small tree that occurs throughout temperate eastern North America (Fernald 1950). At the study site it flowers in late April to early May and ripens fruits in June and early July. Fruits are eaten by a variety of bird species, most of which are seed dispersers (see Results). Chipmunks (Tamias striatus) and probably other rodents are seed predators (Robinson 1986). Fruits are purple when fully ripe, but at this site were often taken while red; hence I consider red fruits "ripe" in this study. Individual trees of A. arborea ripen fruits much more asynchronously than they flower: the average time to ripen 90% of a fruit crop is 20 d, making it one of the most asynchronous of 12 vertebrate-dispersed species studied at the site (Gorchov 1987).

Experiments were done in 1985 and 1986 at the Edwin S. George Reserve in southeastern Michigan. The climate and vegetation have been described in Rogers (1942), Cantrall (1943), Evans and Dahl (1955), and Cooper (1958).

A. arborea is a major understory species in the oakhickory woods in the northern part of the Reserve. A relatively flat area of $\approx 275 \times 125$ m was selected for the fruit display manipulations. All A. arborea plants bearing 50 or more fruit on 20 May 1985 (n = 60) were flagged and mapped. On each tree, crop size was estimated and height was measured to the nearest 0.5 m. Fruit crop size was periodically re-estimated during the ripening period so that current data could be used in the selection of experimental and control trees. The following spring the area was recensused, and 35 additional trees that did not have 50 fruits in 1985, but did in 1986, were mapped and measured. Fruit crop size on each tree was estimated 28–31 May 1986, and re-estimated periodically during the ripening season.

Manipulations were done early in the ripening season each year when *A. arborea* is the only woody vertebrate-dispersed species in the area with ripe fruit. Each year five pairs of trees were selected for fruit display manipulation. Trees were paired based on similarity in: (1) height (usually within 1 m), (2) total fruit crop size (within $\approx 30\%$) and number of fruits ripe, (3) proximity to dirt roads, gaps, and other fruiting conspecifics. To minimize effects of neighboring conspecifics on frugivore foraging behavior (Manasse and Howe 1983) trees were excluded from consideration if located <20 m from a conspecific with a larger fruit crop. Coin toss determined which tree of each pair was manipulated; the other served as the control.

Fruit displays were manipulated by removing a large number of unripe fruits and replacing them with ripe fruits collected off-site. Unripe fruits were cut off with scissors, leaving the pedicel intact, and removed from the site. A ripe (red) or nearly ripe (pink) fruit was placed on each of these pedicels with the pedicel piercing the fruit at its abscission scar. These added ripe fruits appeared exactly like "natural" ripe fruits, except that the pedicels appeared slightly shorter, since the distal 5 mm or so was inside the fruit; pink fruits generally turned red after 1 d. With the use of ladders I was able to manipulate all parts of the smaller trees and nearly all of the larger trees.

At most, one manipulation was set up each day. On the 1st d, fruit crop size was counted or estimated on both the control and manipulated trees, a sample of ripe fruits was marked on each tree, and ripe fruits were added. The number of fruits added in each manipulation is given in Table 1. On one of the 10 manipulated trees additional ripe fruits were added on the 2nd d, and on 2 trees they were added on each of the first 3 d (Table 1). Marked fruits were censused on each of the first 4 d after the initial manipulation. Four days was chosen because added fruits typically began to desiccate after this time: of 34 ripe fruits added inside frugivore exclosures, 33 remained attached after 4 d, at which time only 3 of these had desiccated and another 18 had begun to desiccate (Gorchov 1987).

To keep track of individual fruits, infructescences with "natural" ripe fruits on both manipulated and control plants were marked with 2-cm Avery paper dumbbell tags, and the condition of each fruit recorded daily. Partially ripe fruit were included with ripe fruit in this analysis, since they would ripen during the first 2 d of the experiment. In the 1985 experiments all accessible "natural" ripe fruits were monitored; in 1986 a random sample of \approx 40 ripe fruits was censused on each plant.

To minimize fruit removal by mammals, an aluminum foil pie tin that had been slit radially to its center was placed over the trunks of both control and manipulated trees 30–75 cm above the ground (Willson and Melampy 1983). For the 1985 experiments I also taped black plastic (46 cm broad) above the pie tin on each manipulation and control tree to discourage climbing by mammals. In neither year were mammals observed in these trees during an experiment.

Fruit disappearance, rather than fruit removal per se, was recorded. The inference that disappearance equals removal is justified by the fact that inside frugivore exclosures 94% of natural ripe fruits remain attached, hydrated, and free of noticeable decay for at least 4 d after turning red (median = 8 d, Gorchov 1987).

Manipulation no.

2

3

4

5

6

7

8

9

10

87 (37), 67, 37

100 (18), 64

64 (90)

165 (21)

197 (32)

204 (35)

136 (37)

64 (41)

TABLE 1. Height of manipulated (M) and control (C) trees and initial numbers of total, natural ripe, and added ripe fruits on manipulated trees.

14 (5)

32 (30)

78 (10)

125 (13)

275 (20)

142 (19)

61 (20)

17(3)

*	The percentage of the total fruit crop that was ripe immediately before addition of ripe fruit is given it	n parentheses	in
the	Natural ripe column: that ripe immediately after addition is given in the Added ripe column.		

† First number listed is number of fruits added on the 1st d of the experiment. If additional numbers are listed without parentheses, they give the number of fruits added on the 2nd and 3rd d, respectively.

‡ Removal rate faster on manipulated (M) or control (C) tree. Logrank statistics given in Fig. 1.

270

638

107

784

993

1352

759

303

|| May be slight underestimates.

Μ

5

2.5

4.5

5.5

3

5

3

5

5

5.5

4 7

3

Removal rate was defined as the "survivorship" curve of marked samples of natural ripe fruits over the 4-d course of the experiment. Comparison between the removal rates for the manipulated and control trees of each pair was done by Peto and Peto's logrank test, which tests whether the survivorship curves of two cohorts differ significantly from one another (Peto and Pike 1973, Pyke and Thompson 1986). The logrank statistic (LR) was calculated as:

$$\mathbf{LR} = (O_i - E_i)^2 / E_i$$

where O_i and E_i equal the observed and expected total number of fruits that disappeared in treatment *i* (*i* = 1 for the manipulated tree and *i* = 2 for the control). $E_i = d_k p_{ik}$ where d_k = the total number of fruits that disappeared during time interval *k* and p_{ik} = the proportion of fruits present at the start of interval *k* that are found in treatment *i*. LR was compared to chisquare with 1 df. The logrank test was also used to compare removal of natural vs. added ripe fruits from each manipulated tree, but partially ripe fruit were not included in the latter analyses.

Observation and mist-netting of frugivores visiting *A. arborea* were done in 1984 and 1985 in the same forest, but 300–600 m from the study plot. Netted birds were held in boxes for 30 min after capture, and feces were checked for seeds. Raccoon (*Procyon lotor*) and red fox (*Vulpes vulpes*) scats found anywhere in the George Reserve were also checked for seeds.

RESULTS

Manipulations greatly increased the proportion of a tree's fruit that was ripe, in most cases by a factor of 2 or more (Table 1). The addition of ripe fruit on the 1st d increased the proportion of the fruit crop that was ripe from an average of 11% (range: 0-30%) to an average of 37% (18–90%). The difference in these pro-

portions is similar to the proportion of the fruit crop ripening on the peak day of ripening in a synchronous summer ripener, *Prunus virginiana* L., in 1985 ($\bar{X} = 25\%$, range: 19–30%, n = 6 plants; Gorchov 1987).

Manipulated and control trees had significantly different ripe fruit removal rates in 5 of the 10 manipulations (Fig. 1). In 3 of these 5 manipulations, fruits were removed faster from the control (asynchronous) tree; in the other 2 they were removed faster from the manipulated (synchronous) tree. In one of the remaining manipulations, fruit removal was marginally faster on the control (.05 < P < .10). The outcomes did not differ consistently between the two years.

Removal rates of added ripe fruits were not significantly different than those of natural ripe fruits on 6 of the 8 manipulated trees with sufficient data (total censused fruits \geq 30). Removal of added fruits was faster on the other 2 trees.

Eleven bird species were either observed feeding on A. arborea fruits or had intact Amelanchier seeds in their feces: Cedar Waxwing (69 observations, 0 fecal samples obtained), American Robin (Turdus migratorius) (21, 5 feces with seeds), Tufted Titmouse (Parus bicolor) (10, 1), Blue Jay (Cyanocitta cristata) (8, 1), Scarlet Tanager (Piranga olivacea) (3, 2), Gray Catbird (Dumetella carolinensis) (0, 2), Wood Thrush (Hylocichla mustelina) (0, 2), Red-bellied Woodpecker (Melanerpes carolinus) (1, 0), Veery (Catherus fuscescens) (0, 1), Northern Cardinal (Cardinalis cardinalis) (1, 0), Rufous-sided Towhee (*Pipilo erythrophthalmus*) (1, 0). The last two species are probably seed predators. Robinson (1986) demonstrated that seeds of A. arborea ingested by Cedar Waxwings are excreted intact and germinable. Cedar Waxwings visited A. arborea in flocks of 1-8 individuals ($\bar{X} = 3.5$, sp = 2.1, n = 14) and stayed 1–10 min ($\bar{X} = 5.0$ min, sp = 3.3, n = 55). Chipmunks (seed predators) were observed eating A.

.05 < P < .10 (C)

P > .10

P > .10

 $\bar{P} > .10$

P < .005 (C)

P < .005 (C)

P < .005 (M)

P < .05 (C)



FIG. 1. Fruit removal rate (survivorship of marked sample of "natural" ripe and partially ripe fruit) on manipulated (synchronous) and control (asynchronous) fruit displays on *Amelanchier arborea* trees. Each graph reports data from a manipulated tree and a paired control. (a) Manipulations 1–5, done in 1985. (b) Manipulations 6–10, done in 1986. LR = logrank statistic (see Methods); ns = not significant.

arborea fruits on two occasions. Two of four raccoon scats collected during *A. arborea*'s fruiting season contained intact *Amelanchier* seeds, making them minor seed dispersers at this site.

DISCUSSION

The field manipulations of ripening synchrony on *A. arborea* do not support Thompson and Willson's (1979) hypothesis that asynchronous ripening avoids satiation of frugivores. Removal of ripe *A. arborea* fruits was significantly slower from artificially synchronous trees than from asynchronous matched controls in only 3 of 10 replicates. Ripening synchrony might be expected to cause frugivore satiation only when the number of fruits is large; hence increasing synchrony would be expected to reduce removal rates only for those trees with the largest numbers of fruit. However, no such trend was found among the replicates. Additional experiments with other summer-fruiting species and in other locations are needed to evaluate the hypothesis more completely. However, other evidence conflicts with an unstated assumption of the hypothesis, and the seasonal pattern it was hypothesized to explain.

Earlier authors have emphasized two conditions nec-

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essary for asynchronous ripening to be favored: low disperser abundance (Howe and Estabrook 1977, Thompson and Willson 1979, Stapanian 1982), and low ability of fruit to persist after ripening in a condition acceptable to dispersers. (Species with persistent ripe fruits are likely to be visited before fruits rot or desiccate and would benefit little from asynchronous ripening [Murray 1987]). Factors contributing to interspecific differences in persistence of ripe fruit include seasonal abundance of invertebrates and microbes (Thompson and Willson 1979), chemical and physical defense of ripe fruit (Stiles 1980, Herrera 1982), pulp nutritional composition (Stiles 1980, Herrera 1982, Stapanian 1982, White 1988), and water content (Stapanian 1982, White 1988). Strength of attachment to the plant probably also contributes to fruit persistence.

While the two conditions of low disperser abudance and poor fruit persistence are necessary for this model of the evolution of asynchronous ripening, they are not sufficient. It is also necessary to assume that dispersers do not concentrate their foraging at large, synchronously ripening displays as would be expected for opportunistic frugivores (Howe and Estabrook 1977: model 2). This assumption would hold if dispersers were either (1) relatively sedentary or (2) irregular in their visits to each area. Most previous discussions of fruit-disperser interactions in temperate North America have not addressed this issue of disperser concentration, although emphasis on the movement of dispersers in the fall (Thompson and Willson 1979, Stapanian 1982) suggests an implicit assumption that they are relatively sedentary in the summer. Willson and Thompson (1982) argued that summer frugivores are probably largely restricted in their foraging to their nesting territories (and hence would not concentrate on large displays). However, I present evidence (below) that at any point in the season many frugivorous birds are not territorial, and that some forage over areas much larger than their defended breeding territories.

Amelanchier spp. and other early summer fruits ripen while Cedar Waxwings are still foraging in prenesting flocks, since their breeding season does not typically begin until late June (Putnam 1949, Bent 1950, Wood 1951, Leck and Cantor 1979). Cedar Waxwings are one of the most frugivorous of all North American birds (Martin et al. 1951), although they may be major seed dispersers only in the Great Lakes region, Quebec, New York, and New England, where their summer abundance is greatest (Robbins et al. 1986: Tables 3 and 4).

By the time Cedar Waxwings begin breeding in late June, the other major frugivorous species in eastern North America, such as American Robin, Gray Catbird, and Wood Thrush, are near the end of their nesting period, at least in Michigan (Wood 1951, Kelley et al. 1963). Even while nesting, some frugivorous species regularly leave their breeding territories to forage on fruit (Cedar Waxwing: Saunders 1911, Putnam 1949; American Robin: Hirth et al. 1969; Jamie Smith and Glenna A. Stewart, *personal communication*). During the nesting season, nonbreeding adult Robins form flocks in areas of high fruit abundance (Hirth et al. 1969).

A few weeks after fledging, which begins in June for most frugivorous species in Michigan, the young birds generally leave their natal territory and often aggregate in areas of high fruit abundance (American Robins: Hirth et al. 1969; Northern Mockingbirds: Kale and Jennings 1966). Later in the summer this non-territorial behavior of fledglings and non-breeding adults is also exhibited by adults that have completed breeding.

The above evidence demonstrates that during the summer many frugivorous birds to not confine their foraging to nesting territories; rather, they often travel considerable distances to, and aggregate at, plants with abundant ripe fruit. This implies that fruit removal from individual fruiting trees is not limited by the appetites of a small number of birds whose territories include that tree. Hence relatively synchronous ripening might be favored, since increasing the number of ripe fruits available at one time could increase the probability of a plant's discovery (Murray 1987) or its profitability to a foraging bird.

However, if birds forage for fruit over large areas, their arrival at any one plant would not be particularly reliable. Therefore fruit removal from a particular plant would be patchy and unpredictable in time. Such an irregular pattern of frugivory would provide an alternative mechanism for a dispersal advantage to asynchronous ripening, and appeared to characterize the removal of A. arborea fruits on the study site in both 1985 and 1986. Cedar Waxwings, responsible for most of the fruit removal, usually travelled in flocks of 2-6, visiting some fruiting trees and bypassing others. Flocks remained longer at and often made repeated visits to trees that appeared to have more ripe fruit. A pattern of sporadic frugivory is apparent in the removal curves of censused fruits (Fig. 1): for 18 of the 20 trees, more than half of the censused fruits that were removed from the tree over 4 d were removed in a single day.

I argue that this temporal unpredictability of disperser visits, rather than spatially restricted disperser foraging, provides the third necessary condition for asynchronous ripening to be favored (the others being limited disperser abundance and low ripe fruit persistence). All three conditions may also be met for many fall-ripening species: disperser visits are probably even more unpredictable in the fall (Thompson and Willson 1979, Stapanian 1982), low fruit removal from some fall species (Sherburne 1972, Thompson and Willson 1979, Stiles 1980) suggests dispersers are limiting, and fall fruits vary in their ability to persist (White 1988). If these conditions are met in many fall-ripeners, this would account for the absence of the predicted seasonal pattern in within-plant ripening synchrony among birddispersed plants in northern Florida (Skeate 1987) and among bird-dispersed trees and shrubs in Michigan (Gorchov 1987). I predict that ripening synchrony should be more strongly correlated with the ability of fruits to persist after ripening than with season of ripening. This prediction is supported by my finding that among 12 bird-dispersed trees and shrubs in Michigan, those with more synchronous ripening tend to have more strongly attached ripe fruit (Gorchov 1987). Without strong attachment, chemical defense and resistance to desiccation are of limited value to ripe fruit.

An alternative advantage to asynchronous ripening is that birds spend longer periods of time foraging in, and excrete a greater proportion of seeds beneath, trees with more synchronous ripening (Stiles 1982). Hence asynchronous ripening could improve dispersal success, not by increasing the proportion of fruits removed, but by increasing the proportion of removed fruits that have their seeds deposited away from the parent. This possibility is unlikely to be important for the system described here, since $\approx 79\%$ (n = 85) of the fruit-eating visits by birds lasted ≈ 5 min or less, which is far less than the 30 min required for gut passage of *A. arborea* seeds by Cedar Waxwings (Robinson 1986) and a variety of seeds by American Robins and Hermit Thrushes (Johnson et al. 1985).

Other alternative hypotheses for the evolution of asynchronous ripening have been proposed. Asynchronous ripening may extend the duration of and therefore enhance the effectiveness of bicolored fruit displays caused by dual color change during ripening (Stiles 1982, Willson and Thompson 1982); *A. arborea* fruits, like those of other asynchronous species at this site, do go through a dual color change. Alternatively, ripening rates in some species may be physiologically constrained (Thompson and Willson 1979, Murray 1987), but this seems unlikely in *A. arborea*, because fruit production appears more related to stored reserves than current photosynthesis (Gorchov 1987).

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