

Competition for dispersal agents among tropical trees: influences of neighbors

Robin S. Manasse and Henry F. Howe

Program in Evolutionary Ecology and Behavior, Department of Zoology, University of Iowa, Iowa City, IA 52242, USA

Summary. We distinguish factors influencing seed dispersal that are potentially under the control of parent plants from those that are not in a Panamanian population of the neotropical nutmeg, *Viola surinamensis* (Myristicaceae).

In the first category, we find that individual variation in crop size and nutritional components of the aril failed to explain any variation in the proportion of fruits taken from fruiting trees. The ratio of edible aril to indigestible seed explained a significant but small (13%) portion of variation in the fraction of fruits taken by tropical birds. These results suggest that the potential for ongoing natural selection on fruit and crop characteristics by dispersal agents exists, but is periodic or weak. On the other hand, the number of fruits available to birds within 50 m of any given *Viola* tree profoundly influenced the extent to which it secured dispersal. More than three times as much variation (42%) in relative dispersal could be explained by the number of “competing” *Viola* fruits during the peak of an individual tree’s fruiting season. When isolated plants are eliminated from the analysis, the depressive effect of competition with neighbors explains 72% of the variation in individual dispersal. These results suggest that birds seek out clumps of fruiting trees, but that intraspecific competition for a limited disperser assemblage occurs within the clumps.

Our results are a first step towards separating attributes of the plant that are potentially under the influence of natural selection by dispersal agents from emergent population effects that can override individual advantage in crop or fruit characteristics.

Introduction

Many tropical plants bear fleshy fruits that are consumed by birds and mammals. But fruit-eating animals have varying influences on dispersal; visitors may remove seeds from the vicinity of the parent tree, drop them in place, or destroy them outright (McKey 1975; Howe 1980). Furthermore, a given dispersal agent may prefer to visit some individual fruiting trees rather than others. From the perspective of the plant, both the fact of undepleted crops (McKey 1975) and the observation that crops vary in the extent to which

they are depleted (Howe and Estabrook 1977) suggest competition for dispersal agents. Given the virtual absence of relevant data in the literature, it is clear that investigations of frugivory and seed dispersal are particularly useful when they document factors influencing overall dispersal success and its variance within populations of fruit-bearing plants (Howe and Smallwood 1982). Here we use a Panamanian population of the bird-dispersed canopy tree *Viola surinamensis* (Rol.) Warb. (Myristicaceae) to investigate the factors influencing differential dispersal of individuals.

The proportion of fruits taken from individual crops may depend on the quality or quantity of fruit produced, or upon the proximity of neighbors that compete for dispersal agents. To the extent that attributes of an individual crop influence the outcome of competition for dispersal agents, frugivores may select for parental patterns of investment in fruit quality or quantity (Howe and Estabrook 1977). To the extent that visitation depends on proximity of neighboring plants of the same or different species, chance rather than inherent attributes determine relative dispersal success. Here we re-evaluate the hypotheses that the largest proportion of fruits taken is from (1) crops of intermediate size (small crops are ignored, while large ones satiate the assemblage; see Howe and Estabrook 1977), (2) trees with especially nutritious arils (pulp), and (3) plants bearing fruits with a high ratio of edible aril to indigestible seed. Our tests involve a larger sample of individual trees than previously used, as well as a more exacting laboratory analysis (cf. Howe and Vande Kerckhove 1981). We also uniquely evaluate the effects of neighbors, thereby testing the hypothesis (4) that the proximity of fruiting neighbors depresses individual dispersal. The latter assumes both that fruit-eating animals may perceive clumps of contiguous crowns rather than individual trees, and that foragers are so limited that a clump of trees may produce far more fruits than available animals can eat (Howe and Estabrook 1977).

Methods

We monitored fruit production and depletion of *V. surinamensis* on Barro Colorado Island, Panama from mid-May through early September, 1980. The habitat is a “tropical moist” forest of the Holdridge Life Zone System (Holdridge 1967); its natural history has been described in detail

by Croat (1978). The area used in this study includes the 23 ha in and near Lutz Watershed that was previously used by Howe and Vande Kerckhove (1980, 1981), as well as seven additional ha in nearby Shannon Ravine.

Fruit traps placed beneath the canopies of fruiting 28 (*Viola surinamensis*) trees were used to estimate the amount of fruit falling from the tree crown (see Howe and Vande Kerckhove 1981). Traps consisted of 1 m² plastic frames covered with 1.5 mm mesh mosquito screening. The number of traps placed under a crown thus ranged from 5 to 21 (10 ± 4 SD); amounting to $10.1\% \pm 3.0\%$ SD of the area under the crown. Each trap was leveled by placing it on poles from 0.3 to 1.0 m above the ground, depending on the terrain. Fruit debris included capsules, which permit an estimate of the total crop produced, and undispersed seeds, which permit an estimate of the seed not removed from the vicinity and consequently of those that are dispersed (see Howe 1980; Howe and Vande Kerckhove 1981). A unique estimate was obtained for each tree by dividing the total number of debris components collected from under a crown by the area sampled. Some of the traps were knocked over by coatis (*Nasua nasua*) attempting to remove fruit from the traps. We discouraged these visits by regularly spraying fruit left in the traps with insecticide (Raid) or mosquito repellent. Data were not collected from disturbed traps.

Twenty seeds with fresh arils were removed randomly from underneath each tree and frozen on the day of collection. Traps were emptied weekly. Undamaged fruit was collected beneath the parent tree, usually during the time of maximum (peak) fruit display of individual trees. These arillate seeds were freeze-dried to constant weight in a Labconco Freeze Dry 3. Dried arils and seeds were weighed separately on an analytical balance. All arils were returned to a freezer for storage until the end of the season, when they were transferred to Iowa for nutrient analysis. Lipid, protein, crude fiber, ash and total available carbohydrate of aril samples were determined by methods modified from Horowitz (1980; see Manasse 1982). For all analyses, determinations were made on a collection of arils from each individual tree, since a single aril was too small to provide enough material for a complete nutrient scan.

Pearson product-amount correlations were computed for those variables hypothesized to contribute to the variance in the proportion of seeds dispersed from an individual tree. Variables representing characteristics of individual trees were several measures of profitability with respect to nutrient award and crop size. Population factors hypothesized to contribute to the dispersal success of individual trees were the number of fruit produced by conspecifics within a 50 m radius for both the sum of the entire fruiting season and the week of maximum (peak) fruit availability by the individual tree (hereafter referred to respectively as NFs and NFp; see Table 1), and the proportion of fruit made available by the tree from the total amount of fruit made available by all *V. surinamensis* trees within a 50 m radius for both the entire fruiting season and the week of maximum (peak) fruit availability by the individual tree (hereafter referred to respectively as PFs and PFp, see Table 1). The distance of 50 m represents an estimated maximum distance that a frugivore can see from a tree crown. All proportions were transformed into arcsin square root equivalents before calculations (after Zar 1974). Standard deviations report dispersion around the mean.

Table 1. Abbreviations for variables used in statistical analyses

Variable	Abbreviation
The numbers of fruit produced by conspecifics within a 50 m radius during the entire fruiting season.	NFs
The numbers of fruit produced by conspecifics within a 50 m radius during the week of maximum (peak) fruit availability of the individual tree.	NFp
The fruit made available by the individual as a proportion of the fruit made available by conspecifics within a 50 m radius during the entire fruiting season.	PFs
The fruit made available by the individual as a proportion of the fruit made available by all conspecifics within a 50 m radius during the week of maximum (peak) fruit availability of the individual tree.	PFp

Results

Natural history

Viola surinamensis is a dioecious tree found from Costa Rica and Panama to the Guianas and Brazil, with disjunct populations in the Antilles (Croat 1978). On BCI, *V. surinamensis* is a canopy or emergent tree of primary forest, ranging in diameter at breast height (dbh) from 32 to 115 cm ($\bar{x} = 58 \pm 22$ cm). Orange capsules dehisce from dawn until mid-morning, exposing a gray seed approximately 2 cm long (2.17 ± 0.38 g dry weight) surrounded by a lacinate red aril 1 mm thick (0.97 ± 0.17 g dry weight). Crops ranged from 430 to 31,000 during 1980, with a mean of $8,296 \pm 6,618$. Crop size is correlated with dbh ($r = 0.60$, $P < 0.0001$). During 1980, 24–73% ($\bar{x} = 48 \pm 19\%$) of the seeds were removed by birds and monkeys. The species flowers during the dry season (December through February); most plants drop fruits in June, July and August.

Of 78 birds and mammals that eat fruit in Barro Colorado forests, only 7 are known to eat *V. surinamensis* fruits and regurgitate or defecate seeds in viable condition (Howe and Vande Kerckhove 1981). These dispersal agents, in order of decreasing importance in removing seeds, are: Chestnut-mandibled Toucan (*Ramphastos swainsonii*), Rufous Motmot (*Baryphthengus martii*), Slaty-tailed Trogon (*Trogon massena*), Black-crested Guan (*Penelope purpurascens*), Keel-billed Toucan (*R. sulfuratus*), Spider Monkey (*Ateles geoffroyi*), and Collared Aracari (*Pteroglossus torquatus*). A small cotinga, the Masked Tityra (*Tityra semifasciata*) strips arils off of seeds, but does not ingest or disperse seeds.

Dispersal: individual characteristics

One expects the most efficient dispersal from trees of intermediate crop size (Howe and Estabrook 1977). Kurtosis values indicate considerable variation within *V. surinamensis* populations, ranging from -1.1 to 6.0 ($\bar{x} = 1.6 \pm 1.7$) (Fig. 1). Only two trees had platykurtic distributions, indicating that most phenologies were peaked. A kurtosis value for summed weekly fruit production of all 28 trees is 2.8, indicating a strongly peaked overall fruiting season (see Howe 1982).

Nutritional components of the arils vary greatly from tree to tree (Tables 2 and 3), but no linear correlations indicate an association between nutritional components and the fraction of fruits taken from a tree; correlation coefficients reflecting association between percent of seeds taken and amounts of lipid, protein, carbohydrate, fiber, and ash are -0.24 , -0.17 , -0.28 , 0.34 , and 0.02 , respectively (all $P > 0.05$). Furthermore, there is no detectable relationship between the proportion of seeds removed from a tree and ratios of one nutrient component to another (e.g. $r = 0.04$ for protein:lipid; $r = 0.12$ for protein:carbohydrate). Percentage values in Table 3 do not sum to 100 because volatile chemicals are lost during storage of nutmeg arils (see Chichester and McFeeters 1971; Sanford and Heinze 1971).

Earlier work demonstrated a strong association between the proportion of fruits taken and the mean ratio of aril to seed for each tree ($r = 0.72$, $P < 0.0002$; see Howe and Vande Kerckhove 1980). The association in 1980 was also significant, but less strong ($r = 0.32$, $P < 0.05$). Neither total weight of the arillate seed, aril weight, nor seed weight are

significantly correlated with the fraction of fruits taken ($r = -0.17$, -0.26 , 0.07 , respectively). In this sample, mean aril and seed weight were correlated ($r = 0.53$, $P < 0.002$; see Howe and Vande Kerckhove 1981).

Total crop size produced by individual trees was not correlated with the proportion of seeds removed ($r = 0.17$, $P > 0.15$).

Dispersal: neighborhood effects

Many parts of the BCI forest lack *V. surinamensis*, but where it occurs an average of 3 fruiting individuals occurs within 50 m of any given individual (range 0–5). The sum of all fruits on neighbors (<50 m) of a given individual during the season (variable NFs; see Table 1) is negatively correlated with the proportion of seeds taken from individual trees ($r = -0.36$; $P < 0.05$), indicating that plants do compete with neighbors for dispersal agents. It is obvious, however, that the population is not entirely synchronous (Fig. 1); a tree may be at the height of fruit production

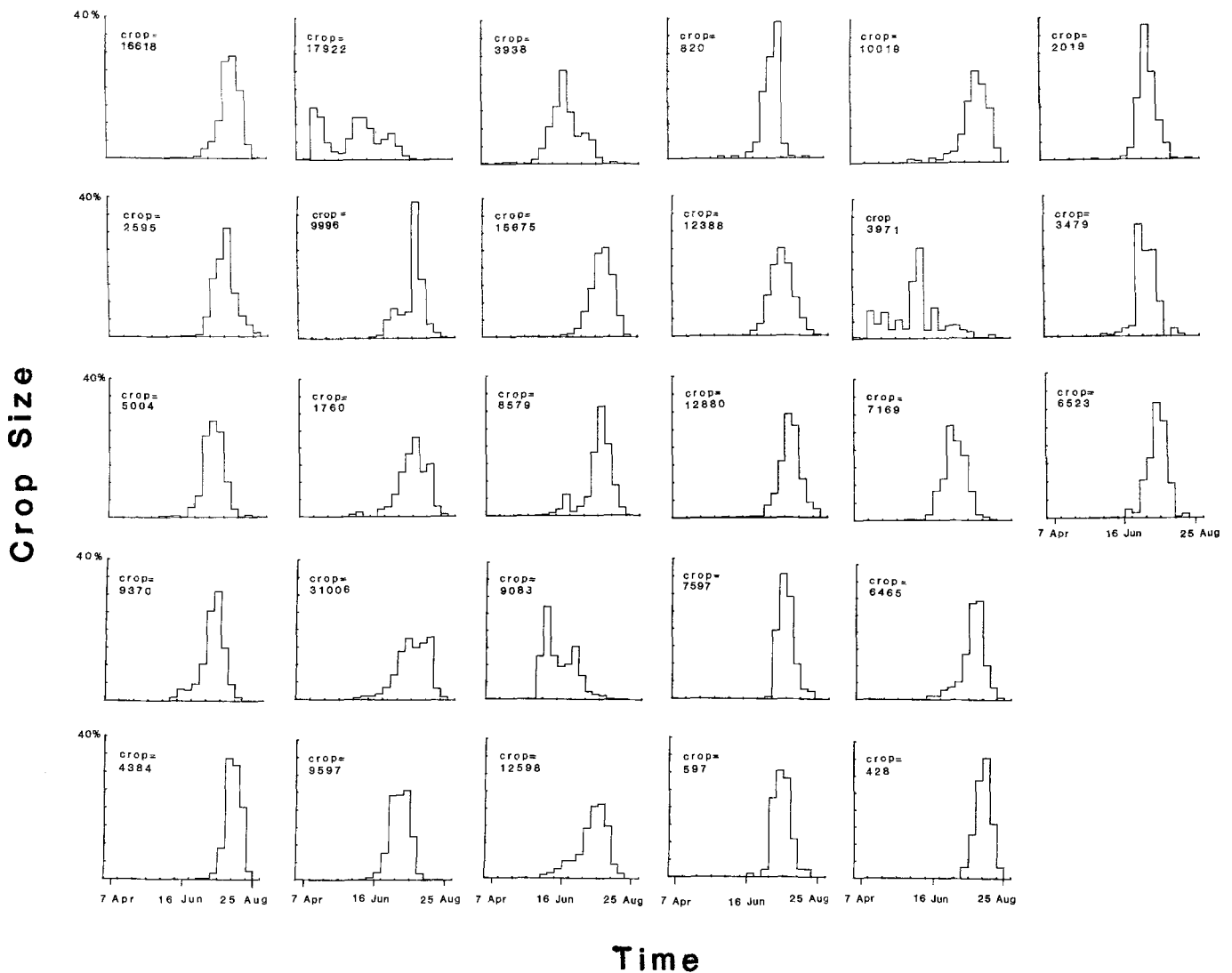


Fig. 1. Fruiting phenologies for individual trees in 1980

Table 2. ANOVA for seed weight, aril weight and aril weight/seed weight

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-Value
<i>Seed weight</i>				
Between trees	16	46.0371	2.8772	57.51*
Within trees	323	16.1589	0.0500	
Total	339	62.1946		

* $R^2 = 0.74$, $P < 0.0001$ *Aril weight*

Between trees	16	9.2360	0.5772	39.78*
Within trees	323	4.4867	0.0145	
Total	339	13.9927		

* $R^2 = 0.66$, $P < 0.0001$ *Aril weight/seed weight*

Between trees	16	2.1343	0.1334	36.65*
Within trees	323	1.7562	0.0036	
Total	339	3.8905		

* $R^2 = 0.64$, $P < 0.0001$

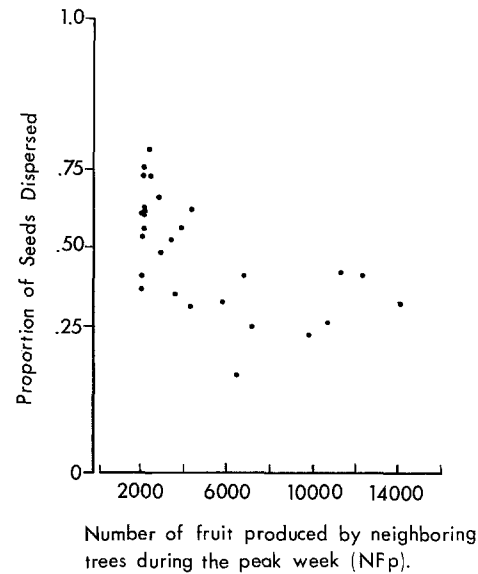
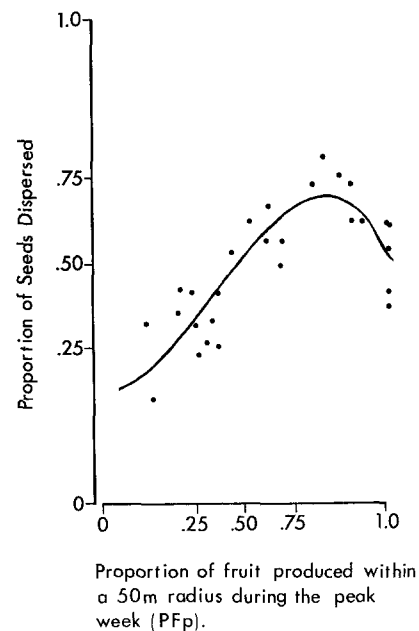
when its neighbors are not. The key competitive effects probably occur at the height of fruit production, designated here as the peak week of production. In fact, the proportion of fruits taken from an individual is negatively correlated with the number of fruits on neighbors during its peak week of production (these competing fruits are the variable NFp; see Table 1) ($r = -0.61$, $P < 0.0005$) (Fig. 2).

Trees may have large or small fruit crops; the relative importance of any given crop with respect to its neighbors may be expressed as the proportion of the total neighborhood fruit production during the season (variable PFs; Table 1). This is not correlated with the proportion of fruits taken from a tree ($r = 0.24$). But the proportion of fruits in a neighborhood produced by a tree during its peak week of production (PFp; Table 1) is clearly correlated with the total fraction of fruits dispersed during the season ($r = 0.65$, $P < 0.0002$), accounting for 42% of the variance in individual dispersal success during 1980. The same general result holds when using only the fraction of fruits dispersed during the peak week and PFp ($r = 0.36$, $P < 0.05$), the difference in results being attributable to the obvious kurtosis in production in this species (Fig. 1; Howe 1982). Plants which produce large displays when their neighbors do not clearly do very well in terms of dispersal.

Further analysis indicates that the relationship between the proportion of seeds dispersed from individual trees and PFp is not strictly linear. The best fit is cubic, with the first-order term equal to zero ($Y = 0.3563 + 1.2433 X^2 + 0.6776 X^3$; $P < 0.0001$ for β_0 , β_1 , and β_2 respectively; see Fig. 3). The five trees producing 100% of the available fruit within a 50 m radius during the peak week were each completely isolated from conspecifics in space as well as time.

Table 3. Nutritional components in the aril

Nutrient	<i>n</i>	Percent composition (mean \pm SD)	g per aril (mean \pm SD)	range (g per aril)
Lipid	28	52.71 \pm 3.07	0.51 \pm 0.10	0.32–0.76
Protein	28	3.81 \pm 0.36	0.04 \pm 0.01	0.03–0.05
Carbohydrate ^a	28	6.23 \pm 2.39	0.06 \pm 0.03	0.01–0.14
Fiber	27	4.14 \pm 1.15	0.04 \pm 0.01	0.02–0.06
Ash	27	1.39 \pm 0.87	0.01 \pm 0.01	0.003–0.043

^a Non-structural carbohydrate**Fig. 2.** Proportion of seeds dispersed plotted against NFp (see Table 1)**Fig. 3.** Proportion of seeds dispersed plotted against PFp (see Table 1)

For these trees, the proportion of seeds dispersed cannot increase linearly with temporal isolation provided by fruiting asynchrony because there are no neighboring fruiting trees. Isolated trees are apparently least likely to be found by a sparse disperser assemblage. Partial discrimination of spatial and temporal effects in the variable PFp can be accomplished by dropping the five entirely isolated trees out of the analysis. For these clumped trees, 72% of the variance in proportion of seeds dispersed is attributable to PFp ($r=0.85$, $P<0.00005$).

Discussion

Our study distinguishes the relative contributions of four kinds of characteristics associated with fruit display to individual variation in dispersal success. We show that three attributes of individual trees contribute little or nothing to the proportion of fruits taken by animals; neither crop size nor nutritional components of the arils of different trees explain any variance in dispersal success, as defined here. Nor does the ratio of aril to seed explain as much individual variation in dispersal as was the case in a previous study (cf. Howe and Vande Kerckhove 1981). However, our analysis does show without a doubt that neighborhood effects can profoundly influence dispersal, and in so doing probably influence individual fitness. Our objectives here are to discuss these results in light of previous studies of this system and to consider them in light of related issues.

The confirmation of rather weak influences of crop and aril qualities on relative dispersal is surprising, in light of the fact that dispersal is incomplete and varies markedly within the *V. surinamensis* population (Howe and Vande Kerckhove 1981; see Howe and Estabrook 1977). Dispersal agents are clearly in limited supply, but they evidently do not place consistently strong selection on either crop size or aril components. Probably numerical superiority of large crops overrides any selection for crop attributes (see Howe 1980; Howe and Vande Kerckhove 1981), and birds may not be able to distinguish minor differences in aril quality. Similarly negative results have been reported for bird choice among fruits of varying quality from different species (Sorensen 1981). It is interesting that the significant correlation between aril/seed ratio and the proportion of fruits taken was replicated, but that the relationship was weaker than that reported during a lean year (Howe and Vande Kerckhove 1980). Median crop sizes were four times larger in 1980 than 1979, and the overall percentage of fruits taken averaged less in the "bumper" year (48%) than in the "lean" year (62%). Our data suggest that the surfeit of food lessened frugivore need to choose carefully among fruiting trees. Continued demonstration of bird preference for fruits with a high ratio of edible aril to indigestible seed is consistent with Herrera's (1981a) profitability analysis of frugivore use of fruits, as well as his demonstration of regional differences in pulp/seed ratios in *Smilax* (Herrera 1981b; see Howe and Smallwood 1982 for alternative interpretations). The overall insight from our study is that potential selection on fruit character due to disperser choice varies markedly from one year to the next.

Of more interest is our discovery that neighborhood effects have potentially profound influences on dispersal. Mack and Harper (1977) and more recently Weiner (1982) note that the fitness of herbs is influenced by the unique neighborhoods in which they occur in natural and experi-

mental populations; conspecific or heterospecific neighbors may depress or enhance seed or seedling survival of any given individual. *V. surinamensis* trees, like other plants in tropical and temperate communities, are clumped (Ashton 1969; Pielou 1974; Hubbell 1979). A consequence is that each individual faces a unique assemblage of competitors that vary in proximity and crop size. Birds evidently visit clumps of contiguous or adjacent crowns as if they were one plant; it is apparently more efficient to visit clumps of superabundant resources than select among widely scattered individuals that might have individually superior crop qualities. The somewhat depressed dispersal of completely isolated plants underlines the need for statistical partitioning of temporal and spatial effects with a much larger sample, particularly in light of Moore and Willson's (1982) discovery that isolated *Lindera* bushes are depleted more rapidly than those in clumps. The issue of fitness in the latter case is moot because all plants are entirely stripped of fruits. But it is clear that birds visiting both *Virola* and *Lindera* are influenced by spatial effects which almost certainly affect individual plant fitness.

Our results further suggest that fruiting asynchrony tends to favor those plants that bear most fruit when neighbors do not. The exception seems to be complete isolation in space or time; birds are less likely to visit plants without fruiting neighbors. Advantages to asynchrony may oppose those to synchrony imposed by seed predators or pollinators that select against outliers (see Janzen 1974; Augspurger 1981); the relative importance of each factor is an open question for any plant population.

Results reported here indicate that studies of the evolutionary ecology of seed dispersal should consider influences quite out of the control of parent plants, such as neighborhood effects, as well as those customarily thought to be under the influence of natural selection.

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