

Annual variation in a neotropical seed-dispersal system

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SUMMARY

- 1 A 3-year study shows that Panamanian *Virola surinamensis* (Myristicaceae) fruits are dispersed by six highly frugivorous birds and one monkey in a forest inhabited by seventy-eight species of fruit-eating birds and mammals.
- 2 The integrity of the disperser assemblage is evidenced by constancy in the face of four-fold variation in median crop size from one year to another and dramatic changes in community phenologies brought about by aberrant rains.
- 3 Neither crop size, kurtosis of individual fruiting schedules, nor nutritional composition of arils influence the proportion of fruits taken from individual trees.
- 4 The ratio of aril to seed weight consistently influences the proportion of fruits taken from individual trees, the effect being most pronounced during seasons or shorter periods of *Virola* fruit scarcity.
- 5 Conspecific fruit produced within the immediate vicinity of individual trees significantly depressed individual dispersal during 2 years; heavy use by birds which had apparently been denied other sources of food and destructive and wasteful use by monkeys obscured any effect during a season of aberrant rains.
- 6 Potential selection on fruit characters is apparently periodic; selection on fecundity *per se* is evidently continual.

INTRODUCTION

Tropical fruits differ enormously in size, abundance, and nutritional properties, implying both distinct phylogenetic trends and a variety of means of attracting and sustaining dispersal agents. On one level, it is important to know what features of a 'dispersal system,' or a fruiting plant and its associated animals, distinguish it from others. Comparative natural histories of different plant species permit association of features of the fruit and crop with attributes of an enormous variety of fruit-eating animals that might serve as dispersal agents (Snow 1971; van der Pijl 1972; McKey 1975). Of interest on a second level are sources of variation in dispersal of seeds of individuals within a population of plants. Direct assessment of properties of the crop, fruit, population, or community that promote or depress fruit removal allows an inference of possible sources of natural selection on plants and their dispersal agents, without the confounding phylogenetic distinctness endemic to comparative studies

(Howe & Estabrook 1977). The objective here is to pose and test hypotheses on each level using the model system of a neotropical nutmeg, *Viola surinamensis* (Rol.) Warb. (Myristicaceae) in the seasonal rain forest of Central Panama.

Viola surinamensis offers a good test of morphological dispersal syndromes. The tree produces a distinctive fruit obviously adapted for animal consumption (Fig. 1). Brilliant red coloration, a scentless and easily detached aril, and dehiscence early in the day foretell dispersal by birds (Van der Pijl 1972). The oily texture of the aril and the large (2 cm long) seed suggest high investment in individual fruits, and consequently predict low fecundity (McKey 1975). Together, these attributes lead to the expectation of a limited assemblage of birds that rely upon such fruits for a major portion of their diets (McKey 1975; Howe & Estabrook 1977). Systematic observations over three seasons should indicate whether such general predictions of natural history have foundation.

Factors that influence fruit removal are poorly understood. Dispersal agents are in limited supply if seed removal is less than complete (McKey 1975), and if differential reproduction *vis à vis* dispersal leads to varying lifetime probabilities of seed removal for different plants within a population (Howe & Estabrook 1977). At a first approximation, it is useful to determine sources of variation in dispersal within populations. Characteristics of either a tree or its surroundings may influence the proportion of seeds taken during any given year. A plant might, for instance, regulate production of fruits so as to make best use of a limited assemblage of dispersal agents. Observable consequences should include relatively high fruit removal from trees of intermediate fecundity, and a positive relation between the proportion of fruits taken and the degree of platykurtosis, or flattening, of the individual fruiting curves. Dispersal agents may also choose trees on the basis of fruit quality. Birds might, for instance, prefer trees with particularly nutritious arils, or they might favour plants which offer a large edible reward for the indigestible seed that must be consumed with the pulp. The surroundings may additionally play a role. If feeding assemblages are truly limited from the perspective of the plant, close proximity of fruiting neighbours should depress removal from an individual tree, thereby giving an advantage to isolated plants or those fruiting out of synchrony with others in the population. The relative importance of factors intrinsic to the plant or imposed by the environment may be expected to vary from season to season, depending upon the abundance and distribution of fruits of the same or other species and the shifting preferences of the frugivore guild.

MATERIALS AND METHODS

Study site and tree

Frugivory and fruit removal at *Viola surinamensis* were studied from April to early September of 1979–1981 at the Smithsonian Tropical Research Institute field station on Barro Colorado Island, Panama. The general features of the island are described by Croat (1978). In 1979 the *Viola* study site included 23 ha in and adjacent to Lutz

Watershed; the following 2 years 10 ha were added in the same area, in addition to 7 ha at the head of Shannon Ravine. Trees were in remnants of 'old forest' thought to be over 460 years of age, surrounded by advanced second growth more than 70 years old (Foster & Brokaw 1982). Although insular since the building of the Panama Canal 70 years ago, the Barro Colorado forest appears representative of seasonal moist forests in the area, harbouring approximately 365 species of trees (Croat 1978). Some insectivorous birds have become extinct since the building of the canal (Willis 1974), but seventy-eight fruit-eating birds and mammals still inhabit the forest (see Enders 1935; Willis & Eisenmann 1979). None of the large frugivores likely to disperse wild nutmegs are extinct; indeed they are well-represented on the island (see Willis 1980). Annual rainfall from 1962 to 1982 averaged 2530 ± 615 mm. Precipitation during 1979 (2664 mm) and 1980 (2105 mm) was unexceptional. A record rainfall during 1981 (4633 mm) was 3.4 standard deviations above the 20 year mean. Similarly, fruit production of other species was unexceptional during the first two seasons, but approached failure for many species during 1981 (R. Foster, pers. comm.; see Foster 1982a, b). In short, the study period encompassed both 'normal' and highly unusual seasons in a typical seasonal moist forest.

Virola surinamensis occurs from Costa Rica and Panama to the Guianas and Brazil, with disjunct populations in the Lesser Antilles (Croat 1978). On Barro Colorado Island this species, known as *V. nobilis* in the older literature, is a canopy or emergent tree of mature forest. Fruits consist of a single grey seed 2 cm long and 1.5 cm wide, surrounded by an easily detached lacinate red aril 1 mm thick, all enclosed in a dehiscent fibrous orange capsule (Fig. 1). The entire dry weight is approximately 5 gm, with the aril weighing approximately 1 gm and the capsule and seed averaging 2 gm each (Howe & Vande Kerckhove 1981). The fruit closely resembles the commercial nutmeg of Asia (*Myristica fragrans*), and is in fact known locally as 'wild nutmeg.' *V. surinamensis* is a dioecious species that flowers during the dry season from January to April. Individual plants may be found fruiting during any month of the year (Croat 1978), but the vast majority bear ripe fruit between April and early September, with a wet-season peak in July or August (Fig. 2). Maximum fruit production precedes the wettest months of the year, probably ensuring seedling establishment well before the onset of severe drought. In the greenhouse, seeds with arils attached were killed by mould, while those with arils removed by animals or me germinated in 2–4 weeks (Howe & Vande Kerckhove 1981). Assuming approximately one mature reproductive per ha in suitable old forest on Barro Colorado Island, the entire breeding population of both sexes probably numbers 700–800 individuals.

General procedures

This outline summarizes general procedures and defines the samples used. More detail is given by Howe & Vande Kerckhove (1981). Between late May and early September 1979, I studied fruit and frugivores at twenty-two *Virola* trees, of which seventeen yielded complete data for the season as well as suitable samples of preserved fruits. From April to early September in 1980 and 1981, I studied fruit and visitors at

twenty-eight trees in the same site and in Shannon Ravine. Fifteen trees were alive and in fruit all 3 years; this is a 'subsample' of use in comparing means from one year to the next. Twenty-five trees were alive and in fruit during 1980 and 1981, permitting a wider sample for a lesser period of time. These 'complete' samples of twenty-five are particularly useful for analyses of correlation and regression in which sample size is critical.

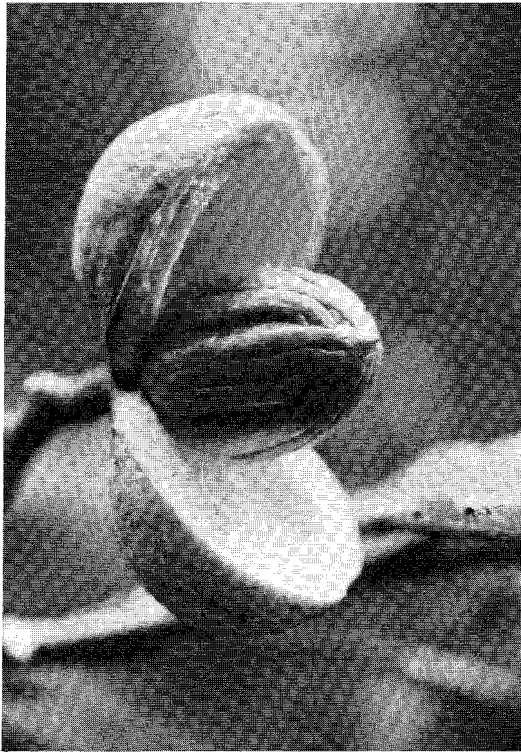


FIG. 1. *Virola surinamensis* fruit, as displayed to fruit-eating animals. The fruit consists of a fibrous capsule that dehisces in early or mid morning to expose a large (2-cm long) grey seed almost completely surrounded by a lacinate, brilliant red aril.

Trees

Fruit traps allow estimation of the quantity of fruit debris falling under tree crowns. Traps covering approximately 10% of the area under the canopies were placed at random. Traps consist of 1 m² plastic frames covered by 1.5 mm plastic mesh. Each horizontal frame is elevated 0.2–1.7 m above the ground, depending on topography. Traps catch all debris, including capsules which permit an estimate of the total crop size and undispersed seeds which permit estimates of the number and proportion of fruits left at the trees. Each set of crop estimates is unique because it is derived by dividing the number of parts (e.g. seeds, capsules) caught by a known area under the crown into the total area sampled. Coatis (*Nasua narica*) that forage for arils (not

seeds) under the canopies are discouraged from tampering with traps by regular sprayings of counted fruits with insect repellent. During fruit scarcity, when animals nonetheless raid traps, weekly counts of trap contents are replaced by daily counts and intensified spraying. Such extreme methods are effective because fruit fall is concentrated during morning hours when traps can be efficiently tended.

Fruits for nutritional analyses and dry weight determinations were picked at random from the ground, frozen, and freeze-dried to constant weight (8–10 days) on

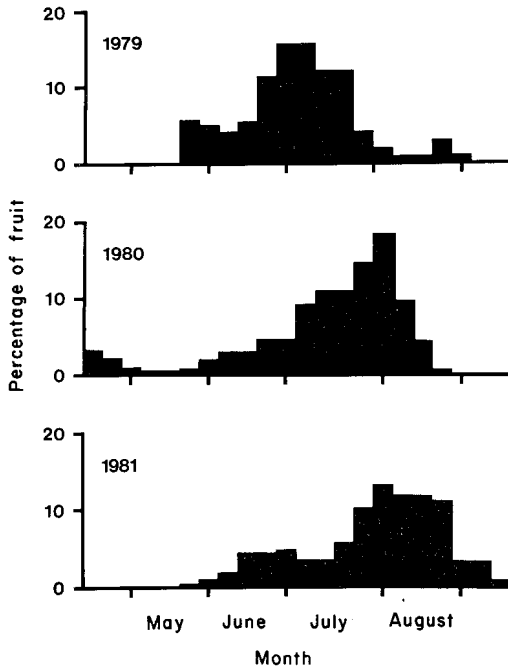


FIG. 2. Weekly fruit production of 15 *Virola surinamensis* trees, expressed as a percentage of the total production during the season.

Barro Colorado Island. Composite samples of 8–15 arils were secured from seventeen trees in 1979. In 1980, samples of twenty arils were obtained from each of twenty-eight trees. Samples of 8–20 arils were taken from twenty-eight trees in 1981, when low production and heavy animal use precluded wider sampling. These samples are unbiased with respect to bird use, as evidenced by equivalence in aril and seed weight of fruits taken from the trees and found underneath (Howe & Vande Kerckhove 1981). Protein, lipid, soluble carbohydrate, and phenolic extractions were accomplished commercially in 1979. Parallel analyses and a fibre analysis were done in my laboratory with 1980 and 1981 samples (Manasse 1982; unpubl.).

In 1979, censuses consisted of four randomly timed rounds of twenty-four trees on 3 days per week, from late May through late August. In 1980 and 1981, five randomly timed rounds of the same trees were accomplished on 2 days per week. For purposes of

comparison, the number of 'tree scans' for all years was standardized at 3400 by randomly eliminating some rounds throughout the 1979 season. In all cases a 'round' consisted of a 2-km walk, accomplished during an hour, to the same trees. Each tree is scanned for presence of dispersal agents, permitting a gross evaluation of visitation throughout the day and season at a large sample of trees. Howe (1980) and Howe & Vande Kerckhove (1981) discuss biases elsewhere. Diurnal censuses were supplemented each year with night censuses of twenty trees between 19.30 and 21.30 hours, at the peak of nocturnal frugivore activity. These night-time censuses during June and July, amounting to 308 tree scans with an electric lamp and binoculars each season, document presence or absence of nocturnal animal activity.

Statistics

Computations were accomplished with the SAS package at the University of Iowa. Parametric analyses are used where assumptions are met; non-parametric analyses are used when normality is in question. Parametric means are accompanied by standard deviations, non-parametric medians by 25–75% quartiles. Parametric statistics on proportions extreme enough (i.e. below 0.25 or above 0.75) to be influenced by a binomial distortion are checked with computations of data transformed with the angular transformation (Sokal & Rohlf 1969). In no case is interpretation altered. Proportions or percentages are therefore given to facilitate interpretation.

RESULTS

Natural history

This tree, according to the existing theoretical framework, should be playing to a small gallery of connoisseurs. The fruit should possess a rich aril capable of ensuring the efficient dispersal of small crops of large seeds. Effective dispersal agents of *Virola* are likely to be birds, attracted by red displays and morning dehiscence. The large size of the seed and relative rarity of such rich fruits should result in facultative specialization by members of a limited assemblage of large frugivores primarily dependent on fruit for food.

First, *V. surinamensis* does produce a rich fruit in relatively limited supply. Howe & Vande Kerckhove (1981) show that the arils are 1.59 ± 0.19 g, surrounding a seed averaging 3.18 ± 0.32 g fresh weight ($n=20$). Composite samples of arils from seventeen trees average $63.1 \pm 14.0\%$ lipid and $2.5 \pm 0.7\%$ protein, leading to an overall mean energetic content of 27.9 ± 0.8 kJ/g. Manasse (1982) replicates these results for two subsequent seasons. Moreover, crop sizes are small by standards of the rain forest. The sub-sample of fifteen trees monitored from 1979 to 1981 indicates a median production per tree well under 10 000 fruits in the year of heaviest production, and medians well under half of that for the other 2 years (Table 1). Wider samples of 17, 25, and 25 trees give virtually identical results, despite inclusion of a greater range of fecundities. The prediction of small crops of rich fruits holds.

TABLE 1. Annual variation in fruit production at *V. surinamensis* trees

| Year | N | Range | Median (25–75% quartiles) |
|------|----|------------------|---------------------------|
| | | Subsample** | |
| 1979 | 15 | 384–10 412 | 2218 (1699–4066) |
| 1980 | 15 | 820–17 922 | 8579 (3939–12880) |
| 1981 | 15 | 927–26 163 | 3931 (2651–6605) |
| | | Entire sample*** | |
| 1979 | 17 | 214–10 412 | 2082 (1326–3584) |
| 1980 | 25 | 428–31 006 | 8579 (4161–12493) |
| 1981 | 25 | 638–26 163 | 3990 (2687–6687) |

Kruskal-Wallis statistic: ** $P < 0.01$; *** $P < 0.001$.

Secondly, few of the seventy-eight fruit-eating birds and mammals in the Barro Colorado forest actually eat *V. surinamensis* fruits. Extended watches that document both visitation and feeding rates show that toucans (*Ramphastos swainsonii*) are by far the most important single dispersal agents, although five other birds and one monkey remove some fruits in viable condition (Table 2). An important point is that some common visitors are ineffectual dispersal agents. At least as many *Ramphastos sulfuratus* toucans visit this tree as their larger congeners, but are far less important because they eat fewer fruits (also see Howe 1981). *Ateles geoffroyi*, a frugivorous monkey, discards more fruits than it eats, and kills some in the gut (Howe & Vande Kerckhove 1981). One common visitor, a small cotinga (*Tityra semifasciata*), is not a dispersal agent; it strips arils from fruits and drops the seeds under the tree crown (but note Howe 1981). *Cebus capuchinus*, a monkey frequently seen during 1980 and 1981, either nips the base of the aril and drops the rest of the aril and seed, or peels and discards the aril and eats the seed. Its destructive effect is obvious. Significantly, censuses over 3 years show the core of the feeding assemblage to be stable, although relative abundances vary (Table 3). The most notable variations are heavy use of *Virola*

TABLE 2. Contributions of different visitors to the removal and waste (seeds dropped) of *V. surinamensis* fruits (modified from Howe & Vande Kerckhove 1981)*

| Binomial | Total handled | |
|-------------------------------|---------------|-------------|
| | Wasted (%) | Removed (%) |
| <i>Penelope purpurascens</i> | 0 | 9 |
| <i>Trogon massena</i> | 0 | 10 |
| <i>Baryphthengus martii</i> | 2 | 14 |
| <i>Pteroglossus torquatus</i> | 0 | 1 |
| <i>Ramphastos swainsonii</i> | 2 | 35 |
| <i>Ramphastos sulfuratus</i> | 2 | 8 |
| <i>Tityra semifasciata</i> | 5 | 0 |
| <i>Ateles geoffroyi</i> | 9 | 3 |

* Derived from sightings and feeding rates recorded during eight 5-hour watches at each of eight trees.

TABLE 3. Annual differences in census counts at twenty-three *V. surinamensis* trees (standardized to 3400 tree checks each)*

| Binomial | Number of sightings | | |
|-------------------------------|---------------------|------|--------|
| | 1979 | 1980 | 1981** |
| <i>Penelope purpurascens</i> | 7 | 6 | 14 |
| <i>Trogon massena</i> | 7 | 12 | 11 |
| <i>Baryphthengus martii</i> | 13 | 4 | 6 |
| <i>Pteroglossus torquatus</i> | 7 | 8 | 16 |
| <i>Ramphastos swainsonii</i> | 31 | 38 | 40 |
| <i>Ramphastos sulfuratus</i> | 52 | 52 | 39 |
| <i>Tityra semifasciata***</i> | 18 | 48 | 20 |
| <i>Ateles geoffroyi</i> | 50 | 57 | 91 |
| <i>Cebus capuchinus***</i> | 0 | 8 | 31 |
| Total | 185 | 233 | 267 |

* During 1980 and 1981, four trees were added to the nineteen censused in 1979.

** Annual distributions differ, $\chi^2=91.2$, $P \leq 0.001$.

*** Not dispersal agents.

fruits by inefficient foragers such as *Ateles* and *Cebus* in 1981, a year of massive fruit failure in the forest. Night censuses indicate heavy use of *Virola* by nocturnal frugivores only during fruit superabundance in 1980, when many fruits remained on the trees until dark (Table 4). No bats were seen eating these fruits in this or other extensive studies on Barro Colorado (Morrison 1978; Bonaccorso 1979). The number of visitors of all species reflected crop size during each season ($r=0.81$, 0.59 , and 0.83 ; all $P < 0.01$), but the number of species eating *Virola* only increased with crop size in 1980 ($r=0.52$; $P < 0.05$). Notably, the addition was the seed-eating *Cebus* rather than a dispersal agent. The prediction seems secure that *V. surinamensis* relies upon a limited, albeit taxonomically heterogeneous, feeding assemblage.

Thirdly, a high proportion of fruits is taken each year. The fifteen trees in fruit each year of the study indicate a depression of fruit removal during the season of plenty in 1980 ($\bar{x}=46\%$), but averages close to 60% during the other years (Table 5). Considerable variation exists, but the evidence at hand shows a rather efficient

TABLE 4. Annual differences at night census counts at twenty-two *V. surinamensis* trees (standardized at 308 tree checks)

| Binomial | Number of sightings | | |
|-------------------------------|---------------------|------|------|
| | 1979 | 1980 | 1981 |
| <i>Didelphis marsupialis*</i> | 0 | 1 | 0 |
| <i>Aotus trivirgatus</i> | 0 | 4 | 0 |
| <i>Nasua narica*</i> | 0 | 1 | 0 |
| <i>Potos flavus</i> | 0 | 18 | 3 |

* Not dispersal agents.

TABLE 5. Annual variation in the percentage of fruits taken from fifteen *V. surinamensis* trees

| Year | Range | Mean (\pm S.D.)* |
|------|-------|---------------------|
| 1979 | 13-91 | 60 \pm 20 |
| 1980 | 24-73 | 46 \pm 15 |
| 1981 | 40-77 | 59 \pm 10 |

* $F=4.08$, $P<0.025$.

dispersal system as compared with others evaluated in like manner (e.g. Howe & De Steven 1979; Howe 1980).

Differential dispersal

In any size category, trees with large crops virtually always disperse more seeds than those with small ones, indicating an ultimate numerical advantage in high fecundity within a tree population (Howe & Vande Kerckhove 1981). But small trees grow into large ones; the lifetime dispersal of a tree is the sum of the proportion taken each season times the number of fruits produced each season. To determine likely sources of natural selection, one must evaluate sources of variance in dispersal, including those under the control of the parent and those over which the parent can exert no influence. The most likely variables in the first category are crop size and phenology, aril composition, and the amount of edible pulp that accompanies an indigestible seed. Ecological circumstance may also account for considerable variance; the most apparent measure available is the number of competing fruits of the same species in the immediate vicinity of an individual tree.

Firstly, crop size does not influence the proportion of fruits removed from individual *V. surinamensis* trees. If birds had difficulty finding small trees and were satiated at large ones, the highest proportion of fruits taken should be from plants of intermediate fecundity. A second order polynomial regression of the proportion taken against crop size shows that neither first nor second order terms explain any variance in dispersal success (Table 6). At a second level of analysis, trees with relatively platykurtotic (flattened) fruiting phenologies should make best use of a limited disperser assemblage, while those with leptokurtic (peaked) displays are likely to satiate the visitor assemblage. Three seasons of weekly phenology data show first that

TABLE 6. Significance of first and second order terms of a polynomial regression of percentage of the crop removed and crop size at *V. surinamensis*

| Year | <i>N</i> | <i>P</i> (χ) | <i>P</i> (χ^2) |
|------|----------|---------------------|-----------------------|
| 1979 | 17 | > 0.58 | > 0.67 |
| 1980 | 25 | > 0.72 | > 0.97 |
| 1981 | 25 | > 0.15 | > 0.26 |

the population as a whole has a sharply peaked fruiting season (Fig. 2), and more importantly that kurtosis values for individual trees average well above 2, indicating strong leptokurtosis (Table 7; see Zar 1974). Furthermore, the expected negative correlation between the proportion dispersed and the degree of leptokurtosis does not materialize; correlation coefficients for analyses for twelve trees with good phenology data in 1979 and twenty-four trees with comparable data in 1980 and 1981 are 0.08, 0.13, and -0.21 , respectively. None approach significance. There is no evidence that either the amount of fruit on a tree or its schedule of production explain any variance in the proportion of fruits taken by animals. Fruiting phenology may be controlled by quite different factors, such as flowering phenology and weather.

TABLE 7. Kurtosis values for crops of *V. surinamensis*

| Year | <i>N</i> | Range | Mean (\pm S.D.) |
|------|----------|---------|--------------------|
| 1979 | 12 | 1.6-4.0 | 2.8 \pm 1.5 |
| 1980 | 24 | 1.4-4.3 | 2.8 \pm 0.6 |
| 1981 | 24 | 1.5-3.6 | 2.3 \pm 0.5 |

Secondly, the nutrient content of the arils does not influence dispersal. Howe & Vande Kerckhove (1981) show up to four-fold differences in the presence of ash (0.9-1.3%), protein (1.6-3.6%), lipid (46.0-86.2%), and nonstructural carbohydrate (6.6-12.6%) in aril samples from seventeen trees; these results are replicated with larger samples by Manasse (1982). Yet none of the differences in absolute or proportional contents of arils account for significant variance in the fraction of fruits removed (Table 8).

Thirdly, the mean ratio of edible aril to seed ballast explains some variance in relative dispersal success (Table 9, 10). By far the strongest association, accounting for 52% of the variation in the proportion of seeds dispersed, occurred in 1979 during a season of relative scarcity of *Viola* fruits. Some variance can be explained by the same ratio during the subsequent 2 years. Such results are consistent with the observation that seeds regurgitated by birds in the forest are significantly smaller than those available on *Viola* trees (see Howe & Vande Kerckhove 1981; p. 1101). As an independent test of the enhanced effect of the aril/seed ratio during scarcity, I divided

TABLE 8. Correlation of the proportion of fruits removed with components of *V. surinamensis* arils*

| Component (g/aril) | 1979 (<i>r</i>) | 1980 (<i>r</i>) | 1981 (<i>r</i>) |
|------------------------|-------------------|-------------------|-------------------|
| Protein | 0.30 | -0.03 | 0.23 |
| Lipid | 0.26 | 0.01 | 0.02 |
| Fibre | — | 0.00 | 0.03 |
| Available carbohydrate | -0.22 | -0.17 | -0.13 |
| Ash | -0.35 | 0.02 | 0.25 |

* For 1979, *N* = 17 trees; for 1980, *N* = 28; for 1981, *N* = 17-25.

TABLE 9. Results of the regression of proportion of seeds removed against the ratio of aril to seed weight in *V. surinamensis*

| Year | r^2 | Significance |
|------|-------|--------------|
| 1979 | 0.52 | 0.001 |
| 1980 | 0.14 | 0.06 |
| 1981 | 0.14 | 0.06 |

the 1980 and 1981 seasons into an 'early' half when fruits were relatively scarce, and a 'late' half when fruits were by comparison superabundant (see Fig. 2). During 1980, sixteen trees bore at least 5% of their crops in each half; during 1981, twenty-three trees did the same. Notably, the ratio of aril to seed was positively correlated with the fraction of fruits taken early in the season, but no correlation could be detected at the peak of the season (Table 10). Even when the overall influence of the aril/seed relation is weak, a retrospective analysis shows that times of scarcity within a season promote selectivity among dispersal agents.

Lastly, the proximity of neighbours plays a role during some seasons. These trees are clumped. Many areas of forest have no adult *Virola* trees, but 0-5 neighbours occur within a 50 m radius of any given tree ($\bar{x}=3$). Here I define the proximate neighbourhood as the number of fruits within a 50 m radius of an individual, corresponding to a guess of what a toucan might easily see from a tree crown. Over the course of a season, the median number of fruits with which a tree must compete for dispersers ranges from 7000 to 18000 (Table 11). Interestingly, the strongest depression of individual dispersal due to the proximity of neighbouring fruits occurred during the year of scarcity, with some depression during the year of plenty (Table 12). No effect could be detected in 1981, when widespread crop failure in other plants evidently led to wholesale exploitation of *Virola* by efficient and inefficient visitors alike.

TABLE 10. Seasonal shift in the influence of the aril/seed ratio on removal of *V. surinamensis* fruits

| Year | <i>N</i> | Early (<i>r</i>) | <i>N</i> | Late (<i>r</i>) |
|------|----------|--------------------|----------|-------------------|
| 1980 | 16 | 0.58* | 16 | 0.38 |
| 1981 | 23 | 0.58** | 23 | 0.40 |

* $P < 0.05$; ** $P < 0.01$.

TABLE 11. Estimates of *V. surinamensis* fruits within 50 m of each of fifteen conspecific individuals during the season

| Year | Median | 25-75% quartiles |
|------|--------|------------------|
| 1979 | 7054 | 2930-9019 |
| 1980 | 17939 | 4758-39096 |
| 1981 | 8267 | 2924-20625 |

TABLE 12. Results of the regression of the proportion of fruits taken on the number of *V. surinamensis* fruits within 50 m of seventeen to twenty-five individual trees

| Year | <i>N</i> | <i>R</i> | <i>r</i> ² | Significance |
|------|----------|----------|-----------------------|--------------|
| 1979 | 17 | -0.53 | 0.28 | 0.05 |
| 1980 | 25 | -0.38 | 0.14 | 0.06 |
| 1981 | 25 | -0.25 | 0.06 | NS |

In sum, the relative contributions of parental and population attributes to individual dispersal vary annually. The systematic exclusion of variables used here reflects the manner in which hypotheses were conceived and tested, but overestimates the total variance explicable in the study. One is tempted to add the variance explained by fruit attributes directly to that explained by neighbourhood effects. During 1979, this would suggest an explained variance of 80%; in subsequent years the totals would be 28% and 14%, respectively. But correlations among variables reduce the totals. A retrospective multiple regression shows the same general trends, but reduces the partitioned and total variances explained (Table 13). However, the primary message remains: attributes of the fruit are far more influential in securing removal during scarcity than superabundance.

TABLE 13. Variance explained by a stepwise multiple regression of the proportion of *V. surinamensis* fruits taken against the aril/seed ratios and number of conspecific fruits within a 50 m radius

| Year | Variation explained (%) | | Total |
|------|-------------------------|------------------|-------|
| | Aril wt/seed wt | Competing fruits | |
| 1979 | 52 | 8 | 60 |
| 1980 | 8 | 6 | 14 |
| 1981 | 8 | 0 | 8 |

DISCUSSION

These results have broad implications, both at the level of comparative natural history and at the more problematic level of identifying features that frugivores use to select among trees. This examination supersedes others in the important respect that it documents a stable disperser assemblage from one year to another, despite broad swings in weather and associated phenomena. It also suggests that selection on fruit attributes is most likely during times of stress. At other times, neighbourhood influences obscure effects of differences among the fruit characteristics of parental trees, perhaps by default leading to selection for high fecundity, *per se*.

In general, results reported here are an overall confirmation of the expectation that *Viola surinamensis* should produce a rich fruit in limited supply, and be dispersed by a restricted subset of birds that vie for a particularly favoured resource (McKey 1975; Howe & Estabrook 1977). That the aril is rich is beyond question: few approach its

energetic reward (see Snow 1962; White 1974). The four-fold range of median crop size measured, from 2000 to 8700 per tree, suggests an ample resource. But many wind-dispersed species are one to two orders of magnitude more fecund in this forest (C. Augspurger, Pers. comm.), while animal-dispersed figs produce millions of seeds in a year (Morrison 1978). Even *Tetragastris panamensis*, which possesses a sugary fruit eaten by monkeys and other frugivores, bears as many as 100 000 arillate seeds in a season (Howe 1980). By comparison, *Viola* produces a small crop. That the feeding assemblage is limited is clear from the replicated observation that only seven to eight animals of the eighty or so fruit-eating animals in the forest regularly eat *Viola* fruits. No comparable data from other communities are available to support the assertion that feeding specialization is facultative (cf. Howe & Vande Kerckhove 1979), but the assertion gains strength from the observation that key members of the feeding assemblage do not co-occur with this tree in South America (Ridgely 1976; de Schauensee & Phelps 1978). Overall, the framework conceived by Snow (1971) and McKey (1975) has stood one of its first major tests.

Perhaps the more important general result is that the 'dispersal system,' defined as *Viola surinamensis* and its associated animals, maintains a remarkable integrity in the face of considerable annual variation in both the properties of the tree population and the community at large. Despite a four-fold variation in median crop size from one year to the next, fruit superabundance only adds one seed predator (*Cebus*) and one common nocturnal visitor (*Potos*) to the assemblage. The influence of the first is obvious; that of the second might be guessed by the anecdotal observation of more than 450 insect-riddled *Viola surinamensis* seeds under a hollow occupied by a kinkajou (H.F. Howe, pers. obs.; see Janzen *et al.* 1976). Still remarkable is the fact, more fully discussed elsewhere, that several common and well-studied frugivores co-exist with *Viola surinamensis* and its small-seeded congener *V. sebifera* and simply do not eat the fruits (Morrison 1978; Bonaccorso 1979; Milton 1977, Howe 1981; Howe & Vande Kerckhove 1981). The integrity of the assemblage even weathered a season of fruit scarcity in the forest, brought on by a record annual rainfall more than three standard deviations above the norm. Under such circumstances one might expect a wholesale scramble for whatever fruit is available, as was observed at some tree species in 1969 (Foster 1982a; see Leck 1972; Foster 1977). But the assemblage remained stable in composition, albeit with heavy and destructive use by monkeys (see below). Given that seed size is not the limiting feature of *Viola* visitation (Howe 1981), I can only speculate that chemical deterrents exclude wasteful frugivory by mammals under all but extreme conditions (Howe & Vande Kerckhove 1981).

The attempt to partition variance in dispersal success has produced several important lessons. First, the observation that some variables thought to be important fail to influence the proportion of fruits taken demands a re-organization of existing theoretical frameworks. Secondly, I do identify a variable (i.e. aril/seed ratio) of obvious interest to dispersal agents, as reflected in the differential dispersal of individual trees. Lastly, the most far-reaching result is the documentation of annual variation in the influence of parental attributes as compared with emergent qualities of the population. The potential for selection is periodic, not constant.

Initial attempts to infer dispersal strategies of tropical trees relied upon comparisons of the size and quality of fruit crops of different species (Snow 1971; McKey 1975), leading to analogous predictions for intraspecific competition for dispersal agents (Howe & Estabrook 1977). Failure of aril quality to influence dispersal success may simply reflect coarse techniques which rely upon composite samples rather than statistical treatments of data derived from single arils. But the results are so overwhelmingly negative that it is reasonable to suppose that frugivores simply do not discriminate minor differences in aril composition. Sorensen (1981) reports comparable negative results in use of berries by English birds. Interspecific choice may involve categorical detection of particularly important nutrients, or a gross assessment of the amount of pulp that can be acquired for the amount of indigestible seed consumed (Herrera 1981a). Perhaps the only active discrimination of *Virola* arils is the rejection of more than half of the fresh fruits handled by *Ateles* monkeys, suggesting a possible chemical defence against inefficient use by monkeys which habitually knock down more fruits than they eat (Howe 1980; Howe & Vande Kerckhove 1981).

Failure of crop size and phenology to influence proportional dispersal is more important, because it pinpoints deficient assumptions in earlier models. Howe & Estabrook (1977) assume, as do others (e.g. Heinrich & Raven 1972), that forager activity is under the control of individual plants. But this carries the implicit assumption that the interaction between animal and plant is independent of other plants. Such would be unlikely unless distributions were uniform or random. I suspect that crop size fails to influence relative dispersal in stands of *Virola* because one or more neighbouring trees strongly influences the amount and quality of visitation at any particular individual. Assuming that tropical trees are generally clumped rather than spaced (Ashton 1969; Hubbell 1979, 1980), the general case must be that each individual plant faces a unique constellation of competitive interactions from neighbours of the same and different species (Howe & Smallwood 1982; see Mack & Harper 1977). This uniqueness is in part a consequence of the enormous diversity of potential neighbours in a tropical community, in part a reflection of the wide range of crop sizes borne by trees of different age and exposure to light. Use by birds of *Virola* stands of varying collective fecundity 'spreads the assemblage thin,' and in so doing blunts the force of interaction between a particular tree and the animals that might visit it.

The influence of aril and seed ratio on individual dispersal is not surprising in light of previous insights from comparative studies. Snow (1971) and McKey (1975) comment that birds are likely to weigh the advantage of selecting one species over another on the basis of the reward obtained for the seed bulk and ballast that must be consumed; this is the concept of foraging 'profitability' applied to frugivory (Herrera 1981b). But the fact that birds use the aril/seed ratio to discriminate among trees within a population presents a paradox, because it suggests directional selection for dispersibility associated with small seed size. Trees with large seeds obviously occur. Howe & Vande Kerckhove (1980) suggest that extremes of the 'reward/bulk continuum' reflect two potent sources of selection in a forest in which frugivores may be either common or scarce (see Foster 1982a). Selection might favour small-seeded

trees with dispersible fruits when fruit-eating animals are common, and large-seeded plants that produce highly competitive seedlings when fruit-eating animals are absent (Howe & Richter 1982). Most trees have fruits of intermediate character, representing a 'trade-off' between sources of selection detectable only at the extremes of the continuum. This view must be altered slightly in view of the observation that the absence of frugivores is not a pre-requisite for an advantage to large seeds and seedlings; large seeds are dispersed as well as small ones when fruits are common. What we apparently witness is a periodic advantage for a high ratio of aril to seed, and frequent advantage to the numerical superiority of large crop size.

At first sight, it seems anomalous that fruit abundance overrides selectivity. Within the framework of predation theory, one expects selectivity to increase as the overall abundance of resources increases (MacArthur 1972). Predators eat prey of unknown distributions as they become available. The prey are independent of one another, and of course attempt to avoid capture. A forager in a 'patch' simply eats more of the best prey, the more easily they are caught. But this study suggests that the rules change when scattered trees of known location produce particularly palatable fruits; the early birds get the best fruits. During scarcity at *Viola*, birds must often travel considerable distances to find trees at which they can efficiently eat their fill. Birds either visit the preferred plants at or close to dawn, or take the documented risk that competitors will deplete the best fruits (Howe 1981; Howe & Vande Kerckhove 1981). During plenty, there is little work involved in finding *Viola* crops, and birds do not compete for fruits. Extreme scarcity might lead to a breakdown of selectivity or force use of alternative foods, but the general message here is that selection on fruit characters occurs only during times of relative dearth. At other times, the trees with the highest fecundity are favoured regardless of fruit character.

Finally, population and community effects need discussion. Neighbourhood effects are well-documented in populations of small herbs (Mack & Harper 1977; Harper 1977). Positive (Silander 1978; Augspurger 1981) and negative (Carpenter 1976; see Lloyd 1980) density-dependence occurs in the effect of flower number on seed set. Depression of dispersal by competing neighbours both shows that the *Viola* assemblage is limited and that neighbour influence occurs in the dispersal of large trees. The absence of such an effect in 1981 is probably attributable to both increased fruit use by proper dispersal agents and opportunistic adjustments by clumsy foragers during a spectacularly aberrant year. The result is bedlam in the data. Record rains caused massive crop failures in other species (R. Foster, pers. comm.; see Foster 1982a, 1982b), offering a rare insight into community effects. *Viola* crops were intermediate between those of other years, indicating unusual stability in fruit production in the face of climatic variation that affected many other species. Paradoxically, these intermediate crops were dispersed with high efficiency without selectivity among trees. Apparent causes were unusually heavy use by birds denied other sources of food, and heavy and destructive use by *Ateles* and *Cebus* monkeys. Part of the commotion in the data is due to the fact that trees favoured by proper dispersal agents were often heavily visited by monkeys as well; in 1981 a negative correlation existed between the fraction of seeds taken and the number of monkeys recorded in censuses ($r = -0.45$, $P < 0.05$),

at those trees actually visited by primates. The scramble for food in general, and the chaotic waste by monkeys in particular, obliterated measurable effects among the trees. What we see is a remarkably stable assemblage exploiting a remarkably predictable food resource, in the face of variation in the fortunes of other animals and plants as extreme as any likely to occur in a diverse tropical rain forest.

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REFERENCES

- Ashton, P.S. (1969). Speciation among tropical forest trees: some deductions in light of recent evidence. *Biological Journal of the Linnean Society*, **1**, 155–196.
- Augsburger, C.K. (1981). Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology*, **62**, 775–788.
- Bonaccorso, F.J. (1979). Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum Biological Sciences*, **24**, 360–408.
- Carpenter, F.L. (1976). Plant–pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). *Ecology*, **57**, 1125–1144.
- Croat, T.B. (1978). *The Flora of Barro Colorado Island*. Stanford University Press, Palo Alto.
- Enders, R.K. (1935). Mammalian life histories from Barro Colorado Island, Panama. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **78**, 385–502.
- Foster, M.S. (1977). Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology*, **58**, 73–85.
- Foster, R.B. (1982a). Famine on Barro Colorado Island. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (Ed. by E. G. Leigh, Jr., A. S. Rand & D. S. Windsor), pp. 201–212. Smithsonian Press, Washington.
- Foster, R.B. (1982b). The seasonal rhythm of fruit fall on Barro Colorado Island. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (Ed. by E. G. Leigh, Jr., A. S. Rand & D. S. Windsor), pp. 151–172. Smithsonian Press, Washington.
- Foster, R.B. & N. Brokaw (1982). General character of the vegetation. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (Ed. by E. G. Leigh, Jr., A. S. Rand & D. S. Windsor), pp. 67–82. Smithsonian Press, Washington.
- Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, New York.
- Heinrich, B. & Raven, P. (1972). Energetics of pollination. *Science*, **176**, 597–602.
- Herrera, C.M. (1981a). Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos*, **36**, 51–58.
- Herrera, C.M. (1981b). Are tropical fruits more rewarding to dispersers than temperate ones? *American Naturalist*, **118**, 132–144.
- Howe, H.F. (1980). Monkey dispersal and waste of a neotropical fruit. *Ecology*, **61**, 944–959.
- Howe, H.F. (1981). Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. *Auk*, **98**, 88–98.

- Howe, H.F. & De Steven, D. (1979). Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia*, **39**, 185–196.
- Howe, H.F. & Estabrook, G.F. (1977). On intraspecific competition for avian dispersers in tropical trees. *American Naturalist*, **111**, 817–832.
- Howe, H.F. & Richter, W. (1982). Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia*, **53**, 347–351.
- Howe, H.F. & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–218.
- Howe, H.F. & Vande Kerckhove, G.A. (1979). Fecundity and seed dispersal of a tropical tree. *Ecology*, **60**, 180–189.
- Howe, H.F. & Vande Kerckhove, G.A. (1980). Nutmeg dispersal by tropical birds. *Science*, **210**, 925–927.
- Howe, H.F. & Vande Kerckhove, G.A. (1981). Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology*, **62**, 1093–1106.
- Hubbell, S.P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Hubbell, S.P. (1980). Seed predation and the coexistence of tree species in tropical forests. *Oikos*, **35**, 214–229.
- Janzen, D.H., Miller, G.A., Hackforth-Jones, J., Pond, C.M., Hooper, K. & Janos, D.P. (1976). Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology*, **57**, 1068–1075.
- Leck, C.F. (1972). Seasonal changes in feeding pressures of fruit and nectar eating birds in the Neotropics. *Condor*, **74**, 54–60.
- Lloyd, D.G. (1980). Demographic factors and mating patterns in angiosperms. *Demography and Evolution in Plant Populations* (Ed. by O. Solbrig), pp. 67–88. Blackwell, Oxford.
- MacArthur, R. (1972). *Geographical Ecology*. Harper & Row, New York.
- Mack, R. & Harper, J. (1977). Interference in dune annuals: spatial pattern and neighborhood effects. *Journal of Ecology*, **65**, 345–363.
- Manasse, R.S. (1982). *The impact of neighborhood effects on the dispersal success of wild nutmeg*. M. S. Thesis, University of Iowa.
- McKey, D. (1975). The ecology of coevolved seed dispersal system. *Coevolution of Animals and Plants* (Ed. by L. E. Gilbert & P. Raven), pp. 159–191, University of Texas Press, Austin.
- Milton, K. (1977). *The foraging strategy of the howler monkey in the tropical forest of Barro Colorado Island, Panama*. Ph.D. thesis, New York, University. New York, New York.
- Morrison, D.W. (1978). Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology*, **59**, 716–723.
- van der Pijl, L. (1972). *Principles of Dispersal in Higher Plants*. 2nd edn. Springer-Verlag, Berlin.
- Ridgely, R.S. (1976). *A Guide to the Birds of Panama*. Princeton University Press, Princeton.
- de Schauensee, R.M. & Phelps, W.H., Jr. (1978). *A Guide to the Birds of Venezuela*. Princeton University Press, Princeton.
- Silander, J.A., Jr. (1978). Density-dependent control of reproductive success in *Cassia biflora*. *Biotropica*, **10**, 292–296.
- Snow, D. (1962). The natural history of the Oilbird, *Steatornis caripensis*, in Trinidad, W. I. II. Population, breeding ecology, and food. *Zoologica*, **47**, 199–221.
- Snow, D. (1971). Evolutionary aspects of fruit-eating in birds. *Ibis*, **113**, 194–202.
- Sokal, R.R. & Rohlf, F.J. (1969). *Biometry*. Freeman, San Francisco.
- Sorensen, A. (1981). Interaction between birds and fruit in a temperate woodland. *Oecologia*, **50**, 242–249.
- White, S.C. (1974). *Ecological aspects of growth and nutrition in tropical fruit-eating birds*. Ph.D. thesis, University of Pennsylvania, Philadelphia.
- Willis, E.O. (1974). Populations and local extinctions of birds of Barro Colorado Island, Panama. *Ecological Monographs*, **44**, 153–169.
- Willis, E.O. (1980). Ecological roles of migratory and resident birds on Barro Colorado Island, Panama. *Migrant Birds in the Neotropics* (Ed. by A. Keast & E. S. Morton), pp. 205–225. Smithsonian Press, Washington.
- Willis, E.O. & Eisenmann, E. (1979). A revised list of birds of Barro Colorado Island, Panama. *Smithsonian Contributions to Zoology*, **291**, 1–31.
- Zar, J.H. (1974). *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.