Fecundity, Fruiting Pattern, and Seed Dispersal in *Piper amalago* (Piperaceae), a Bat-Dispersed Tropical Shrub

Theodore H. Fleming

Department of Biology, University of Miami, Coral Gables, Florida 33124, USA

Summary. This paper describes the nightly and seasonal production of ripe fruit by *Piper amalago* (Piperaceae), a patchily distributed, bat-dispersed forest shrub, at Parque Nacional Santa Rosa, Costa Rica. Phenological observations over several years indicate that individuals produce a low (usually 1–3) and variable number of ripe fruit each night for 3–4 wks in the early wet season (June and July). Observations of the disappearance rates of marked fruits and fruit manipulation experiments indicate that fruit removal probabilities are high (often nearly 1.0) and independent of nightly and seasonal ripe fruit crop size. Data from previous feeding and foraging studies of the bat *Carollia perspicillata* (Phyllostomidae) are used to estimate the mobility of *P. amalago's* seeds. Most seeds (>90%) are deposited ≥50 m from parent plants under night feeding roosts. Relatively few seeds move >300 m, and movements this long are more likely to occur early and late in the fruiting season when bats change feeding sites more frequently. Seed experiments indicate that *P. amalago* seedling establishment probabilities are higher in light gaps than under forest canopy. The dispersal quality (*sensu* McKey 1975) of *P. amalago's* chiropteran seed dispersers is directly proportional to the number of seeds they excrete in actual or incipient light gaps.

Introduction

Beginning with the seminal papers of Snow (1971) and McKey (1975), ecological and evolutionary interactions between fruiting plants and their vertebrate seed dispersers have recently received considerable attention from both tropical (e.g. Howe 1977, 1980, 1981; Howe and DeSteven 1979; and Howe and Vande Kerckhove 1979, 1980) and temperate (e.g. Stiles 1980; Thompson and Willson 1978) workers. To date, most attention has been focussed on fecundity and its consequences for the removal probabilities of avian-dispersed seeds. Few quantitative data are available on how far birds actually carry seeds before regurgitating or excreting them or on other dispersal systems.

The conceptual framework for these studies involves the apparent dichotomy that exists between high fecundity (in terms of number of seeds produced per fruit crop) plants that produce sugary fruits consumed by a variety of opportunistic frugivores and low fecundity plants that produce more nutritious fruits consumed by a restricted number of specialized frugivores. Examples of the former strategy include various species of *Ficus* (Moraceae) (Janzen 1979) and *Tetragastris panamensis* (Burseraceae) (Howe 1980) and of the latter strategy, *Casearia corymbosa*

(Flaucourtiaceae) (Howe 1977) and *Virola sebifera* (Myristicaceae) (Howe 1981). Compared with "specialized" plants, "opportunistic" plants are thought to receive low quality dispersal from their vertebrate visitors, where quality refers in part to the dispersal of seeds to safe germination sites (McKey 1975). A further distinction between these two fruiting strategies is that the proportion of seeds removed from opportunistic plants should increase monotonically with increasing fruit crop size whereas intermediate-sized fruit crops should experience proportionally higher seed removal in specialized plants (Howe and Estabrook 1977). Data for two species, *Casearia corymbosa* and *Tetragastris panamensis*, provide weak statistical evidence that percent seeds dispersed is curvilinearly-related to fruit crop size.

The purpose of this paper is to describe the fecundity and fruiting pattern of a bat-dispersed tropical shrub, *Piper amalago* (Piperaceae), to document via observation and experimentation the relationship between nightly and total plant fecundity and fruit removal probabilities, and to estimate the dispersal distances of seeds ingested by bats. Previous experimental work with this species (Fleming et al. 1977; Lockwood et al. 1981) has demonstrated that *P. amalago* fruits are highly sought-after by several species of bats of the family Phyllostomidae. Because individuals bear low numbers of ripe fruit each night for extended periods and its fruit are eaten by a limited number of species, *P. amalago* can be considered a "specialized" plant, and the following two questions arise about its fruiting strategy: (1) is the probability of its fruit removal curvilinearly-related to fruit crop size, and (2) do its dispersal agents deposit most of its seeds in good germination sites? Data presented in this paper indicate that the answer to both of these questions is "No".

Study Area and Methods

This study was conducted at Parque Nacional Santa Rosa, Guanacaste Province, Costa Rica during the wet season months of June and July in 1975, 1976, 1979, and 1980. Vegetation and climate of Santa Rosa, which lies within Holdridge's (1967) Premontane Moist Tropical Zone, are described by Heithaus and Fleming (1978) and Fleming and Heithaus (1981).

A variety of techniques was used to document the fecundity and fruiting pattern of *Piper amalago*, a 1–3 m tall, multiple-stemmed understory shrub whose density ranges from a few to over 200 plants per ha in my study area. Fruits (actually infructescences) weigh about 1.6 g, are about 48 mm long by 4 mm wide, and are vertically exerted away from the foliage of these shrubs. Total fruit crop size was determined in two areas (sites B and C of Fleming et al. 1977) by censusing 30–60 plants prior to fruit maturation in 1976, 1979, and 1980. Number of stems and stem lengths (in cm) were also recorded for each plant.

The general maturation (disappearance) rate of fruit in these areas was determined by labeling 60 randomly-selected fruits (5 per plant on 12 plants) and noting the date each fruit disappeared in 1975, 1976, and 1979 in areas B and C and in area B in 1980. In 1980 the daily maturation rate of the fruit crops of 20–30 plants at site B was monitored during the 4-wk fruiting season. Nearly all fruits disappear on the first night they are ripe and are principally eaten by two bat species, *Carollia perspicillata* and *Glossophaga soricina*, both of which are common to abundant in Santa Rosa forests (Fleming et al. 1977). *P. amalago* density in areas B and C, respectively, is 222 and 398 plants per ha (Fleming et al. 1977). Its dispersion pattern is clumped in both areas, and mature plants are often ≦1 m apart.

Three sets of data were used to examine the relationship between nightly availability of ripe fruit and their disappearance probabilities and rates. First, I determined the probability of a ripe fruit being taken as a function of the number of ripe fruits on a plant by labeling 1–8 fruits on 19–20 plants in both areas and counting the number missing the following morning. Second, I determined the disappearance rates of ripe fruits within one night on 4 occasions by labeling 60 fruits (1–6 on each of 12–20 plants depending on the number of ripe fruit available) in 3 areas (sites B, C, and A, which was near a *Carollia-Glossophaga* roost cave) and counting the number of fruit missing at 0.5 h intervals from 1800 to 2200 CST and again at 0600 the next morning. Third, I experimentally manipulated the number of ripe fruits on plants in areas B and C on 7 occasions as follows: (1) 1–4 ripe fruits were pinned to the branches of 10 plants bearing known numbers of ripe fruit twice each in both areas; equivalent numbers of ripe fruits were simultaneously labelled on 10 control plants; and (2) one ripe fruit was pinned to 10 plants bearing only unripe fruit and 10 plants bearing no fruit on 3 occasions (once in area B, twice in area C). These experiments were set up in the mid-morning of one day, and the plants were checked for missing marked fruit early the next morning.

Dispersal distances of seeds were estimated from a previous radio-tracking study of *Carollia perspicillata*, the principal disperser of *P. a-malago's* seeds (Heithaus and Fleming 1978). That study provided detailed information about the location of individual's nightly feeding areas, how long individuals remained in each area, and the approximate paths taken by bats between feeding areas. Additional insight into the feeding behavior of *Piper*-eating bats was gained by mapping and monitoring 10 night roosts in area C between 22 July and 2 August 1976. The number of ripe *P. amalago* fruit under the roosts, which are secluded bowers of vegetation, and the approximate proportion of seeds removed per fruit was recorded daily. Data from Lockwood et al. (1981) on the feeding and seed passage rates of *C. perspicillata* were used to calculate the residence time of *P. amalago* seeds inside a frugivorous bat.

A series of experiments using fresh, air-dried seeds was conducted to assess the effect of different microhabitats on seed germination and seedling establishment probabilities. One hundred seeds were cast onto the litter and soil of one-half of 0.25 m² plots located in 4 different microhabitats: a *P. amalago* patch growing in heavy forest cover (site B); known night roosts, also in heavy forest, in a site B; heavy forest cover away from *P. amalago* plants but near other *C. perspicillata* food plants, *Chlorophora tinctoria* trees; and at the edge of a large light gap. The other half of each plot was used to control for natural seed input and germination. Four replicate plots were established at each site on 1 August 1979 and were checked for seedlings on 5, 15, and 28 September 1979, 28 January 1980, and 1 August 1980. Each plot was covered until 28 September 1979 by a wooden frame 2 cm high covered with 1.5 mm fiberglass window screening to prevent predators (e.g. ants and rodents; see Perry and Fleming 1980) from removing seeds.

Results

Characteristics of the P. amalago fruit crop. P. amalago is a rather low fecundity plant whose fruit ripen and are removed over a 3–4 wk period in early-to-mid rainy season. Initiation of fruiting varies from year to year depending on the onset and intensity of rains early in the wet season, which usually begin in mid-May.
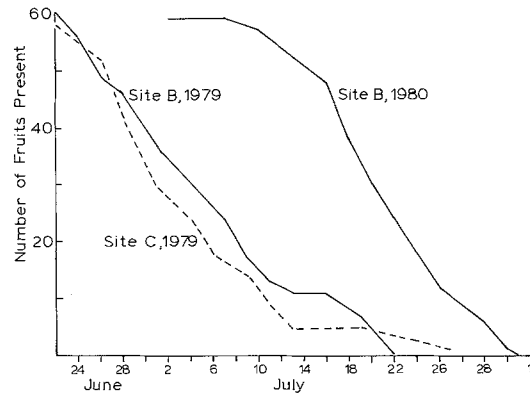

Fig. 1. Disappearance curves for marked fruits of *Piper amalago* in 1979 and 1980

For example, ripe *P. amalago* fruits were available earlier in 1979 than in 1980 because of the earlier and more intense rains in 1979 (Fig. 1). Between sites and years, fruits ripened and disappeared at a similar and constant rate (Fig. 1), although, as described below, there was considerable variation in daily fruit maturation among different individuals.

Total fruit crop size in plants ≧1 m tall, the minimum height of sexually mature individuals, varied between sites and years. In general, fecundity of site C plants was over 2X greater than that of site B plants (1976 means: 41.0 ± 6.2 (SE) vs. 25.5 ± 4.5; 1979 means: 47.3 ± 7.8 vs. 16.8 ± 4.6; 1980 means: 67.8 ± 7.9 vs. 24.9 ± 3.5). Frequency distributions of fruit crop sizes were non-normal in both areas with small crops (≦20 fruits) predominating in area B and small and large crops (up to 192 fruits) more equally-represented in area C. Multiple regression analysis using sites and years as dummy variables (Kleinbaum and Kupper 1978) revealed that total fruit crop size (transformed to ln (fruit crop size $+1$)) was significantly correlated with greatest plant height and number of stems per plants ($p < 0.001$ in partial F tests). Regression equations by site and year are: site B, 1979: $Y = -2.04 + 0.019X_1 + 0.28X_2$; site B, 1980: $Y = -1.21 + 0.019X_1 + 0.10X_2$; site C, 1979: $Y = -1.00 + 0.019X_1 + 0.28X_2$; site C, 1980: $Y = -1.00 + 0.19X_1 + 0.10X_2$ where $Y = \ln$ (fruit crop $+1$), $X_1 =$ greatest height, and $X_2 =$ number of stems.

Sexually mature plants bear only a few (usually 1–3) ripe fruits each night (Fig. 2A). Temporal variation in mean number of ripe fruits per day in 13–30 area B plants in 1980 is shown in Fig. 2B. At the beginning of the season, few plants bore ripe fruit and, as indicated by the high variance:mean ratio of the number of ripe fruits per plant, these fruits were spatially clumped. As the season progressed, the mean number of ripe fruit per plant increased, and ripe fruits were more randomly-distributed among individuals (Fig. 2B). At the end of the season, the mean again declined, but ripe fruits were still randomly-distributed among plants.

Several fruiting characteristics are correlated with total fruit crop size. Both the mean number of ripe fruits per night and its variance: mean ratio are linearly-related to total fruit crop size (Fig. 3A, B). These relationships mean that although more fecund plants bear more ripe fruits per night, they are also temporally more variable in ripe fruit production than are less fecund plants. The number of days on which ripe fruits are available is curvilinearly-related to fruit crop size; an asymptote of about 21 days is reached at a fecundity of about 60 fruits (Fig. 3C). The proportion of days in which plants bear ripe fruit is also curvilinearly-related to total fecundity; an asymptote of about 0.85 is reached at a fruit crop size of about 40 (Fig. 3D).
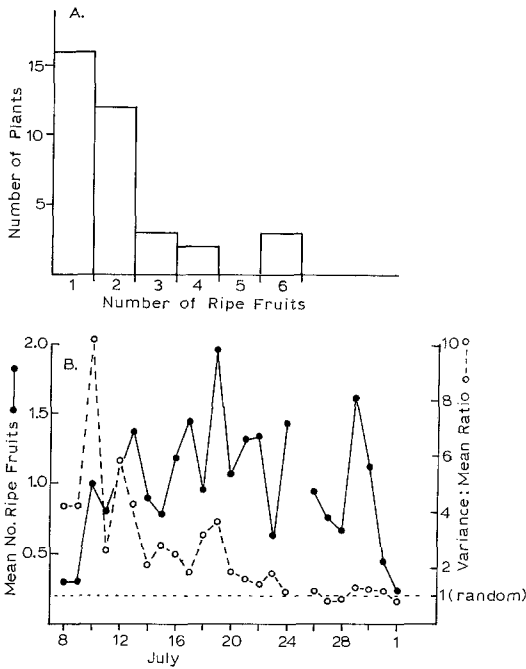
Fig. 2. A Frequency distribution of number of ripe fruits per plant per night in area B in 1979. Data from other sites and years are similar. B Temporal changes in mean number of ripe fruits and its associated variance: mean ratio in area B in 1980. Daily sample sizes range from 13 to 30 plants
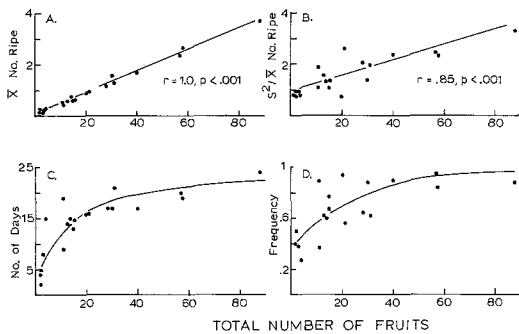

Fig. 3A–D. Correlates of total fruit crop size in area B in 1980. A Mean number of ripe fruit per plant per night. B Variance: mean ratio in number of ripe fruits per plant per night. C Number of days between first and last ripe fruits on 20 marked plants. D Probability that a marked plant will bear ≥ 1 ripe fruit each day during its fruiting season. The nonlinear curves were fit by eye

Infructescences bear variable numbers of small, single-seeded fruits. Seeds are about 1.5 mm long and weigh about 1.6 mg. Total seed number per infructescence is linearly-related to infructescence length by the equation $Y = 3.70 \pm 2.88X$ ($r = 0.77$, df = 18, $P < 0.01$). Median seed number for a random sample of 20 site B and C fruits was 132 (range = 22–205). Plants bearing an average of 17 to 68 fruits per season thus produce 2,244 to 8,976 seeds annually.

Disappearance Rates and Probabilities of P. amalago Fruits. The disappearance rates of ripe fruits within a night are correlated with the density of bats in different *Piper* patches. As shown in Fig. 4, the rate at which ripe fruits disappear was highest close to the *Carollia-Glossophaga* roost (site A) and lowest at site B. Mean number of frugivorous bats captured per net-hour
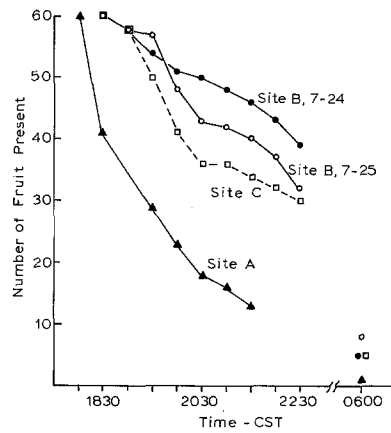

Fig. 4. Disappearance curves for marked ripe fruits within one night in 3 areas in 1976

(=one mist net opened for one h) at sites, A, B, and C in 1974–1975, respectively was 1.74 (SD = 1.07), 1.10 (0.48), and 1.35 (0.56) (Fleming et al. 1977). More recent netting data (unpubl.) corroborate these results. The disappearance rates of these marked fruits did not vary as a function of number of ripe fruit marked per plant (which usually included all ripe fruit on each plant). Twenty-two of the 41 singles and pairs of fruits (53.7%) disappeared by 2200 compared with 91 of the 143 fruits (63.6%) marked in groups of 3 or more; these proportions do not differ significantly ($X_1^2 = 1.34$; $P > 0.25$). Few of these fruits remained on plants the next morning (Fig. 4).

Two sets of observations indicate that the disappearance probabilities of ripe fruit are independent of nightly and/or total fruit crop sizes. First, all of the 66 marked ripe fruit (29 and 37 marked in areas B and C, respectively), including 25 singles, 7 pairs, 5 triplets, and one group each of 4 and 8, disappeared the first night they were available to bats. Second, the proportion of fruits removed from the 1980 site B plants that were censused daily was nearly 1.0 (mean = 0.99 $\pm$ 0.003 SE, $n = 29$).

Results of the fruit manipulation experiments also indicate that disappearance probabilities of ripe fruits are high and independent of the number of ripe fruits per plant. In the 4 experiments in which ripe fruits were added to plants bearing 1 or more ripe fruits, X^2 analysis revealed no difference between sites or treatments (i.e. experimental or control fruits) so the data were combined. Results (Fig. 5) show that there are three peaks regarding the probability that a ripe fruit will disappear; these include 1 ripe fruit per plant, 4–5 per plant, and 7–9 per plant. In the second series of fruit manipulations, a single ripe fruit was added to either barren plants ("experimentals") or plants bearing only unripe fruits ("controls"). Twenty-five of the 28 control fruits (89.3%) and 19 of the 27 experimental fruits (70.4%) were removed; these proportions do not differ significantly ($X_1^2 = 3.07$; $0.10 > P > 0.05$).

Dispersal Distances of Seeds. Radiotracking has shown that *Carollia perspicillata* is a relatively sedentary bat, especially when feeding on fruits of *P. amalago*, and hence it provides relatively little mobility for *P. amalago* seeds. Individuals typically visit 2–3 different feeding areas (FAs), which are located up to 1.6 km apart, each night. Usual distances between FAs, however, are <700 m (Heithaus and Fleming 1978). Bats spend a majority (ca. 60%) of their time in one FA, and they often shuttle back and forth between FAs at an average rate of once every 1.6 h. Rate of movement between FAs is depressed under conditions of bright moonlight.
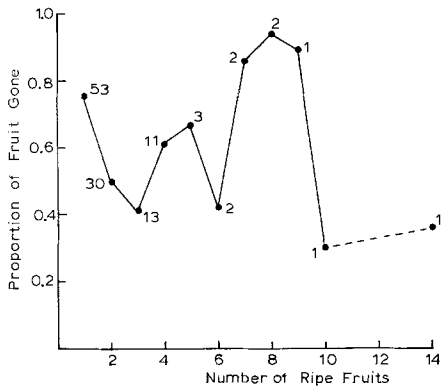
Fig. 5. Probability that a ripe *P. amalago* fruit will disappear as a function of the number of ripe fruits on a plant. Numbers beside each data point indicate sample size (number of plants). Data from experimental and control plants in areas B and C are combined
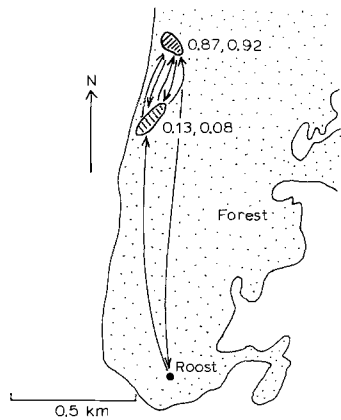

Fig. 6. Typical July nightly foraging bout of *Carollia perspicillata*. Values beside each feeding area indicate proportion of time spent in each area followed by the estimated proportion of total ingested seeds deposited there. Modified from Heithaus and Fleming (1978)
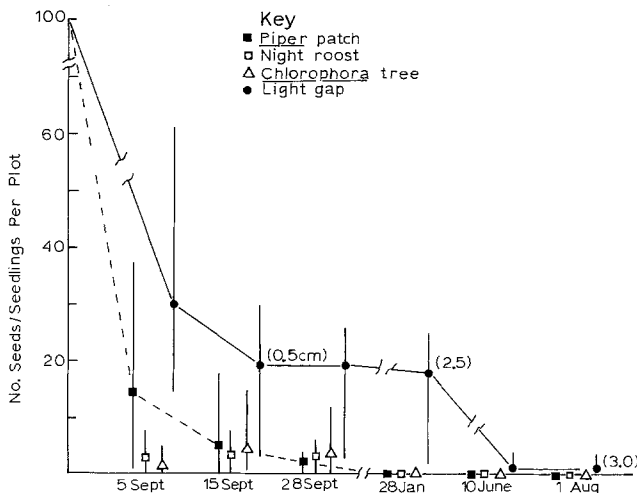

Fig. 7. Results of the 1979–1980 seeding experiments. Values presented are mean and range of values for 4 replicate plots. Means are based on the net number of experimental seedlings in each plot after correcting for seedlings growing on control sides. Numbers in parentheses indicate average height of seedlings

Within FAs, bats pluck one ripe fruit at a time and carry it to a night roost for consumption. In area C in 1976, 10 night roosts averaged 37.8 ± 3.4 (SE) m from the center of the *P. amalago* patch. Judging from the low (<10) number of fruits that accumulated under night roosts on most nights, bats use more than one night roost when feeding in a FA. *C. perspicillata* eats about 35 *P. amalago* fruits each night, and about 60% of the pulp and seeds is removed from each fruit before it is dropped. Fruits are consumed at 16–17 min intervals, and the seeds of each fruit are excreted 20–40 min after ingestion (Lockwood et al. 1981).

The above information can be used to estimate the mobility that individuals of *C. perspicillata* provide for *P. amalago* seeds. A typical nightly foraging bout is shown in Fig. 6. This bat visited 2 FAs located about 300 m apart and spent 79 min (13.4%) in FA 1 and 512 min (86.6%) in FA 2. Assuming the bat ate one fruit every 16 min and excreted one-half of the seeds it ingested from the previous fruit every 20 min, it consumed 32/36 fruits in FA 2 and deposited 90% of the seeds it ingested (ca. 2,930 seeds) there. Relatively few seeds (ca. 7.6%) moved between FAs. The remaining 92.4% of the seeds were deposited within ca. 40 m of the parent plants. The bulk of these seeds probably ended up under the bat's night roosts, where large numbers of seeds of several species can accumulate (Fleming and Heithaus 1981).

Results of the seeding experiments indicate that *P. amalago* seedling establishment probabilities are higher in open sites than in heavily-canopied sites. By 5 September, an average of 30% of the seeds placed in the light gap plots had germinated compared with an average of $\leq 15\%$ in the forest plots (Fig. 7). Seedling mortality was lower in the light gap plots than in other plots during the wet and early dry seasons. Mortality then increased during the rest of the dry season. One year after the plots were established, only 4 seedlings (all in one light gap plot) were alive, and these averaged 3.0 cm in height.

Discussion

Piper amalago is a low fecundity, steady-state (*sensu* Gentry 1974) fruiting plant that depends on a limited number of bat species to disperse its seeds in Tropical Dry or Premontane Moist Forest (Heithaus et al. 1975; Fleming et al. 1977). Its fruiting phenology has presumably evolved under natural selection to maximize the number of seeds that are dispersed to safe germination sites. Its "strategy" for accomplishing this is for individuals to "dribble" out a few fruit each night over about a 3–4 wk period rather than to ripen all of its fruit in only a few days. This phenological strategy, which conforms to model 1 of Howe and Estabrook (1977), gains the attention of specialized frugivores and reduces the likelihood that individual plants will compete among themselves for dispersal services. Interspecific competition for dispersal services between sympatric *P. amalago* and *P. pseudofuligineum*, however, has helped mold the timing of *P. amalago's* fruiting season. Less than one week after *P. amalago* has ripened the last of its fruit crop, *P. pseudofuligineum's* fruit ripen and are eaten by the same bat species (Fleming et al. 1977 and unpubl. data).

Although fruits of *P. amalago* at Santa Rosa are eaten by 2–3 bat species, which in the case of *Carollia perspicillata* are known to prefer these fruits over several others in their diet (Lockwood et al. 1981), it is unlikely that these fruits are highly nutritious. Of 7 fruit species in *C. perspicillata's* wet season diet, *P. amalago* ranks 7th in the ratio of pulp dry wt: seed dry wt (ratio = 0.61), in available kJ/fruit (0.62), and in net energy

gained per unit of handling time (Lockwood et al. 1981). Nutrient content of its pulp has not yet been determined, but it is unlikely that the pulp is highly nutritious. The pulp is juicy, sweet-tasting, and is not oily. In contrast, specialized bird fruits are often highly nutritious because of their high lipid and protein content (Snow 1971; Howe 1981). Bats such as *Carollia* and *Glossophaga* apparently do not prefer *P. amalago* fruit for its nutritional content as much as for its spatio-temporal predictability.

Howe and Estabrook (1977) have predicted that model 1 fruit species experience stabilizing selection for an optimal fruit crop that maximizes proportion of seeds that are successfully dispersed. Data for *P. amalago* do not conform to this prediction because fruit removal probabilities are high and independent of nightly or total fruit crop size (but see below). Bats are very thorough in their search for these fruit, and relatively few escape their detection.

Since *P. amalago* plants typically bear 1–3 ripe fruits each night, the question arises, Does this nightly production represent an optimum that minimizes seed wastage? In a short-term (nightly) sense, the answer to this question is "No" because the fruit manipulation experiments indicate that plants producing more ripe fruits each night (up to 10/plant) do not suffer greater fruit and seed wastage than do plants of lower productivity (Fig. 4). Instead of being a short-term optimum, the observed low nightly fruit production appears to be a means by which plants maximize the length of their fruiting season and hence the reliability of visitation by specialized frugivores. Bats benefit from this phenological pattern by having a reliable food source for several weeks, which ultimately reduces their food search costs and flight time. Reduced flight times are particularly important for small (i.e. 10–20 g) bats such as *C. perspicillata* and *G. soricina* for both energetic and predator-avoidance reasons (Heithaus and Fleming 1978).

Although bats find most ripe fruit each night, plants producing large ($\geqq 10$) numbers of ripe fruit on an irregular nightly basis may be at a selective disadvantage to less productive plants because a lower proportion of their fruits is removed by bats (Fig. 4). This result suggests that Howe and Estabrook's (1977) prediction that model 1 plants experience stabilizing selection to produce an optimal fruit crop size should be amended to include the existence of daily or nightly ripe fruit optima. Daily avoidance of disperser satiation, which is probably a major selective force behind the evolution of reduced fruit output, will clearly help to maximize seasonal seed dispersal success.

Although bats remove most fruits from plants, relatively few seeds move farther than ca. 50 m from parent plants. Approximately 40% of *P. amalago*'s seeds remain on their infructescences when these are dropped under night roosts. Within 2 days after being dropped, these seeds are fungus-covered and probably die. Most of the remaining 60% of the seeds are also deposited under night roosts, usually close to parent plants. Seed mobility, as measured by the distances seeds travel from their source, probably changes significantly during *P. amalago*'s fruiting season. Mobility is likely to be higher at the beginning and end of the season when fruit density is low and bats change feeding areas more often than in the middle of the season when fruit density is high and bats are more sedentary (Heithaus and Fleming 1978).

As is true for most plants (Harper 1977), the "average" seed produced by *P. amalago* has an infinitesimally small chance of surviving to become a reproducing adult. Results of the seed plot experiments suggest that seed and seedling stages are periods of very high mortality. To the extent that they deposit seeds

under forest cover rather than in open sites, frugivorous bats such as *C. perspicillata* kill (probably indirectly rather than directly) many more seeds than they disperse to safe sites. From *P. amalago*'s viewpoint, the dispersal quality of these bats is directly proportional to the number of seeds they excrete in actual or incipient light gaps.

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