AVIAN SEED DISPERSAL OF NEOTROPICAL GAP-DEPENDENT PLANTS

By

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In cloud forest at Monteverde, Costa Rica, I investigated reproductive consequences of avian seed dispersal for three species of gap-dependent plants: Phytolacca rivinoides (Phytolaccaceae), Witheringia solanacea, and W. coccoloboides (Solanaceae). Of six bird species that consumed fruits of these plants, only three (Myadestes melanops (Muscicapidae), Phainoptila melanoxantha (Ptilogonidae), and Semnornis frantzii (Capitonidae) dispersed seeds in viable condition. I estimated quality of dispersal service provided by these species by comparing the seed shadows they produced with spatial and temporal distributions of establishment sites for the plants.

I estimated seed shadows from data on gut passage rates of seeds and on movement patterns of radio-tracked birds. Seed shadows produced by all three effective dispersers were extensive, with few seeds deposited near the parent plant, and some moved > 500 m.

Seeds of the species examined germinate in forest gaps formed by treefalls or landslides. Germination success varies with gap size and age, but the relationship is different for each species; both Witheringia species germinate well in gaps as small as 15 m^2 or as old as 6 months, whereas P. rivinoides germinates well only in gaps > 70 m^2 or < 4 months. Consequently, establishment sites for all three plants are both rare and ephemeral, but to differing degrees.

Seeds that are not dispersed to suitable habitat patches can remain dormant in the soil until a gap is formed overhead.

To determine consequences of dispersal and dormancy for plant reproductive success, I developed a simulation model that uses data on seed shadows, germination requirements, seed dormancy, and forest dynamic processes to estimate reproductive output (total offspring produced during an individual's lifetime) and relative "fitness" (an estimator that discounts the contribution of offspring produced after a long period of dormancy). Results show that (1) dispersal by any of the three effective dispersers increases reproductive output 16-36 times, even without seed dormancy. (2) dormancy capabilities up to two years greatly enhance both reproductive output and "fitness", but greater capabilities increase only reproductive output. (3) Without dispersal, dormancy has little effect on either reproductive output or fitness. Thus, both dispersal and dormancy ("dispersal" in time) are essential to these gap-dependent plants.

INTRODUCTION

Recent interest in the ecology and evolution of plant-frugivore mutualisms focuses largely on the reproductive consequences, to plants, of fruit consumption by different animals (e.g., Snow 1965, 1971; McKey 1975; Howe and Estabrook 1977; Howe and De Steven 1979; Howe and Vande Kerchove 1979, 1980, 1981; Thompson and Willson 1979; Howe 1980; Stiles 1980, 1982; Herrera 1981, 1984; Sorensen 1981, 1983; Thompson 1981; Stapanian 1982; Skeate 1985). Most studies deal with fruit removal or qualitative aspects of dispersal only: they distinguish between regular and occasional visitors to fruiting plants (e.g., Leck 1972, Howe and Primack 1975, McDiarmid et al. 1977, Howe 1977, 1980, Howe and De Steven 1979, Howe and Vande Kerchove 1979, Hilty 1980, Greenberg 1981), between animals that pass seeds in viable condition and those that destroy seeds (e.g., Howe 1980), or between animals that disperse seeds away from the parent plant and those that drop seeds directly beneath it (e.g., Howe 1977, 1980, 1982, Howe and Vande Kerchove 1979, 1981). However, few studies directly address the contributions to plant reproductive success resulting from the spatial distributions of seeds, or "seed shadows," produced by dispersers.

This study deals with the reproductive consequences of avian seed dispersal in three gap-dependent plant species of neotropical cloud forest. Using data on the dynamics of gap formation and the seed germination requirements of plants, I first identify the spatial and temporal distributions of suitable habitat patches ("gaps" formed by treefalls or landslides) within the forest. Second, I compare the distribution of suitable patches with the "seed shadows" produced by different frugivorous birds. Finally, I evaluate the impacts of fruiting phenology, plant longevity, seed dormancy, and other plant life history traits on plant reproductive success and on the ecology and evolution of plant-disperser interactions.

In spite of the recent explosion of research on plant-frugivore interactions (reviewed by Howe and Smallwood 1982, Janzen 1983a; see also Estrada and Fleming 1986), knowledge of their ecology and evolution lags behind that of plant-pollinator interactions (reviewed by Feinsinger 1983, Jones and Little 1983, and Real 1983). This discrepancy occurs because the reproductive consequences of pollen dispersal by animals are more easily quantified than the consequences of seed dispersal (Wheelwright and Orians 1982). In plant-pollinator systems, both the origin of, and "target" for, pollen grains are specific and easily recognized by dispersers and ecologists alike. Furthermore, pollinators are rewarded for delivering pollen grains to the target--the stigma of a conspecific flower. Thus, we can determine the relative advantages of pollen dispersal by different animals by determining which ones are most likely to deposit pollen grains on the stigma of a conspecific flower. In contrast, the only target for dispersed seeds is generally a patch of soil with a combination of physical, chemical, and biotic characteristics that make it a suitable site for germination and growth (i.e., a "safe site," *sensu* Harper 1977). Furthermore, no reward is offered to vectors that deposit seeds in such sites. For most plants, we lack detailed knowledge of the characteristics of suitable target sites for seeds, let alone their spatial and temporal distributions. As a result, we know little about the reproductive advantages of dispersal for most plants, and even less about the consequences of dispersal by particular animals.

To understand plant-frugivore relationships and the phenotypic traits associated with them, we must identify the spatial and temporal distributions of seed "targets" and evaluate the likelihood of dispersal to those sites by different animals. Howe and Smallwood (1982) proposed three alternative functions of seed dispersal. First, dispersal may result in decreased density- or distance-dependent mortality on seeds or seedlings near the parent plant (e.g., Howe and Primack 1975, Janzen et al. 1976, Platt 1976, Salmonson 1978, Clark and Clark 1981, Augspurger 1983a,b, 1984a,b, Howe et al. 1985). Second, dispersal by certain means (e.g., by ants that carry seeds to rotting logs) may result in non-random seed movement to particular sites where the probability of survival is especially high (Docters van Leeuwen 1954, Handel 1978, Culver and Beattie 1980, Thompson 1980, Davidson and Morton 1981a,b). Third, widespread dispersal may allow colonization of ephemeral, spatially unpredictable patches of disturbed habitat (cf., Augspurger 1983a,b, 1984a,b, Platt 1975, 1976).

Although the three functions proposed by Howe and Estabrook are not mutually exclusive, the third may be most important for many plants. In most tropical and temperate forests, recruitment of many plant species occurs only in patches created by canopy disturbances such as treefalls and landslides (Richards 1952, Schultz 1960, Whitmore 1975, Hartshorn 1978, Brokaw 1980, Denslow 1980). Such gap-dependent or "pioneer" species typically germinate in forest gaps soon after formation, grow rapidly to reproductive size, and produce large numbers of seeds. They often die out as the gap is closed by lateral growth of trees on the gap's border and by vertical growth of other plants within the gap. In most gap-dependent species, germination is stimulated by the increased red/far red ratio of incident light (e.g., Vazquez-Yanes 1977, 1980, Vazquez-Yanes and Smith 1982, Vazquez-Yanes and Orozco-Segovia 1984) or increasing soil temperature fluctuations (Aubreville and Leroy 1970, Vazquez-Yanes 1976, Vazquez-Yanes and Orozco-Segovia 1982, 1984) that characterize recent gaps (Schultz 1960). Such plants are ideal for studies on seed dispersal. The spatial and temporal distributions of suitable habitat patches can be determined by first establishing the range of gaps in which germination and establishment occur, and then measuring the distribution of those gaps over the landscape.

STUDY AREA

From June 1981 through July 1983, I studied the interactions between frugivorous birds and *Phytolacca rivinoides* Kunth & Bouche (Phytolaccaceae), *Witheringia solanacea* L' Her, and *W. coccoloboides* (Damm.) Hunz. (Solanaceae) in the Monteverde Cloud Forest Reserve, Costa Rica ($10^{o}18'$N, $84^{o}48'$W). Lawton and Dryer (1980) provide a thorough description of the geography, climate, and forest types of the Reserve. The Monteverde area lies on a gently sloping plateau, on the Pacific slope of the continental divide in the Cordillera de Tilarán. Local weather patterns and vegetation of the area are strongly influenced by the northeast trade winds. Blowing mist is a nearly constant source of water for plants near the continental divide, even during much of the dry season (January to early May). Forest types in the area range from Lower Montane Rain Forest (Holdridge life zone classification system, Holdridge 1967) near the continental divide, through Lower Montane Wet Forest to Lower Montane Moist Forest and Premontane Wet Forest zones along the lower edge of the plateau.

Sites used in this study were all located between 1450 and 1650 m elevation, within either Lower Montane Rain Forest (oak ridge forest, windward cloud forest, and swamp forest, *sensu* Lawton and Dryer 1980), or within the Lower Montane Wet Forest - Rain Forest transition zone (leeward cloud forest, *sensu* Lawton and Dryer (1980)). Dominant overstory vegetation within the study area includes many species of Lauraceae, Moraceae, and Araliaceae, in addition to *Meliosma* sp., *Sloanea megaphylla*, *Guarea* spp., *Hieronyma poasana*, *Ardisia palmana*, and *Clusia alata*. The understory is dominated by Rubiaceae, Solanaceae, Acanthaceae, Gesneriaceae, Piperaceae, and Palmae. Many species occur most commonly in light gaps formed by falling branches or trees, including the "pioneer" trees *Cecropia polyphlebia*, *Urera elata*, *Trema micrantha*, *Sapium pachystachys*, *Heliocarpus popayensis*, *Clibadium leiocarpum*, and several species of *Miconia* and *Conostegia*. Several shrubs and large herbs also occur commonly in gaps, e.g., *Solanum acerosum*, *S. hispidum*, *Witheringia* spp., *Phytolacca rivinoides*, *Heliconia tortuosa*, *Bocconia frutescens*, and *Eupatorium sexangulare*.

Seedlings of *Phytolacca rivinoides*, *Witheringia solanacea*, and *W. coccoloboides* are very common in recent treefalls, especially on soils disturbed by uprooted trees. Within one month of formation, these "pits and mounds" (*sensu* Putz 1983) are generally covered by hundreds of seedlings of these and other species, especially *Cecropia polyphlebia* and *Bocconia frutescens*. A typical treefall examined approximately one month after formation contained 79 seedlings of *P. rivinoides* on the "mound" area alone (Murray, unpubl. data). Of the many gap-dependent species at Monteverde, I concentrated on *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* because they have similar fruits (small, multiple-seeded berries) and growth forms, but slightly different life history traits. By doing so, I hoped to evaluate the consequences of dispersal by similar assemblages of frugivores to plants with different reproductive schedules, longevities, and germination requirements.

METHODS

Crop Size, Fruiting Phenology, and Fruit Removal Rates

I collected data on fruit crop sizes and fruiting phenology using monthly censuses of 8, 36, and 33 individuals of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides*, respectively. Plants occurred in several different building-phase (*sensu* Whitmore 1975) treefall plots and in larger, man-made clearings within the reserve. During each census, I counted all flowers, green fruits, and ripe fruits on each plant.

Since most flowering and fruit development in both *Witheringia* species occurs well before ripening begins, I defined the total fruit crop in those species as the largest number of green fruits counted on that plant during any census in that fruiting episode. In *Phytolacca*, I estimated total fruit crop as the product of the number of infructescences formed and the average number of fruits per infructescence. I computed population-level fruiting phenology of each species (i.e., that of the "average" individual) by first determining the proportion of each individual's fruit crop that ripened each month (number of ripe fruits censused in each month divided by the sum of all ripe fruits censused on that plant over the fruiting season), and then averaging this proportion over all individuals censused. Thus, individuals with large fruit crops and those with small fruit crops were weighted equally in determining the fruiting phenology of the "average" individual.

To determine rates of fruit removal from individual plants, I counted the number of ripe fruits on marked branches (Witheringia) or infructescences (Phytolacca) on each census plant on one day, and then counted those remaining 24-72 hours later. For purposes of the analyses reported here, each observation consisted of two such censuses on one plant. During the first count, I removed any damaged or desiccated fruits that might abscise spontaneously before the next census. In most cases (77% of all observations), I counted all ripe fruits on the plant. On very large plants or those with inaccessible fruits (23% of all observations), I marked and counted only a subsample of branches or infructescences. Plants were checked in this way for 2-4 consecutive days each month. Eighty-six percent of the observations were from plants re-censused after 24 hours. In those checked after 2 or 3 days, I divided the number of fruits removed by the number of days between censuses. All removal data are thus reported on a per day basis. I could not obtain information on removal rates by direct observation; the birds responsible for removing most fruits from these plants are extremely wary, and generally avoid feeding in the understory anywhere near an observer.

Seed Germination Experiments

I conducted experiments to determine germination success of P. rivinoides, Witheringia solanacea, and W. coccoloboides in closed-canopy forest and in treefall gaps of various sizes and ages. Seeds used in all experiments were collected from several plants, mixed, and assigned to different treatments at random. Since many comparisons had to be made at different times of year, strict controls were not possible for all experiments. In such cases, I attempted to eliminate most of the obvious biases introduced by seasonal weather conditions. For example, during the driest months (March and April) when germinating seeds desiccate easily, I watered all seeds 1-2 times per week. Although this practice may result in an overestimate of seed and seedling survival in gaps during very dry periods, it provides unbiased data for answering the more immediate question of the relationships between germination success and gap size and age.

To compare germination success in closed-canopy forest with that in large gaps, I planted 100 seeds of each species in cups of sterile soil in a large (ca. 2440 m^2) man-made gap and 100 others (in like fashion) in adjacent forest. Gap seeds received full sunlight for most of the day, whereas canopy cover over forest seeds was greater than 98%, as determined by a canopy densiometer. Both groups of seeds were covered with a screened (ca. 1 mm mesh) enclosure to exclude herbivores and seed predators. Setups were checked for germination and seedling survival at 1-14 day intervals for 14 months.

I measured the effects of smaller gaps on germination success by planting 50 seeds of each species in small cans of soil (10 seeds/can) near the centers of six recent treefall gaps of different sizes. Where necessary, I placed cans above any ground-layer vegetation so that shading was due solely to the crowns of trees bordering the gap. By thus eliminating shade from rapidly growing plants within gaps, effects of gap age (see below) on germination success were controlled. These setups were checked at weekly intervals for 2-3 months. I determined gap size using the formula for the area of an ellipse

($A = \pi \cdot L \cdot W / 4$, where L and W represent the lengths of the major and minor axes of the ellipse), since most gaps were roughly elliptical.

Because light quality and intensity within a gap decrease over time as a result of shading from rapidly growing vegetation within it, I also determined the effects of gap age on germination success. Experiments were conducted in four gaps as they aged naturally. Three of the gaps were formed during a severe windstorm on 13-14 November 1982, the fourth during a storm on 11 January 1983. I planted fifty seeds of each species, in 5 groups of 10 seeds each, in small metal cans along transects running through the centers of the gaps. Setups were checked at weekly intervals for 1.5-2.5 months. The first run of this experiment was started 2-4 weeks after gap formation, and was repeated in each gap with 50 new seeds at 3-4 month intervals for one year.

Seed Dormancy Experiments

To estimate how long seeds of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* can remain dormant in the soil, I determined the viability of cohorts of seeds buried for different periods of time. In December 1981 I collected approximately 850 seeds from 5 to 20 individuals per species. After combining seeds taken from all individuals of a particular species, seeds were randomly assigned to treatments (burial for different periods of time) and then packed in small bags of mosquito netting or in microcentrifuge vials with mesh coverings. All seeds were then buried approximately 15 cm deep at a forest site with approximately 98% canopy cover.

At one to two month intervals over the next 17 months, I recovered 50 seeds of each species from the burial site and planted them in plastic cups of forest soil in the center of a large, man-made clearing 40 m away. Seeds were checked at least once every two days for germination. During the dry season, seeds were watered at least every other day.

In March 1984, I recovered an additional 50-75 seeds of each species from the burial site and planted them in plastic cups of potting soil in a greenhouse on the University of Florida campus. These seeds, like those germinated in the field, were checked at least every two days until all seeds had germinated, or until no further germination had occurred for four weeks.

Gap Dynamics of the Monteverde Cloud Forest

From May to July 1983 I set up five permanent 500 m line transects through representative areas of the Lower Montane Wet Forest and Rain Forest zones in the reserve. For each "expanded" gap (the area bounded by lines connecting the trunks of trees bordering the canopy gap; see Runkle 1982) encountered along a transect, I measured the transect interval within the canopy gap (defined as the land area directly beneath the canopy opening), length and orientation of the major and minor axes of the canopy gap, and height of the surrounding canopy. I sampled even the very small gaps (down to 1.6 m^2) formed by single branches, because data from germination experiments suggested that even gaps of that size affected germination success in *P. rivinoides*, *W. solanacea* and *W. coccoloboides*. I also subjectively estimated gap age in years. This was easily done for gaps formed in the previous year, because most still contained intact twigs and leaves of the fallen tree, as well as many epiphytes. The proportion of land area occupied by gaps less than one year old was computed as the length of transect under those canopy gaps divided by the total transect length. Gap area was determined using methods described above. I censused the transects again in March 1984 to collect data on gaps formed since the previous July.

Mist Netting and Analysis of Fecal Specimens

From June 1981 through July 1983, I regularly mist-netted birds in 14 study plots: six in treefall gaps from 1.5 to 3.5 years old, four in large, man-made clearings (hereafter termed "cutover" plots), and four in mature forest with intact canopy. Plots were chosen primarily for another study, and are described in detail in Feinsinger et al. (in review). From June 1981 through July 1982, I netted for the first six hours of daylight (ca. 0515-1115) in two plots of each of the three habitat types each month. Plots used each month were alternated so that sampling effort was approximately equal in all forest and cutover plots, and most treefall plots, over the first 12-month period. From September 1982 through July 1983, I netted at least one day (i.e., for the first 6 hours of daylight) per month in each of three plots, one in each habitat type. For this 11-month period, the same three plots were sampled each month. Additional netting in these and other plots was conducted on an irregular basis. I also netted in one of these plots from 4 to 20 March 1984.

All birds captured were weighed, measured, and checked for breeding condition and molt. Frugivores were marked with unique color combinations using plastic leg bands and then retained from 5 to 45 minutes in small holding cages (ca. 20x20x30 cm) to obtain fecal specimens. I also collected samples from many, but not all, insectivorous species. Fecal specimens were stored in 70% ethanol. In the laboratory, I counted and identified all seeds in each sample using a reference collection made over the two-year study. I also visually estimated the percent arthropod composition of each sample to the nearest 10%.

Fruit Handling, Gut Treatment, and Seed Passage Rates

To determine the consequences to *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* of fruit consumption by different bird species, I conducted feeding experiments with captive individuals of six bird species observed to eat their fruits. Birds were captured in mist nets and maintained in a small (1x1x1m) cage during the experiments. Between trials, fruits other than the experimental species, as well as water, were provided *ad libitum*. In all but two cases, trials were completed and the bird was released on the same day. After introducing the experimental fruits into the cage, I noted whether or not birds consumed the fruits, how fruits were ingested (e.g., swallowed whole vs. eaten piecemeal), whether the ingested seeds were voided intact, and whether they were defecated or regurgitated. Recovered seeds, or a subset if many trials were run, were then planted in plastic cups of soil under a screened enclosure in a large clearing. I checked seeds at least once every two days for germination, and watered them when necessary.

To determine gut passage rates, I conducted feeding trials in a similar fashion. Approximately 7-15 fruits of either *P. rivinoides*, *W. solanacea*, or *W. coccoloboides* were introduced on the cage floor, and all other fruits were removed from the cage. I observed subsequent events through a small hole cut in one opaque side of the cage. Birds usually descended from perches to feed within a few minutes after the test fruits were introduced. All uneaten fruits were removed 5 min. after the first fruit was consumed. The midpoint of the interval during which fruits were eaten was considered as the time of ingestion for all fruits in a particular trial.

Each time a bird defecated, I recorded the time and the location of the fecal mass on the floor of the cage. After 3-5 fecal masses had accumulated, I removed the paper from the bottom of the cage and replaced it. At the end of the feeding trial, all fecal masses were recovered; seeds were later identified and counted. Successive feeding trials were done approximately 30 min apart; i.e., the next trial (with a different fruit species) began 30 min after the beginning of the previous trial. In this way, I could usually complete 1-2 feeding trials on each bird with each of the three fruit species before releasing it on the afternoon of the same day it was caught.

After counting seeds in the fecal masses, I grouped the data into 5-min classes, recording the proportion of all seeds voided in each 5 min time segment following ingestion.

Movement Patterns of Frugivores

To determine the movement rates and patterns of birds taking *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* fruits in the field, I fitted mist-netted birds with small (ca. 3.5g) radio transmitters and followed their movements for 3-8 days. Transmitters used were homemade units similar to those available from a number of commercial telemetry suppliers. I used an LA-12DS receiver (AVM Instrument Company, Dublin, CA) and a homemade 5-element yagi antenna.

Transmitters were attached to the skin and feathers on a bird's back (just anterior to the synsacrum) with Super Glue^{tm}. Birds fitted with transmitters were held in the field in a small cage for approximately 30 min to ensure that they were healthy when released.

By using a carefully mapped network of trails, I could often remain within sight of radiotagged birds for long periods of time. Each time the bird moved to a new location, I simply recorded the time and the bird's location on a map of the study area. When I was out of visual contact with the bird, I determined its location by triangulation. I took compass bearings on the direction of the strongest signal from two points, separated by at least 50 m, on the mapped trail system. After taking the second bearing, I rechecked the first to ensure that the bird had not moved. I took new bearings as soon as the signal received indicated (by a change in signal strength or direction) that the bird had moved. In the absence of any such indication, I took two new bearings every 3-5 minutes to check the bird's location.

RESULTS

Natural History of the Plants

Phytolacca rivinoides is a large herb ranging from Mexico to Bolivia (including the Antilles, Raeder 1961) at elevations from sea level to 3000 m (Standley 1937). Usually among the first colonists of treefalls and landslide edges, individuals commonly spread to cover approximately 25 m^2 within 1-2 years of seedling establishment. Plants begin to ripen fruits at about one year of age, but most die (presumably as a result of shading and/or root competition) within 2.5 years of establishment. Of the eight individuals I monitored closely, the median age at death was 24 months (range 21 to 31 months). During the single, extended fruiting season, individuals produce 1,500-30,000 (median = 4700) fruits borne on axillary racemes containing ca. 30-100 fruits each. The fruits are purple-black, about 7.5 mm in diameter, and contain 5-12 (x=9.4, n=20) seeds in a watery pulp.

Witheringia solanacea and W. coccoloboides are both shrubs attaining heights of about 1.5-2.5 m. Witheringia solanacea ranges from Mexico to Brazil, including the Antilles (D'Arcy 1973), occurring from sea level to 2000 m (Standley 1937). Witheringia coccoloboides is typical of cloud forests from Costa Rica to Colombia at elevations from 300 to 2500 m (D'Arcy 1973). Both species grow much more slowly than does P. rivinoides; although seedlings are common in young gaps, they do not attain reproductive size for about 3-5 years, and they usually live for 8 or more years before being shaded out by the reestablishing canopy. Fruits of both *Witheringia* species are red, ca. 10-12 mm in diameter, and are borne in axillary fascicles. Fruit crop size and seed number are highly variable in both species. Total seasonal fruit crops in *W. solanacea* ranged from 5 to 1084 (median=154, n=121), and seed number per fruit ranged from 6 to 39 (x=22.8, n=44). Seasonal fruit crops in *W. coccoloboides* ranged from 5 to 1150 (median=120, n=84), and seed number ranged from 46 to 73 (x=59.1, n=17).

Fruits of all three species show typical adaptations for bird dispersal (van der Pijl 1972). Removal by animals other than birds is probably rare. Although rodents are known to eat fruits of some understory plants, including *P. rivinoides* (Denslow and Moermond 1982), I found no evidence of removal by rodents at Monteverde. Early morning counts of fruits marked on the previous afternoon showed no evidence of nocturnal removal, and no fruits were removed from two plants each of *W. solanacea* and *W. coccoloboides* from which birds, but not rodents, were excluded by screened enclosures left open at the bottom (Murray, unpubl. data). In addition, an intensive concurrent study of frugivorous bats revealed no evidence of these fruits in bat fecal specimens (E. Dinerstein, pers. comm.).

Fruit Consumers

The disperser assemblages for *P. rivinoides*, *W. solanacea* and *W. coccoloboides* at Monteverde are surprisingly limited. Data from ca. 200 fecal samples collected from mist-netted frugivores, as well as extensive observations by several investigators (Wheelwright et al. 1984), suggest that only ten bird species commonly consume fruits of any of these plants in the Monteverde vicinity. The limited size of the disperser assemblage comes about because few species of frugivorous birds commonly descend to the forest understory or into treefall gaps; similar fruits of canopy trees and epiphytes are often taken by a much larger number of bird species (Wheelwright et al. 1984). The three major dispersers for all three plant species in cloud forest above 1500 m are Black-faced Solitaires (Myadestes melanops, Muscicapidae), Black and Yellow Silky Flycatchers (Phainoptila melanoxantha, Ptilogonatidae), and Prong-billed Barbets (Semnornis frantzii, Capitonidae). Of the 360 seeds of these three plant species recovered in fecal specimens from 196 frugivores, all were from these three bird species. Furthermore, these data also suggest that Myadestes is responsible for far more dispersal of these plants than are either Semnornis or Phainoptila: 84% of recovered seeds were from Myadestes alone.

Although P. rivinoides, W. solanacea, and W. coccoloboides are highly dependent upon a very few bird species for dispersal services, none of the birds is similarly dependent upon any of the three plant species. The known diets of Myadestes, Phainoptila, and Semnornis include fruits of 51, 14, and 30 species, respectively (Wheelwright et al. 1984; K. G. Murray, unpubl. data). In fact, fruits of the three plants are of relatively minor importance in the diets of these birds. Of the 154 fecal specimens collected from these three species, only 35% contained seeds of P. rivinoides, W. solanacea, or W. coccoloboides. The ecological relationships between these three plants and their dispersers are thus highly asymmetrical.

Seven other bird species removed fruits from at least one of the plant species. The tanagers Chlorospingus opthalmicus and Tangara dowii and the finch Pselliophorus tibialis occasionally removed fruits, but failed to ingest most seeds (see below). Of the remaining four species recorded feeding on P. rivinoides, W. solanacea and W. coccoloboides, only one was a frequent visitor to any of these plants: at elevations below approximately 1420 m, seeds of W. solanacea were commonly found under display perches of Long-tailed Manakins (Chiroxiphia linearis, Wheelwright et al 1984).

Data from mist net captures (Table 1) also suggest the unequal importance of these ten bird species as dispersers for P. rivinoides, W. solanacea, and W. coccoloboides. Of the three primary dispersers, M. melanops was the most frequently captured in all three habitats. In fact, M. melanops may be the most important disperser for all understory plants with bird-disseminated seeds within the Monteverde Cloud Forest Reserve.

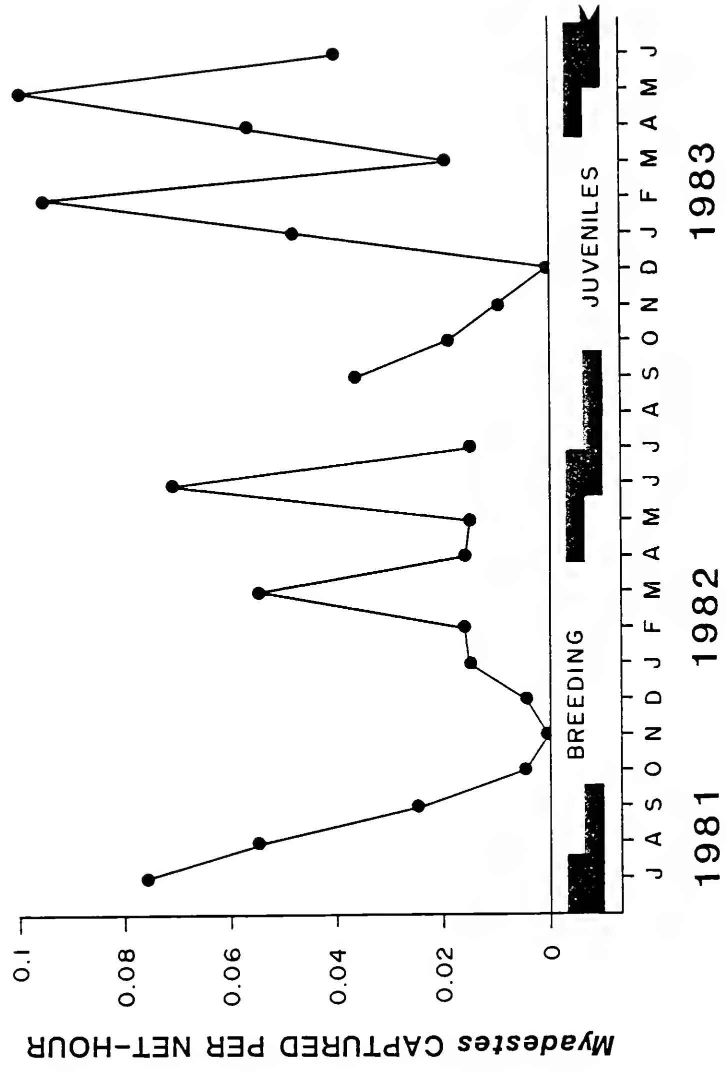
Capture rates for Myadestes were highly variable over time, however (Fig. 1). While usually very common in the reserve from February through August, they were all but absent from late October through early January. The seasonal decline in capture rate was due to emigration of both adults and young following the breeding season. Visual and auditory censuses confirmed this seasonal pattern of abundance (K. G. Murray, unpubl. data). Where Solitaires go when they leave the Monteverde area remains somewhat a mystery, but D. J. Levey (personal communication) has caught several individuals during this season at Finca La Selva, at ca. 50 m elevation in the Atlantic lowlands. Although some other species of frugivorous birds at Monteverde are also altitudinal migrants (e.g., Three-wattled Bellbirds, Procnias tricarunculata, and Resplendant Quetzals, Pharomachrus moccino; Wheelwright 1983, and K. G. Murray, personal observation), I have no

Table 1. Capture data for bird species feeding at least occasionally on fruits of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* at Monteverde. Total numbers of mist net hours in forest, treefall, and "cutover" (see text) plots were 1158, 1164, and 1449, respectively.

Species	forest	treefalls	"cutovers"[a]
Myadestes melanops	66	30	33
Phainoptila melanoxantha	1	0	4
Semnornis frantzii	0	0	3
Chlorospingus opthalmicus	10	9	5
Tangara dowii	0	0	1
Pselliophorus tibialis	1	0	2

[a] Capture data from these unusually large (1155-2442 m^2) man-made clearings are not included with those from natural treefalls. Plant and bird assemblages in the large clearings were more typical of early second growth habitats than those of natural forest or treefall gaps.

Figure 1. *Myadestes* capture rates and breeding activity from July 1981 to June 1983. Bars at bottom of figure indicate the presence of breeding adults (i.e., with brood patches) and young of the year on study plots.


Myadestes CAPTURED PER NET-HOUR
0.1
0.08
0.06
0.04
0.02
0
J A S O N D J F M A M J J A S O N D J F M A M J
1981
1982
1983
BREEDING
JUVENILES

evidence that any other disperser of P. rivinoides, W. solanacea, and W. coccoloboides undertakes such annual movements.

Fruit Handling and Seed Treatment in the Gut

Consumers of P. rivinoides, W. solanacea, and W. coccoloboides at Monteverde handled fruits by one of two methods. Myadestes, Phainoptila, and Semnornis invariably swallowed fruits whole, with little or no manipulation in the bill. In contrast, the tanagers Chlorospingus opthalmicus and Tangara dowii, and the finch Pselliophorus tibialis, mashed fruits extensively in the bill before swallowing. This behavior resulted in the fruit skin and many of the seeds being dropped before the pulp was ingested. Field observations of these and other tanager and finch species suggest that most handle fruits in this manner. As a result, these birds ingest and disperse few, if any, of the seeds they remove from most plants.

The probability of seed ingestion in tanagers and finches seems to depend at least in part on seed size. In Pselliophorus, Chlorospingus, and Tangara, most seeds were discarded along with the fruit skin during handling (Table 2). Nevertheless, some W. solanacea seeds (ca. 1.5 mm diameter) were ingested by all three species, especially by Pselliophorus. In contrast, none of the birds ingested any of the larger seeds of W. coccoloboides (ca. 2.4 mm diameter); all were discarded with the fruit skin. For seeds of a given size, the probability of ingestion increases with bird size. P. tibialis (ca. 30.5 g; gape 10.3 mm) ingested 71% of the W. solanacea seeds offered, whereas C. opthalmicus (ca. 20.0 g; gape 9.1 mm) and T. dowii (ca. 20.0 g; gape 8.5 mm) ingested only 10.7% and 15.8%, respectively.

Apparently, larger seeds are more easily separated from the fruit pulp during manipulation in the mandibles, especially by birds with smaller bills. Data on the seed loads recovered from mist-netted tanagers at Monteverde support this suggestion: feces of these birds generally contained only the minute (ca. 0.2-.06 mm diameter) seeds from species of Ericaceae, Melastomataceae, and Gesneriaceae (K. G. Murray, unpubl. data). Small tanagers such as Chlorospingus and Tangara may act as dispersers only for plants with such minute seeds.

The effect of gut passage on seeds also varies among bird species. Data from feeding trials suggest that although many seeds of W. solanacea may be ingested by Pselliophorus, very few survive passage through the gut (Table 2). Instead, most seeds were apparently ground up in the gut; feces of the individual used in this experiment contained large numbers of recognizable W. solanacea seed fragments. Only two W. solanacea seeds emerged intact, and these were inviable (Table 3). The absence of seed fragments in feces of the same bird after feeding on W. coccoloboides fruits again strongly suggests that seeds of this species are not ingested by Pselliophorus. Data for Chlorospingus and Tangara suggest that the few W. solanacea seeds that are ingested pass through the gut intact (Table 2); no evidence of destruction in the gut (such as seed fragments in the feces) was found, and the few seeds recovered from feces were fully viable (Table 3).

Seeds eaten by Myadestes, Phainoptila, and Semnornis were always voided intact. Although I found no evidence of either increased or decreased germination success (defined simply as the percent of seeds that germinated following gut passage) as a result of gut passage in any of these birds, the rate at which seeds of all three plant species

Table 2. Fruit handling techniques and gut treatment effects on seeds eaten by captive individuals of six frugivore species.

Bird species[a]	Plant species[b]	seed diameter (mm)	fruits eaten	seeds dropped	seeds ingested	voided intact[c]
M.m.	P.r.	2.0	53	0	411	411
	W.s.	1.5	69	0	1366	1366
	W.c.	2.4	36	0	1206	1206
P.m.	P.r.		17	0	168	168
	W.s.		19	0	447	447
	W.c.		18	0	524	524
S.f.	P.r.		36	0	413	413
	W.s.		7	0	145	145
	W.c.		8	0	477	477
C.o.	W.s.		3	16	3	3
	W.c.		4	36	0	-
T.d.	W.s.		2	25	3	3
P.t.	W.s.		9	38	95	2
	W.c.		4	111	0	-

[a] M.m.= Myadestes melanops, P.m.= Phainoptila melanoxantha, S.f.= Semnornis frantzii, C.o.= Chlorospingus opthalmicus, T.d.= Tangara dowii, P.t.= Pselliophorus tibialis

[b] P.r.= Phytolacca rivinoides, W.s.= Witheringia solanacea, W.c.= Witheringia coccoloboides

[c] Of seeds ingested

Table 3. Effects of gut passage on germination success and germination rate. Data on untreated controls taken from Table 4.

		percent germination (n)		days to 95% germination[c]	
Bird species[a]	Plant species[b]	treated	untreated	treated	untreated
M.m.	P.r.	78 (100)	89 (100)	22	49
	W.s.	73 (100)	86 (100)	45	56
	W.c.	d	86 (100)	31	56
P.m.	P.r.	89 (100)	89 (100)	37	49
	W.s.	d	86 (100)	73	56
	W.c.	d	86 (100)	54	56
S.f.	P.r.	75 (100)	89 (100)	26	49
	W.s.	d	86 (100)	19	56
	W.c.	d	86 (100)	19	56
C.o.	W.s.	100 (3)	86 (100)	d	d
T.d.	W.s.	100 (3)	86 (100)	d	d
P.t.	W.s.	0 (2)	86 (100)	d	d

[a] M.m.= *Myadestes melanops*, P.m.= *Phainoptila melanoxantha*, S.f.= *Semnornis frantzii*, C.o.= *Chlorospingus opthalmicus*, T.d.= *Tangara dowii*, P.t.= *Pselliophorus tibialis*

[b] P.r.= *Phytolacca rivinoides*, W.s.= *Witheringia solanacea*, W.c.= *Witheringia coccoloboides*

[c] Of those that germinated

[d] Insufficient number of seeds available for experiment

germinated was often enhanced by gut passage (Table 3). Thus, although treatment in a bird gut is not required for germination in any of these plants, seedlings from treated seeds may gain a competitive advantage through rapid germination in a newly created patch of suitable habitat.

Spatial and Temporal Distribution of Suitable Colonization Sites

Germination Requirements

Gap vs. understory comparisons. Results of forest vs. gap germination experiments (Table 4) show that after 60 days, all three species had significantly higher germination success under gap conditions than under closed canopy. Many *Witheringia* seeds did eventually germinate in the forest after more than a year. These seeds, however, were protected from litter fall by the screened enclosure. Ordinarily, seeds on the forest floor would be covered by leaf litter and incorporated into the soil seed bank in a dormant state long before they germinated.

Germination success vs. gap size. Germination success increased with increasing gap size in all three species (Fig. 2). In fact, slopes of the regressions (on transformed variables; see Fig. 2 legend) of germination success on gap area do not differ significantly among the three species (F_s=1.550 with df=2,15, $0.1 < P < 0.25$). Furthermore, analysis of covariance shows that the regression lines for the two *Witheringia* species are indistinguishable (F_s=0.07 with 1,17 df, $P > .75$), but that the adjusted mean germination success in *P. rivinoides* is less than that for the other two species (F_s=12.82 with 1,17 df, $P < .005$). Equations for the adjusted (by analysis of covariance) regressions are $y = 6.84x + 12.88$ for both *W. solanacea* and *W.*

Table 4. Percent germination success in forest and large gap habitats. Sample size for all experiments was 100. Differences between gap and forest values were tested with a test for equality of two percentages (Sokal and Rohlf 1969: 608).

	gap	forest	p
		after 60 days	
Phytolacca rivinoides	89	0	<.001
Witheringia solanacea	86	14	<.001
Witheringia coccoloboides	86	2	<.001
		after 410 days	
Phytolacca rivinoides	89	0	<.001
Witheringia solanacea	86	61	<.001
Witheringia coccoloboides	86	87	>.5

coccoloboides, and $y = 6.84x + 1.14$ for *P. rivinoides*, where y is the arcsin transform of the proportion of seeds germinating and $x = \ln(\text{gap area} + 1)$. Thus, germination success increases with gap size at the same rate in all three species, but for a given gap size, germination success in *P. rivinoides* is always less than for either species of *Witheringia*. Consequently, *P. rivinoides* requires larger gaps than either species of *Witheringia* for germination. Such differences in the relationship between gap size and germination success translate directly into differences among species in the distribution of suitable germination sites over the landscape.

Germination success vs. gap age. Seeds of *P. rivinoides*, *W. solanacea* and *W. coccoloboides* also differ in the relationship between germination success and gap age (Fig. 3). Because the gaps used were of different sizes, data plotted in Figure 3 were adjusted to control for the effects of gap size, according to the relationships in Figure 2. To facilitate comparison among species, data were also scaled such that the highest germination success attained in each species was set at 100%.

Germination success decreased with increasing gap age in all three species, presumably as a result of decreasing light intensity (or quality) as the understory vegetation within the gap grew and shaded more of the soil surface. The initial increase in germination success of *P. rivinoides* may have resulted from increased light intensity or quality in the first few months after gap formation, as the leaves and epiphytes on fallen trees and branches decayed and fell to the ground. Such an increase in light intensity or quality would be expected to have the greatest effect on an extremely shade-intolerant species such as *P. rivinoides*.

Figure 2. Germination success vs. gap area. Results from germination experiments in 6 recent gaps and 1 forest understory site (gap area=0). Curves shown are de-transformed linear regressions of the proportion of seeds germinating (arcsin transformed) on ln(gap area + 1). Equations, F-values, and significance levels for *P. rivinoides*, *W. solanacea* and *W. coccoloboides* are $y = 6.99x + 0.54$ ($F=71.8$, $p < .001$), $y = 5.15x + 20.08$ ($F=10.11$, $p < .05$), and $y = 8.36x + 6.35$ ($F=40.35$, $p < .002$), respectively.

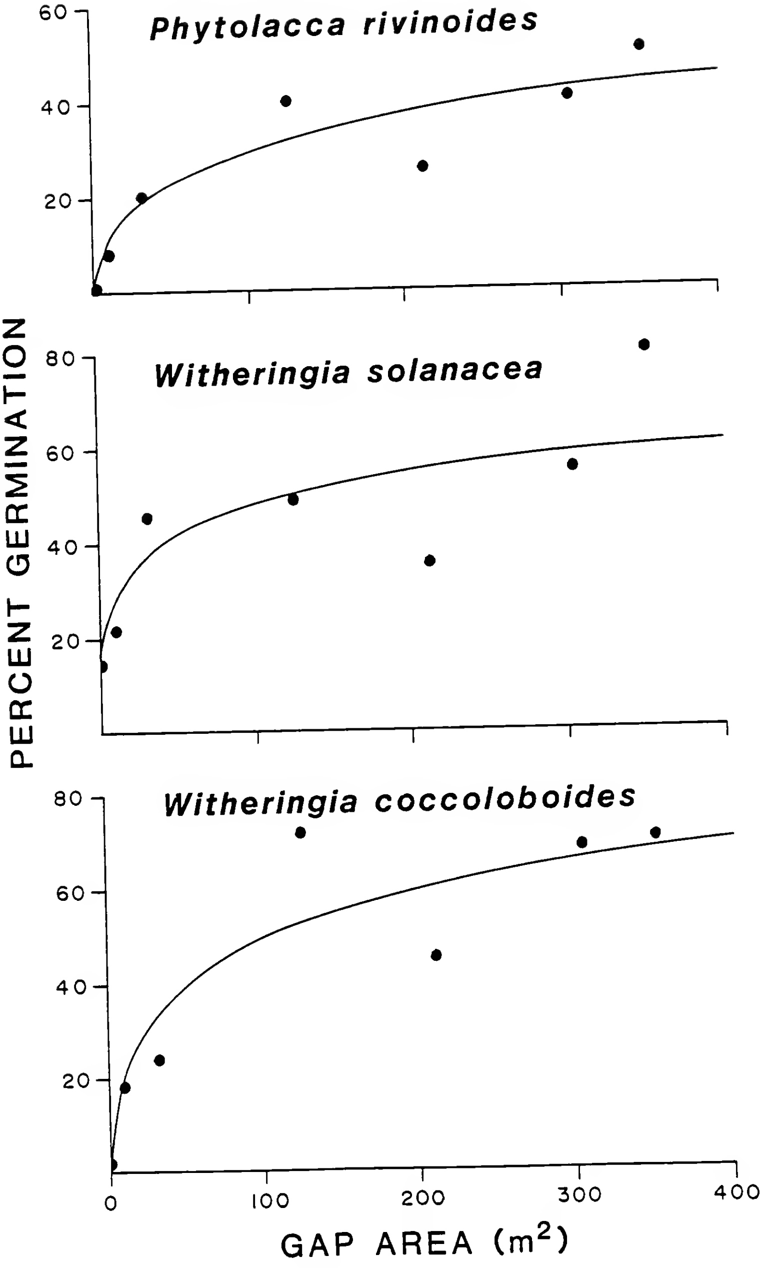
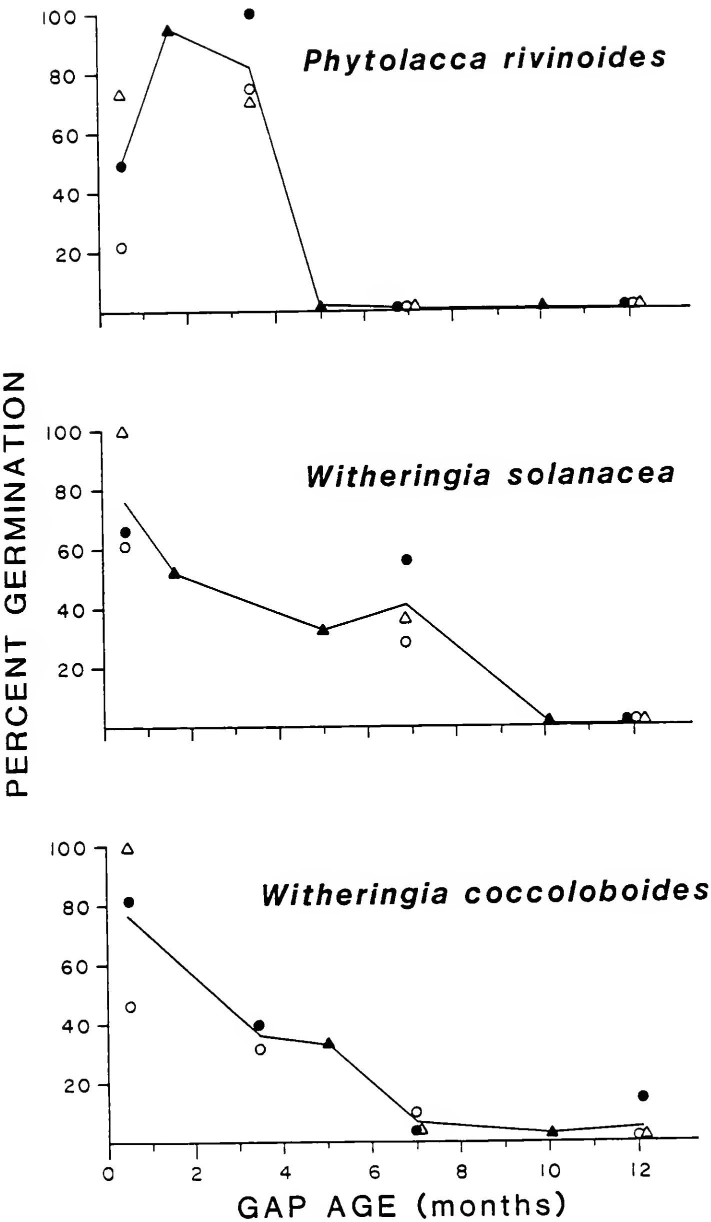

Phytolacca rivinoides
60
40
20
Witheringia solanacea
80
60
40
20
Witheringia coccoloboides
80
60
40
20
PERCENT GERMINATION
0
100
200
300
400
GAP AREA (m^2)

Figure 3. Germination success vs. gap age. Results from germination experiments in 4 gaps as they aged naturally (see text). Missing data for *W. solanacea* at 3.5 months and for *W. coccoloboides* at 1.5 and 3.5 months are due to a lack of sufficient seeds for those experiments. Different symbols indicate values for each of the 4 gaps. Lines connect mean germination success values at each gap age.


Phytolacca rivinoides
Witheringia solanacea
Witheringia coccoloboides
PERCENT GERMINATION
100
80
60
40
20
0
2
4
6
8
10
12
GAP AGE (months)

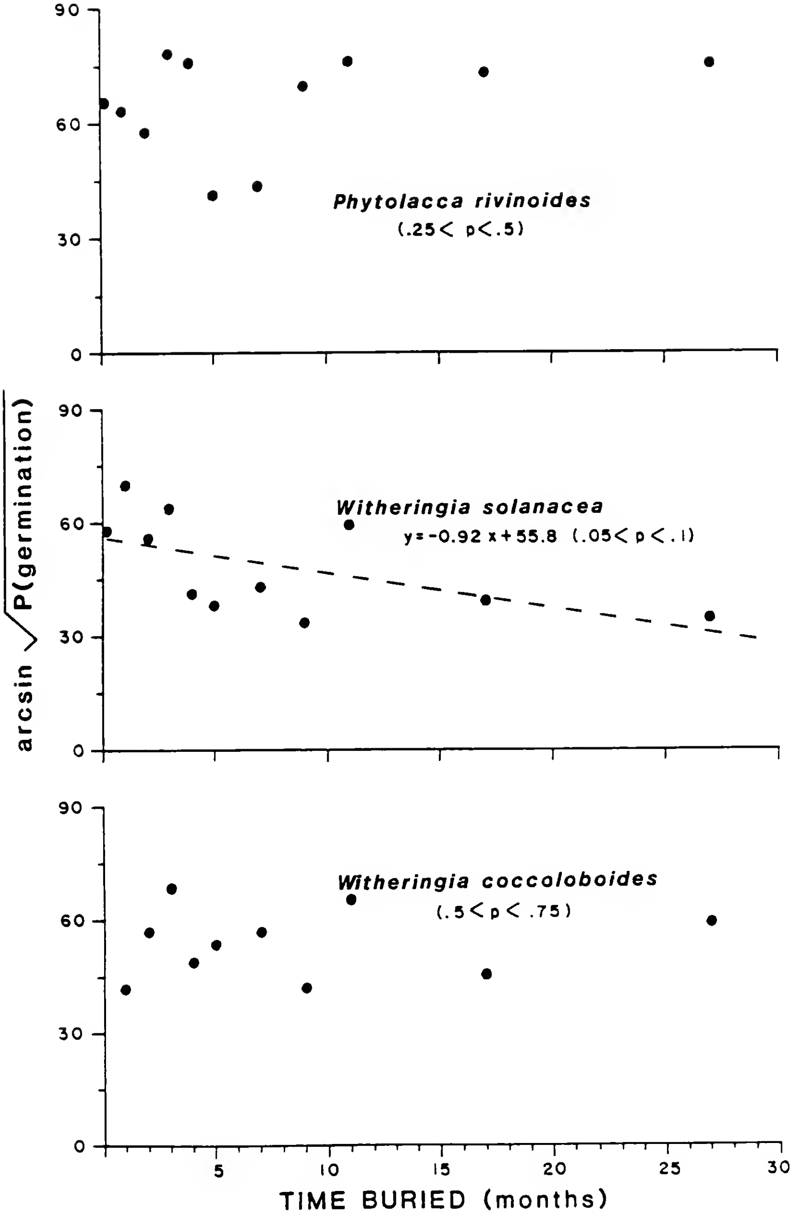
Following the initial increase in P. rivinoides, germination success decreased with increasing gap age much more rapidly than in either species of Witheringia. In fact, germination success in P. rivinoides was negligible by 7 months after gap formation, whereas some W. coccoloboides seeds germinated in gaps as old as 12 months. Germination success decreased least rapidly with increasing gap age in W. solanacea, although it reached zero by 10 months (Fig. 3). Thus, a given gap remains open for colonization by W. coccoloboides and W. solanacea for some time after it is no longer suitable for P. rivinoides.

Seed dormancy. In all three plant species, seeds buried for up to 27 months showed no significant decrease in viability (Figure 4). Mean germination success for all seeds was similar in all three species; values for P. rivinoides, W. solanacea, and W. coccoloboides were 65%, 50%, and 55%, respectively. In a similar experiment (K.G. Murray, unpubl. data), I collected 100-200 seeds of each species at approximately two-month intervals for the same 27-month period and buried these seeds together in a similar forested site. These seeds were recovered in March 1984 and planted in the greenhouse. The results of this experiment were similar to those obtained in the previously described one: no decrease in seed viability was demonstrated in the first 27 months of burial.

Spatial Distribution of "Safe Sites"

New canopy gaps covered approximately 1.5% of the total land area sampled by forest transects each year. Percentages of the five forest transects under new canopy gaps (less than 1 year old) were 0.2, 3.1,

Figure 4. Results of seed dormancy experiments with *P. rivinoides*, *W. solanacea*, and *W. coccoloboides*, and results of regression analyses on germination success vs. seed burial period.


90
60
30
0
Phytolacca rivinoides
(.25< p<.5)
arcsin √P(germination)
90
60
30
0
Witheringia solanacea
y=-0.92 x+55.8 (.05< p <.1)
90
60
30
0
Witheringia coccoloboides
(.5< p < .75)
5
10
15
20
25
30
TIME BURIED (months)

3.1, 1.5, and 0.5, respectively, for the 1983 census, and 0.7, 2.1, 1.3, 1.3, and 1.1 for the 1984 census. Most gaps were formed during severe windstorms, which occur primarily from November through January at Monteverde.

The size distribution of canopy openings associated with the 90 "expanded" (sensu Runkle 1982) gaps sampled is shown in Figure 5. It is typical of such distributions in that very small gaps are exceedingly common, whereas very large gaps are exceedingly rare. Most gaps smaller than 10 m^2 were formed by one or more branches falling from the canopy, although entire trees occasionally formed gaps as small as 5 m^2.

The gap size distribution shown in Figure 5 slightly overrepresents large gaps, since the probability that a gap will be sampled by a line transect is directly proportional to its size. To construct an unbiased gap-size distribution, I weighted the number of gaps in each size class by first dividing that number by the diameter of a circular gap equal in area to the median-sized gap in that class. I then determined the proportion of all weighted values occurring in each size class. The resulting adjusted gap-size distribution is very similar to the unweighted one in Figure 5, and is not shown here. However, all estimates of the density of gaps in each size class, and the proportion of land area they occupy (see below), are based upon the unbiased gap-size distribution.

Assuming that the canopy disturbance rate of 1.5% per year and the adjusted gap-size distribution are representative for the Monteverde cloud forest over the long term, I determined the density of gaps of various sizes over the landscape and the amount of land area they occupy. I first divided the range of observed gap sizes into the

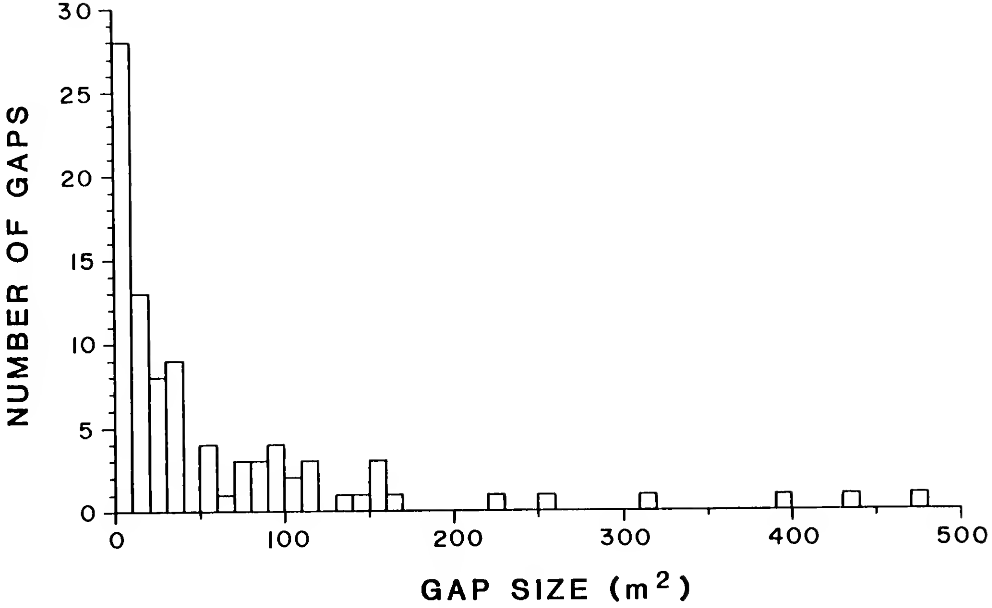


Figure 5. Size distribution of 90 canopy gaps formed over a 2-year period from ca. March 1982 - March 1984.

following 16 size categories: $\leq$ 4.9, 5-9.9, 10-14.9, 15-19.9, 20-24.9, 25-29.9, 30-39.9, 40-49.9, 50-59.9, 60-79.9, 80-99.9, 100-149.9, 150-199.9, 200-299.9, 300-399.9, and > 400 m^2. To determine the density and coverage (proportion of land area) of gaps in each category that are formed each year, I used a modification of the methods of Lucas and Seber (1977) for line transect data. Because the gaps censused in this study were actually formed over a period of several years, I weighted the coverage estimates such that the total area in gaps (over all size categories) equals 1.5% of total land area. Density estimates were weighted in a similar manner, so that all final values are expressed on a per-year basis.

I used this analysis to approximate the availability of suitable germination sites over the landscape. For purposes of illustration, let us arbitrarily define a "safe site" with respect to gap size as any gap in which germination success is at least 25%. My use of the term "safe site" here is not exactly equivalent to that of Harper (1977), since one gap could provide many germination sites, and each of these would be termed a "safe site" by Harper's definition. Figure 6 shows the density of safe sites and the proportion of land area they occupy as a function of minimum safe site area, using the gap density and coverage estimates derived above. Both density and land area covered decrease rapidly with increasing minimum safe site area. For a plant that requires a gap of at least 100 m^2 (e.g., a circular gap of 11.3 m diameter) as a safe site, for example, there is approximately 1.0 safe site per hectare, and 0.62% of the total land area is available for colonization. For a plant whose seeds can germinate in a much smaller gap, however, say 10 m^2 (e.g., a circular gap of 3.6 m diameter), suitable patches for colonization are much more common: 6.0 "safe sites" per hectare, representing 1.32% of the total land area.

Similar analyses demonstrate that suitable germination sites are indeed distributed differently for the species in this study. Minimum gap sizes in which germination success is at least 25% (based on the regression lines in Figure 1) are 66.7, 5.9, and 15.9 m^2 for P. rivinoides, W. solanacea, and W. coccoloboides, respectively. Thus, from Fig. 6, we can estimate approximately 1.6, 8.8, and 4.3 suitable patches per hectare, representing 0.8, 1.4, 1.2% of the total land area.

The foregoing discussion treated the availability of suitable patches only on the basis of gap size and its effect on germination success; i.e., it assumes that all gaps formed in a particular year are equally suitable for colonization at any time. Since germination success varies among the species with respect to gap age as well as to gap size, however, the availability of suitable colonization sites varies among species temporally as well as spatially. If we again arbitrarily define the length of time a gap remains open for colonization as the length of time during which germination success remains at least 25%, then for P. rivinoides, W. solanacea, and W. coccoloboides gaps remain open for colonization for approximately 4.5, 8.0, and 5.5 months, respectively. Figure 7 shows the density of safe sites and the proportion of land area they contain as a function of time of year, for plants that can colonize gaps up to 4, 6, and 8 months old. The figure was generated by multiplying both the canopy disturbance rate of 1.5% / year or the overall gap density of 17.5 gaps / hectare / year by the estimated proportion of gaps occurring in each month. The result (the line labelled "0 months") is the density of gaps formed that month, or the proportion of land area they occupy. Other lines in the figure were generated by including, for each month, the density of new gaps or the proportion of land area disturbed in the 4, 6, or 8 previous months. For species capable of invading only very young gaps, suitable colonization sites are available for only a short period of time each year (Fig. 7). For species capable of colonizing older gaps, however, the availability of suitable colonization sites remains high for a much longer period of time. For example, suitable colonization sites for *W. solanacea* are relatively common for 9 months of the year, while those for *P. rivinoides* are common for only 5 months.

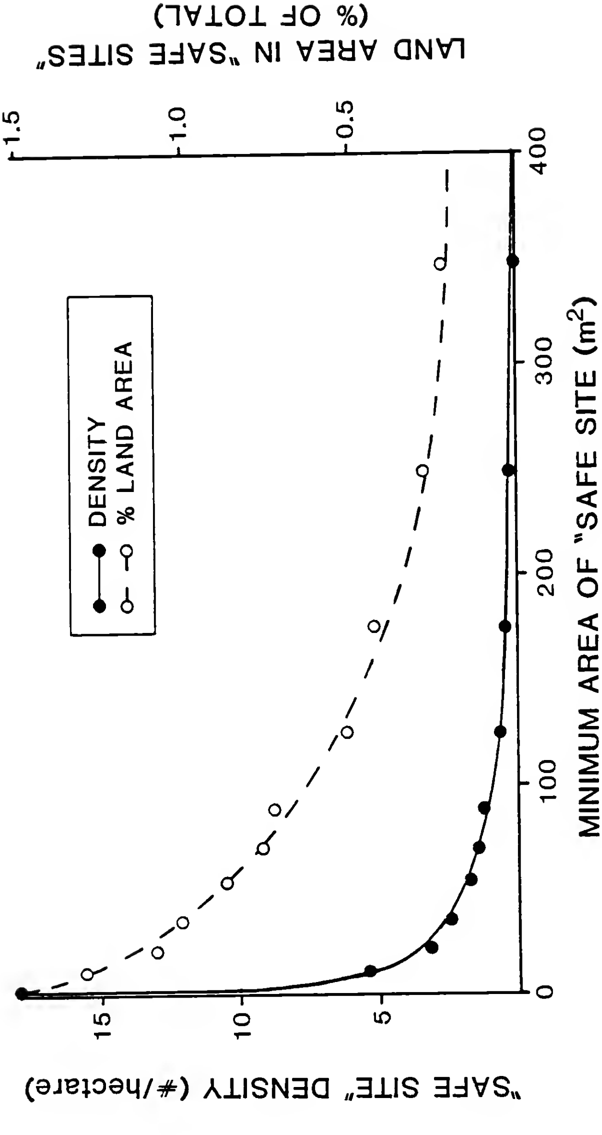
Although these analyses are useful for gaining a qualitative impression of the relationship between germination requirements and the availability of suitable habitat patches over the landscape, data presented in Figures 6 and 7 clearly show that applying the concept of "safe site" to treefall gaps oversimplifies the relationship between germination requirements and availability of suitable patches over the landscape. The effects of gap size and age on germination are not threshold effects, in which germination success in gaps below a certain size or above a certain age is zero and that in younger or larger gaps is 100%. Instead, germination success is a continuous function of both gap size and age, and each gap size has an associated germination probability for each plant species.

Seed Shadows Produced by Birds

Seed Passage Rates

Most birds fed on fruits placed in the experimental cage soon after the fruits were introduced. In most cases, birds ate 4-10 fruits

Figure 6. Density and areal coverage of "safe sites" (see text) vs. minimum safe site area.


LAND AREA IN "SAFE SITES"
(% OF TOTAL)
1.5
1.0
0.5
DENSITY
% LAND AREA
"SAFE SITE" DENSITY (#/hectare)
15
10
5
0
100
200
300
400
MINIMUM AREA OF "SAFE SITE" (m^2)

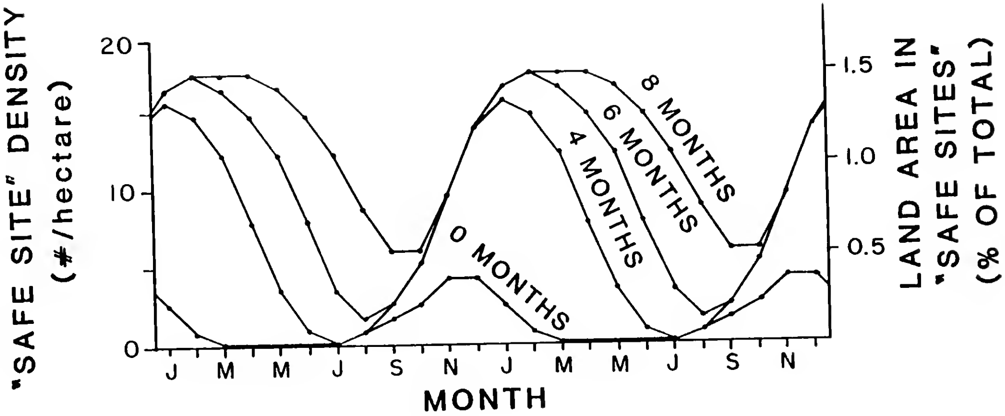


Figure 7. Density and areal coverage of "safe sites" as a function of time of year. Lines labelled 0, 4, 6, and 8 months show the density and coverage of gaps 0, $\leq$ 4, $\leq$ 6, and $\leq$ 8 months old.

(depending upon fruit and bird species) and then perched for approximately 10-15 minutes. During this time, birds generally closed their eyes, puffed out their feathers, and remained nearly motionless. Similar behavior was often observed in actively foraging birds in the field: after taking a number of fruits from a plant (and presumably filling the gut), birds often flew to a perch in a neighboring tree or shrub and remained there for 10 or more minutes. This period of inactivity almost always continued until the first defecation of material from the previous foraging bout. Birds became progressively more active after each successive defecation, as fruits were processed through the gut.

Data on gut passage times for seeds of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* are shown in Figure 8. Although variation in gut passage time is considerable at all levels (i.e., among seeds of a particular plant species ingested at the same time, among plant species in a given bird species, and among bird species), it is useful to ask whether gut passage rates vary among plant species and bird species in a systematic way. To determine whether seeds of some plant species are processed more quickly than others, I compared median passage times for the three plant species in the three bird species. In all three bird species for which I have detailed data, median passage times were longest for seeds of *P. rivinoides*, intermediate for *W. coccoloboides*, and shortest for *W. solanacea* (Table 5). All else being equal, *P. rivinoides* seeds should thus travel farther than those of either species of *Witheringia*. The reasons for these consistent differences are as yet unclear; fruits of all three species are similar in size, have fruit skins of similar thickness and toughness, and contain seeds that seem to

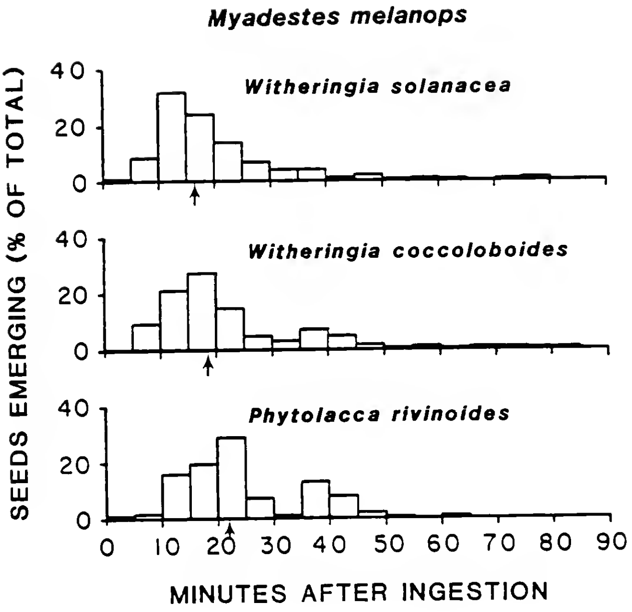


Figure 8. Seed passage rates for the three plant species in Myadestes melanops, Phainoptila melanoxantha, and Semnornis frantzii. Arrows indicate median passage times.

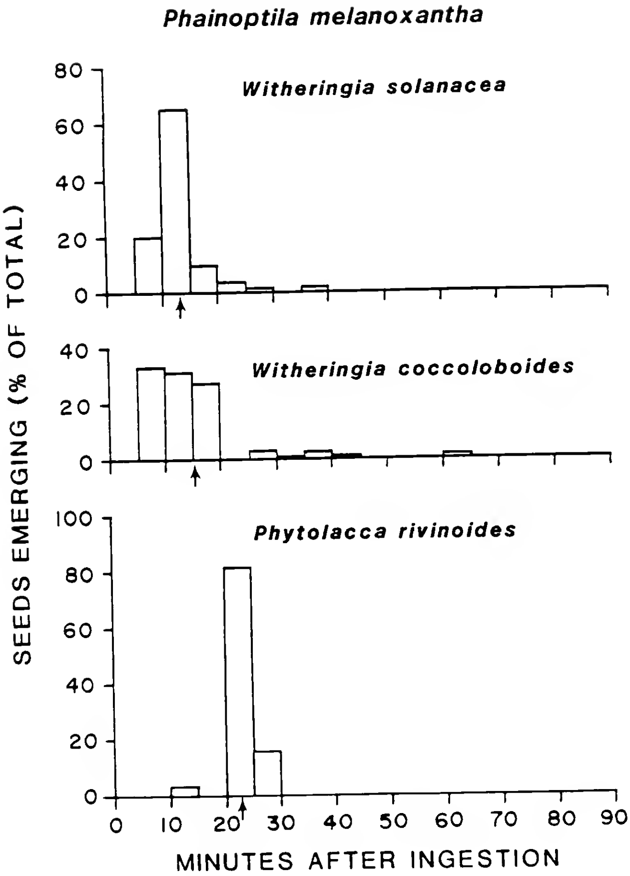


Figure 8 -- continued

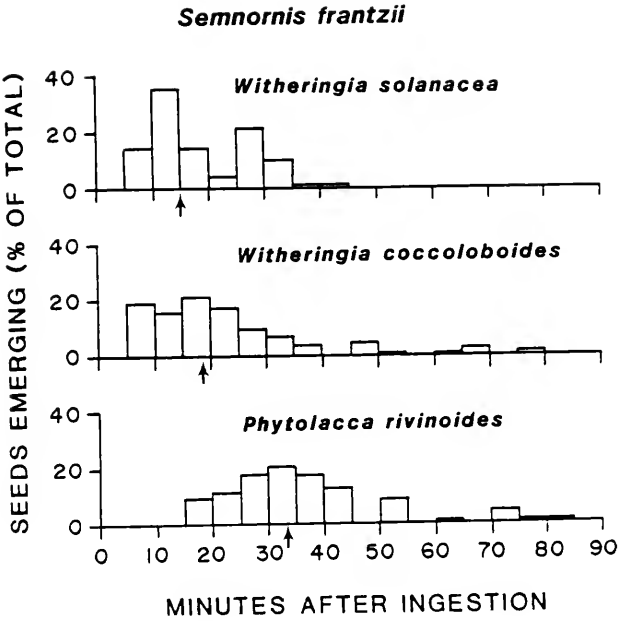


Figure 8 -- continued

Table 5. Summary of differences among median seed retention times, (A) among bird species within plant species, and (B) among plant species within bird species. Based on multisample median tests (Zar 1984:179-180) and subdivisions of the multisample contingency tables (Zar 1984: 69-70).

A.

plant species	comparisons				
Phytolacca rivinoides	Sf	$>^{**}$	Mm	$=$	Pm
Witheringia solanacea	Sf	$=$	Mm	$>^{**}$	Pm
Witheringia coccoloboides	Sf	$=$	Mm	$>^{**}$	Pm

B.

bird species	comparisons				
Phainoptila melanoxantha	Pr	$>^{**}$	Wc	$>^{**}$	Ws
Myadestes melanops	Pr	$>^{**}$	Wc	$>^{**}$	Ws
Semnornis frantzii	Pr	$>^{**}$	Wc	$>^{*}$	Ws

$^{*}p < .05$

$^{**}p < .005$

be about equally easily extracted from the pulp. In fact, *P. rivinoides* fruits are slightly smaller than those of either *Witheringia* species and have a more watery, amorphous pulp. It would seem that seeds would be most easily separated from this pulp, yet retention times were consistently longer in *P. rivinoides* than in the two *Witheringia* species. Fruits of *W. solanacea* and *W. coccoloboides* may contain a compound with laxative properties, or perhaps *P. rivinoides* contains a compound having the opposite effect.

Median passage times vary systematically among bird species as well. For seeds of all three plant species, passage times are longer in *Semnornis* than in *Phainoptila* (Table 5). Median passage times in *Myadestes* were generally intermediate between those in *Semnornis* and *Phainoptila*, but were statistically indistinguishable from those of one or the other bird species for seeds of each plant.

Several features of the seed retention distributions in Figure 8 are important to the relationship between gut passage times and the spatial patterns of seeds produced by an actively foraging bird. First, seeds ingested at one point in time do not emerge from the gut together; in these experiments, the last seeds emerged more than 75 minutes after the first-emerging seeds ingested at the same time. Second, the distributions of retention times are not symmetrical, but instead are skewed to the right. As a result, neither the length of time for the appearance of the first-voided seeds, pulp, or marker stain (e.g., Herrera 1984, Holthuijzen and Adkisson 1984, Sorensen 1984) nor the mean seed retention time (e.g., Walsberg 1975) is likely to provide complete information for inferring seed dispersal patterns. Third, although retention times are variable in all cases, the variation is greater in some bird species than in others. For example, coefficients of variation for P. rivinoides passage times in Myadestes, Semnornis, and Phainoptila were 44.5, 35.9, and 9.2, respectively. Clearly, any inferences about the seed shadows produced by animals must be based on a consideration of the entire frequency distribution of retention times, rather than on a descriptive statistic (e.g., mean, median, mode, etc.) derived from it.

Movement Patterns of Frugivorous Birds

A total of 195.7 hours of data on movement patterns was collected from 8 birds of three species. Totals for Myadestes melanops, Phainoptila melanoxantha, and Semnornis frantzii, respectively, were 4 individuals for 96.2 total hours, 3 individuals for 90.3 hours, and 1 individual for 9.3 hours. I also attached transmitters to eight other individual Myadestes, one Phainoptila, and one Semnornis, but I was unable to collect enough data on these birds to include here. Transmitters fell off two of these birds less than one day after the birds' release. In five other cases, the tagged individual moved out of the area before I could begin tracking it. These five individuals were non-territorial birds that foraged over very large areas of the forest. The few hours of data collected from two of these birds indicate that they did not move more rapidly through the forest than those on well-defined home ranges; rather, their movements were simply more linear than those of other individuals of the same species, which turned more often. Seeds dispersed by a particular widely foraging bird are thus unlikely to travel much farther from their source than those dispersed by birds with more restricted home ranges.

Birds fitted with transmitters generally showed no adverse effects of carrying the 3.5 g package. Within 2 hours of release, most individuals had begun foraging actively and chasing territory intruders. Data from two individuals that did not adjust quickly to carrying the transmitter were not used in the analysis.

Foraging behavior of the primarily frugivorous Myadestes, Phainoptila, and Semnornis resulted in very different movement patterns than those of primarily insectivorous birds. Whereas most insectivores seem to move through the forest almost continuously while feeding, the frugivores studied here punctuated brief episodes of rapid movement with relatively long stationary periods. Radio tracking data indicate that birds generally spent 7 to 12 minutes in one location (Table 6), presumably consuming and processing fruits, and then moved rapidly to another location without feeding along the way. Not surprisingly, this pattern corresponds well with the patchy distribution of fruiting plants. In addition, the mean times between successive movements in Table 6 correspond closely with behavior I noted during feeding experiments with captive birds: after eating a number of fruits, most birds perched nearly motionless for approximately 10 minutes before moving about the cage in search of more fruit. The fact that data from remotely monitored birds correspond well with the behavior of closely observed individuals again suggests that the transmitters did not interfere with normal foraging activity.

Movement patterns of radio-tracked birds did not suggest any tendency for gap-to-gap movement. Rather, birds seemed to travel rapidly between well-defined fruit sources, regardless of where they occurred. Locations to which birds returned frequently were always found to be large fruiting plants such as trees, rather than gaps. Furthermore, data from mist-net captures and analysis of fecal specimens suggest no tendency for preferrential foraging in gaps. First, none of the frugivore species was captured more frequently in gaps than in forest (Table 1). Indeed, one species (*Myadestes melanops*) was captured significantly more often in forest ($X^2 = 12.942$, $p < .001$; expected values corrected for differences in sampling effort). Second, over 82% of the fecal specimens from mist-netted *Myadestes*, *Phainoptila*, and *Semnornis* contained seeds of canopy or subcanopy trees and epiphytes, suggesting that these birds concentrate much of their foraging outside gaps. Thus, although these three bird species are the primary dispersers of the gap-dependent *P. rivinoides*, *W. solanacea*, and *W. coccoloboides*, there is no reason to suspect that they commonly transport seeds of any of these plants directly to other gaps in a non-random fashion.

Mean distances and time intervals between successive bird movements varied more among individuals of a given species than among species (Table 6). This variation may reflect different densities of fruit sources within different birds' feeding ranges or between different seasons. Without collecting data from numerous individuals of each species throughout the year, it is impossible to identify sources of variation in movement patterns more precisely. Because variation among individuals within species was so high, data from each individual were weighted equally for purposes of estimating seed shadows. Individuals from which I was able to collect more extensive data are thus not overrepresented in the analysis.

Table 6. Movement data from individual frugivores fitted with radio transmitters. A) Descriptive statistics on number of foraging movements, mean time interval between successive movements, and mean distance per movement. Standard deviations in parentheses. B) Results of nested ANOVA on time intervals between movements in *Myadestes melanops* and *Phainoptila melanoxantha*. C) Results of nested ANOVA on mean distances moved by individual *Myadestes* and *Phainoptila*. Because movement data were collected from only one *Semnornis frantzii*, those data could not be included in the ANOVAs.

A. Descriptive statistics

bird species	individual	recorded movements	time interval (min) between movements	movement distance (meters)
Myadestes melanops	KN/rt	258	9.1 (4.94)	106.9 (90.67)
	KB/lt	21	7.2 (4.58)	59.7 (64.29)
	BO/rt	158	10.3 (6.90)	51.8 (37.18)
	OG/lt	178	7.7 (7.47)	16.4 (17.16)
Phainoptila melanoxantha	YY/rt	114	12.0 (9.54)	39.1 (33.54)
	OO/rt	189	11.5 (7.05)	100.3 (85.01)
	OY/rt	80	8.7 (10.98)	44.4 (40.03)
Semnornis frantzii	YW/rt	45	9.8 (8.78)	38.8 (26.28)

B. Time intervals between successive movements

source	df	SS	MS	F
among species	1	1064.8	1064.8	4.48 (ns)
within species	5	1189.5	237.9	4.43 ($p < .001$)
error	991	53185.8	53.7	
total	997	55440.1	55.6	

Table 6 -- continued

C. Movement distances

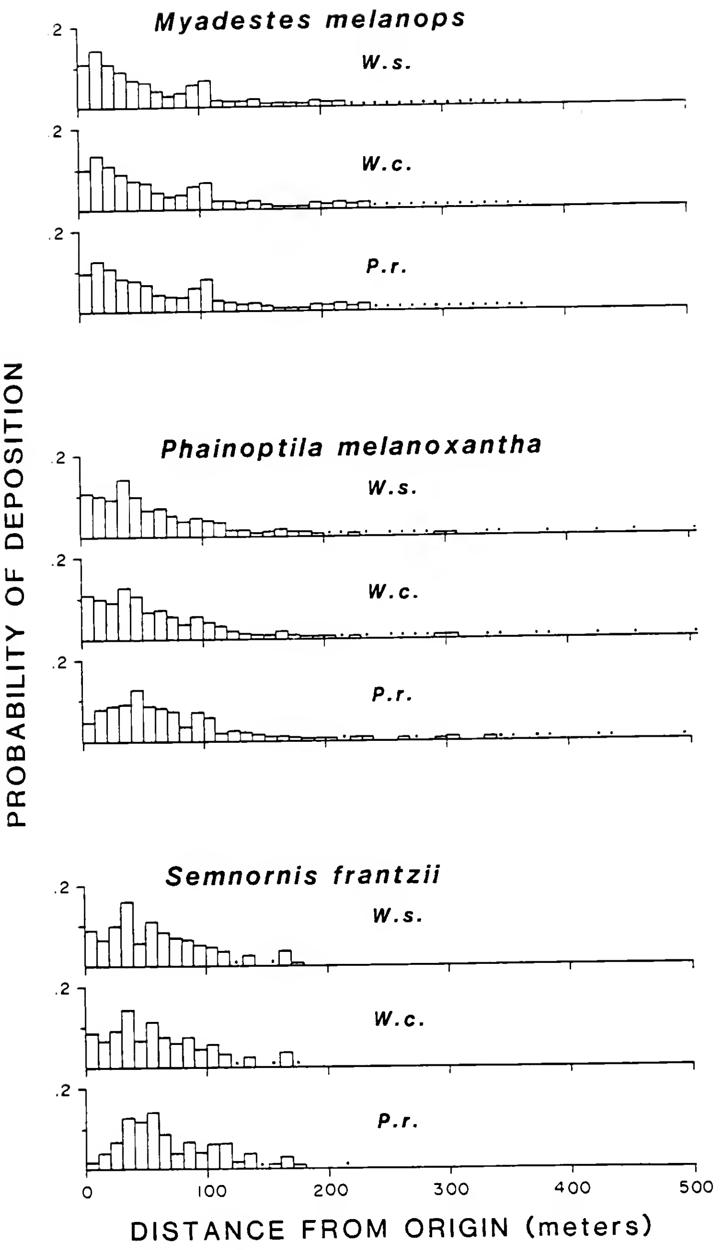
source	df	SS	MS	F
among species	1	7080	7080	0.029 (ns)
within species	5	1236278	247256	60.101 ($p < .001$)
error	991	4076727	4114	
total	997	5320085	5336	

Estimation of Seed Shadows

I estimated seed dispersal distances from data on bird movement patterns and seed passage times as follows. Each time a bird moved to a new location, I recorded the time and that location on a map of the study area. These data allow relatively precise measurement of the distances between all mapped locations and the time spent at each. By knowing the bird's distance from each location during each subsequent minute, and by combining these data from many such "initial" locations, I constructed a probability matrix of distance versus time. Thus, I computed the probability that a given bird will be at a distance of d meters from an initial location at time t. Multiplying this matrix by the probability distributions of seed passage times resulted in probability distributions of seed movement distances for all three plant species. This method assumes that an individual's behavior after leaving each initial location is not different from that after leaving a fruiting *P. rivinoides*, *W. solanacea*, or *W. coccoloboides*. Data from initial locations at which the bird spent more than 30 min were not used in the analysis, because they indicate non-foraging periods or long visits to plants with very large fruit crops, such as trees. The appendix demonstrates the use of this method to estimate seed shadows.

The estimated seed shadows produced by the three bird species are shown in Figure 9. Those for *Myadestes melanops* and *Phainoptila melanoxantha* are very similar: only 20-36% of seeds are deposited within 30 m of the parent plant, and some seeds may be moved up to 370 m by *Myadestes* and 510 m by *Phainoptila*. Estimated seed shadows for *Semnornis frantzii* are similar to those of the other two species in that the probability of seed deposition within 30 m of the parent is low (12-

Figure 9. Estimated seed shadows produced by *Myadestes*, *Phainoptila*, and *Semnornis* around individuals of *Witheringia solanacea* (*W.s.*), *W. coccoloboides* (*W.c.*), and *Phytolacca rivinoides* (*P.r.*). Dots indicate probability of deposition less than 0.005.


Myadestes melanops
W.s.
W.c.
P.r.
Phainoptila melanoxantha
W.s.
W.c.
P.r.
Semnornis frantzii
W.s.
W.c.
P.r.
.2
PROBABILITY OF DEPOSITION
0
100
200
300
400
500
DISTANCE FROM ORIGIN (meters)

25%), but the estimated maximum dispersal distance is only 220 m. This estimate is based on movement data from only one individual, however, and with a larger sample size the estimated extreme dispersal distances might approach those of the other two species more closely.

Mediation of Plant Reproductive Success by Birds

A Model of Plant Reproductive Success

Because germination success is a continuous function of both gap size and gap age, suitable colonization sites are not discrete, recognizable units, even for the gap dependent-plants studied here. As a result, evaluating the effect of different seed shadows, temporal fruiting patterns, and seed dormancy characteristics on plant reproductive success is complex. For example, we cannot simply determine the probability with which seeds fall into gaps of a particular size or age, and asssume that they will have encountered safe sites. In order to compare the reproductive consequences of different seed shadows, phenological patterns, and dormancy capabilities then, I designed a computer simulation model that estimates the potential maximum lifetime reproductive success of individual plants. Parameters of the model include the phenology of fruiting and gap formation, the seed shadows produced by animals, the relationships of germination success to gap size and age, and the density of, and area occupied by, gaps in various size categories.

Based on either an empirically derived or hypothetical seed shadow, the model first computes the density of seeds in each of a series of concentric distance intervals away from the parent plant. Densities are incremented monthly according to the observed fruiting phenology and seed dormancy capabilities of each species. Using data on observed gap-size distributions and rates of canopy disturbance, the model then determines for each distance interval the amount of land area occupied by gaps in each of 16 gap size categories. Gaps are "formed" according to the estimated phenology at Monteverde. The number of seeds potentially germinating in each distance interval equals the density of seeds in that interval (at that time) times the area in gaps that size, summed over all 16 gap size categories. Within this operation, a similar one based upon the relationship between gap age and germination success takes place. Because a relatively small number of seeds can survive to reproduce in any one gap, another function limits the total number of offspring in gaps of various sizes to the maximum number observed in gaps of that size in the field. For *P. rivinoides*, this number varied from zero in gaps smaller than 10 m^2 to four in the largest gaps. For both *W. solanacea* and *W. coccoloboides*, the maximum number varied from one to five.

The model can be stated mathematically as

$$RO = \sum_{m=1}^{nm} \sum_{i=1}^{51} \sum_{j=1}^{16} \left[\left(\sum_{k=1}^{12} SN_{i,m} \cdot GS_j \cdot PS_j \cdot GA_{k,m} \cdot PA_k \right) \text{ or } \left(GN_{i,j} \cdot MX_j \cdot GF_m \right) \text{, whichever is smaller} \right] \quad (1)$$

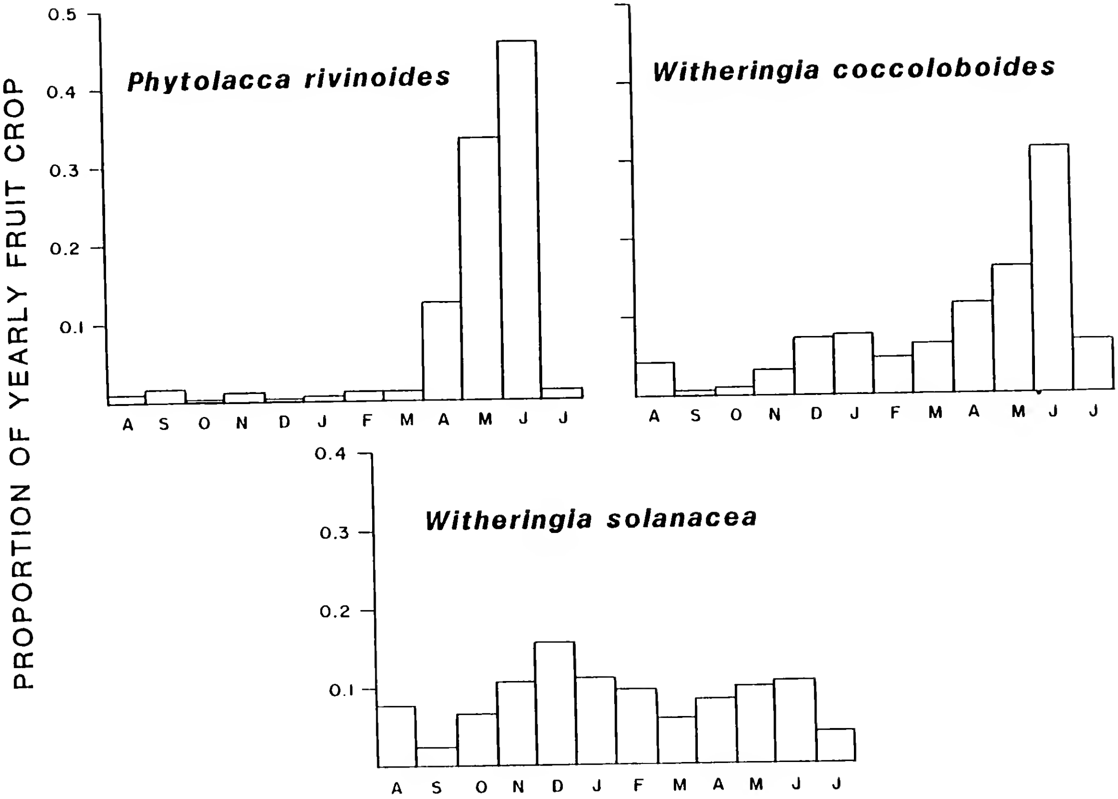
where RO is potential lifetime reproductive output, $SN_{i,m}$ is the number of seeds in distance interval i during month m, GS_j is the proportion of land area in gaps of size category j, PS_j is the probability of germination in gaps of size category j, $GA_{k,m}$ is the proportion of gaps of age k (in months) during month m, PA_k is the probability of germination in gaps of age k, $GN_{i,j}$ is the number of gaps of size category j in distance interval i, MX_j is the maximum number of seeds that can survive to maturity in gaps of size category j, and GF_m is the proportion of gaps (out of those formed in one year) occurring during month m. Here I distinguish "reproductive output", which I define as the total number of offspring produced during an individual's lifetime, from relative fitness, which depends upon the age-specific schedule of reproduction (see below). Note that the model estimates potential lifetime reproductive output only; although it limits the number of germinated seeds that survive in any one gap (simulating competition with siblings), it does not include any other sources of mortality, e.g., predators, pathogens, or accidents such as treefalls. RO as used here is thus not exactly equivalent to the net reproductive rate, R_o. Although a Monte Carlo simulation using a stochastic model might yield more realistic results, the deterministic model is more suitable for the present purpose, due to its relative simplicity and to the fact that with a large number of runs, results from a stochastic model should converge on those from the deterministic one.

Dispersal Effects on Reproductive Output (RO), Assuming No Seed Dormancy

To evaluate the reproductive consequences of dispersal by *Myadestes*, *Phainoptila*, and *Semnornis*, I first ran the model described above four times for each plant species; once with each of the seed shadows in Figure 9, and a fourth time using a seed shadow in which all seeds are deposited within 10 m of the parent plant. This last run thus approximates the case of no dispersal, or the fate of most seeds removed by tanagers and finches. Other parameters of the model were the same for each run on a particular species, and were taken from data collected at Monteverde. The relationships between germination success and gap size are the adjusted regressions given previously. Relationships between gap age and germination success were interpolated from the lines connecting observed mean values in Figure 2. The availability of gaps of different sizes was estimated directly from data on the canopy disturbance rate and adjusted gap size distribution. Fruiting and gap formation phenologies were those shown in Figures 10 and 11. Yearly seed crops, estimated by multiplying the mean number of seeds per fruit by the median yearly fruit crop sizes for each species, were 8,345, 13,061, and 44,180 for *W. solanacea*, *W. coccoloboides*, and *P. rivinoides*, respectively. Because both *Witheringia* species produce two fruit crops per year, crop sizes used here were yearly medians, rather than the seasonal medians reported above. The number of reproductive seasons was assumed to be that estimated for plants at Monteverde: one in *P. rivinoides*, and five in *W. solanacea* and *W. coccoloboides*.

Estimates of total lifetime reproductive output (assuming no seed dormancy) using the four seed shadows are shown in Figure 12. For each plant species, the advantage of dispersal by any of the three legitimate dispersers is obvious. Within 10 m of the parent plant, very few suitable germination sites are available, and density-dependent mortality among seedlings within them is high. Seed shadows produced by *Semnornis*, *Phainoptila*, and *Myadestes* result in much higher estimates of reproductive output, because seeds are distributed over a greater number of suitable patches. However, these estimates are for seeds that are

Figure 10. Fruiting phenology of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* at Monteverde. Values given are for the "average" individual of each species (see text).


PROPORTION OF YEARLY FRUIT CROP
Phytolacca rivinoides
0.5
0.4
0.3
0.2
0.1
A S O N D J F M A M J J
Witheringia coccoloboides
A S O N D J F M A M J J
Witheringia solanacea
0.4
0.3
0.2
0.1
A S O N D J F M A M J J

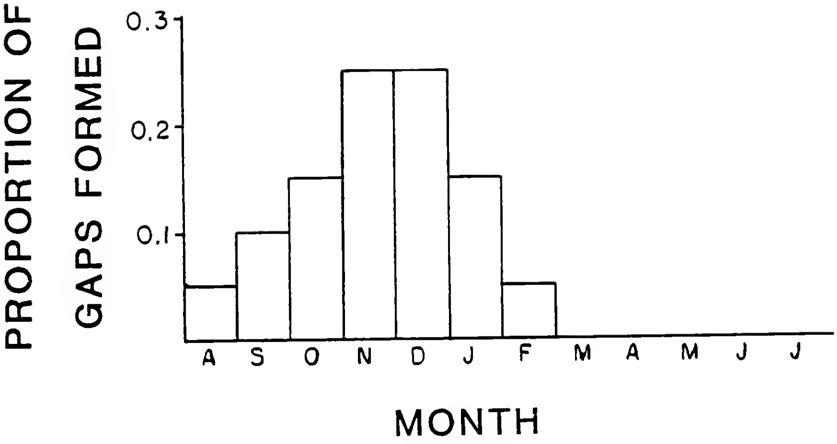
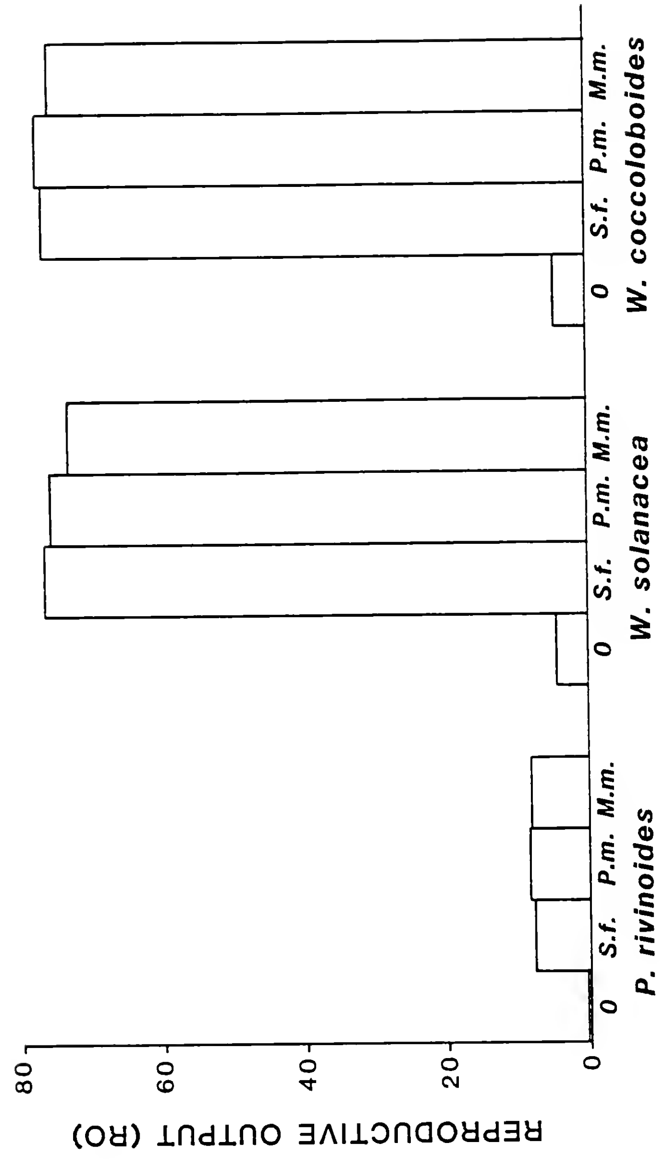


Figure 11. Estimated phenology of gap formation at Monteverde. Values given are the proportions of all gaps formed in a particular year that occur each month.

Figure 12. Estimated lifetime reproductive output (RO; assuming no seed dormancy) of plants receiving all dispersal service from *Semnornis* (S.f.), *Phainoptila* (P.m.), *Myadestes* (M.m), or having all seeds deposited within 10 m of the parent (0).

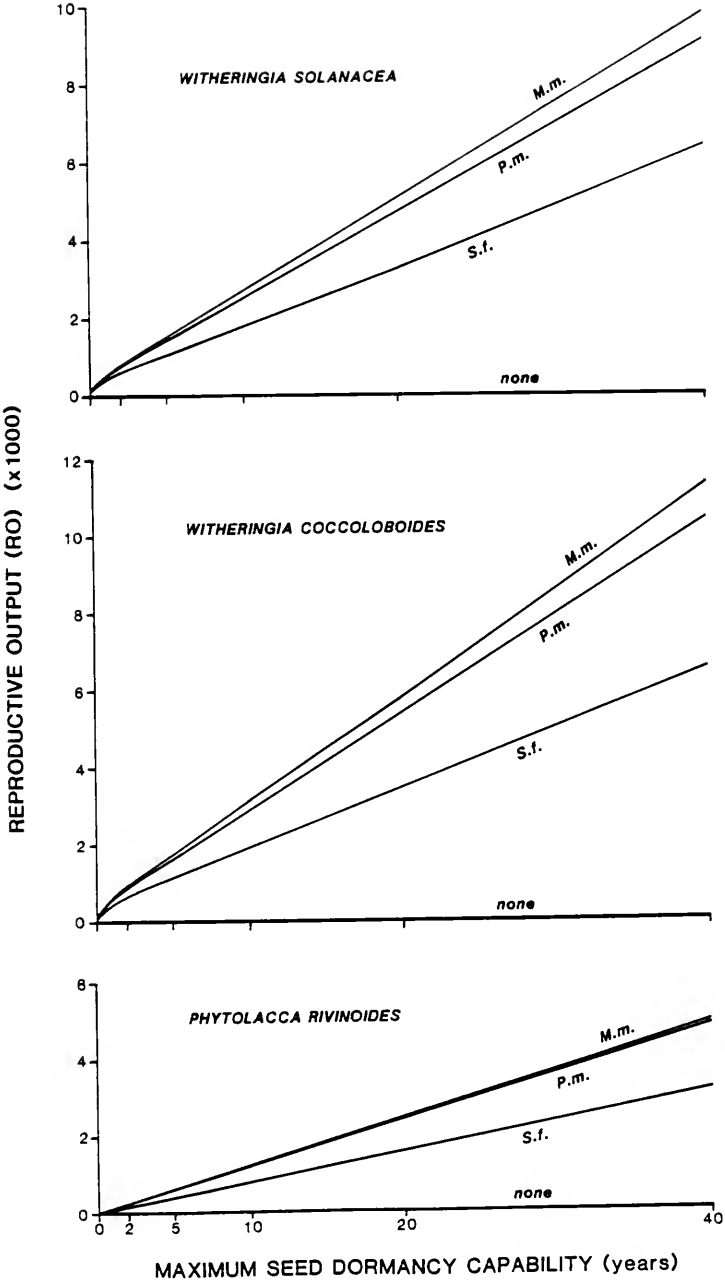

REPRODUCTIVE OUTPUT (RO)
0
20
40
60
80
0
S.f.
P.m.
M.m.
P. rivinoides
0
S.f.
P.m.
M.m.
W. solanacea
0
S.f.
P.m.
M.m.
W. coccoloboides

dispersed to sites currently suitable for germination, and thus germinate in the same month they are dispersed. These estimates do not include later reproduction from dormant seeds that germinate after a new canopy gap occurs overhead. Yet seeds of P. rivinoides, W. solanacea, and W. coccoloboides exhibit "enforced" seed dormancy (sensu Harper 1977), and are capable of remaining dormant in the soil for at least 2.5 years with no detectable decrease in viability, and probably for much longer (Fig. 4).

Reproductive Consequences of Seed Dormancy

Effects on reproductive output (RO). Because plant reproductive success should be enhanced by enforced seed dormancy, I repeated the four model runs for each species, this time allowing any ungerminated seeds to remain dormant for maximum periods of 2, 5, 10, 20, and 40 years. Not surprisingly, potential reproductive output increases dramatically with increased dormancy capabilities of seeds (Fig. 13). For example, plants whose seeds are capable of remaining dormant for just two years can potentially produce 11 to 31 times as many offspring as plants whose seeds die if they are not dispersed directly to sites immediately suitable for germination. If seeds can remain dormant for up to 40 years, up to 611 times as many offspring may be produced. Even more interesting, however, is the fact that the relative differences in estimated reproductive output using different seed shadows are greatly magnified when we also consider reproduction from dormant seeds. Thus for P. rivinoides, dispersal by Myadestes results in only a 4% increase in RO over dispersal by Semnornis, considering only those seeds encountering currently suitable sites when dispersed (Fig. 12).

Figure 13. Estimated lifetime reproductive ouptut (RO) vs. seed dormancy capability, for plants receiving all dispersal service from Semnornis (S.f.), Phainoptila (P.m.), Myadestes (M.m.), or having all seeds deposited within 10 m of the parent (none).


REPRODUCTIVE OUTPUT (RO) (x1000)
WITHERINGIA SOLANACEA
M.m.
P.m.
S.f.
none
0
2
4
6
8
10
WITHERINGIA COCCOLOBOIDES
M.m.
P.m.
S.f.
none
0
2
4
6
8
10
12
PHYTOLACCA RIVINOIDES
M.m.
P.m.
S.f.
none
0
2
4
6
0
2
5
10
20
40
MAXIMUM SEED DORMANCY CAPABILITY (years)

However, if we also consider seeds that can remain dormant in the soil for up to two years until a gap is formed overhead, dispersal by *Myadestes* confers a 54% increase over dispersal by *Semnornis* (Fig. 13). Furthermore, if seeds can remain dormant for even longer periods, these differences become even larger.

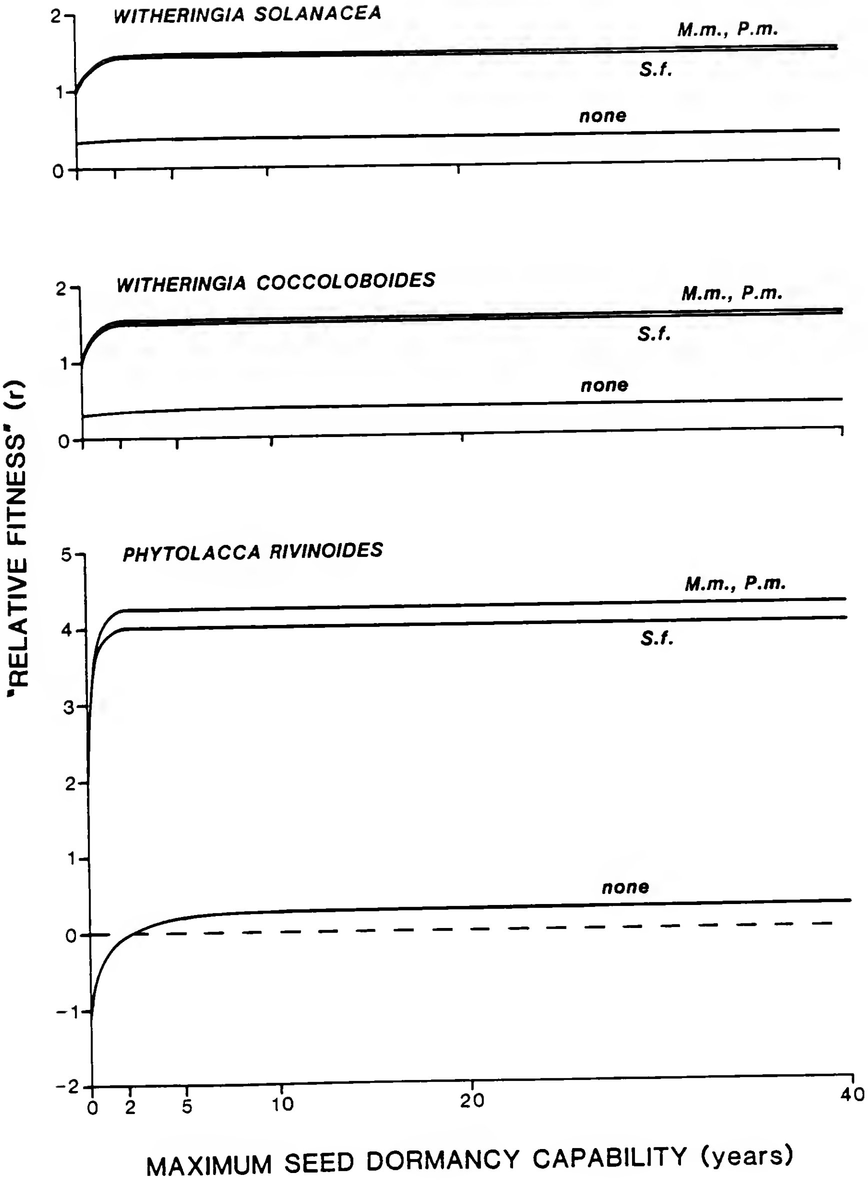
Effects on relative fitness. Although Figure 13 clearly shows that the total number of potential offspring is greatly increased by seed dormancy, it gives a misleading impression of the influence of seed dormancy on relative fitness. The estimator of reproductive output computed by equation 1 is most useful for plants without overlapping generations or age-structured populations, e.g., monocarpic plants without seed dormancy. In such plants, RO will be an unbiased estimator of relative "fitness", and comparisons among treatments (e.g., different seed shadows) yield unbiased information about the fitness consequences of the different treatments. If fecundity and/or survival are age dependent, however, the total number of offspring produced by an individual is not an unbiased estimator of relative fitness, because seeds produced later in life, or those that germinate after a long period of dormancy, contribute less to the population gene pool than those germinating earlier. Fecundity, at least, is age-dependent in all three species considered here. Both *W. solanacea* and *W. coccoloboides* typically produce seeds for five or more years. More importantly, all three species demonstrate the capacity for enforced seed dormancy, which has the effect of greatly increasing the parent plant's reproductive lifespan. Therefore, I computed a less biased estimator of relative fitness by solving for r the equation

$$1 = \sum_{x=0}^{YP+YD} e^{-rx} \cdot l_x \cdot m_x, \qquad (2)$$

where l_x is the probability of seed survival in the soil for x years, and m_x is the number of seeds germinating in year x. This equation is commonly used to compute the exact value of the intrinsic rate of natural increase of a population. Here, r is not the intrinsic rate of natural increase, but an estimator of relative fitness that discounts the contribution of offspring produced later in the parent's life relative to that of those produced earlier. The parent plant germinates in year 0, and x can take on values from 0 to YP + YD, where YP is the last year of seed production and YD is the maximum number of years that seeds can remain dormant. Survival of ungerminated seeds (l_x) was assumed to equal 1.0 for all years up to the maximum dormancy period, followed by complete mortality. Values of m_x were the yearly estimates of seeds germinating generated by the model, which summed to the value for RO given in Fig. 13. The age at first reproduction and number of years of seed production were those estimated for plants at Monteverde. In *P. rivinoides*, all seed production occurs in year 1 (plants between 1 and 2 years of age). In the two *Witheringia* species, seed production was assumed to begin at age 3 and continue for 5 years.

Estimates of relative fitness based on equation 2 are shown in Figure 14. The figure shows that seed dormancy indeed greatly enhances plant fitness, but that most of this enhancement is due to short-term, rather than long-term dormancy. Dormancy capability of more than two years does little to increase the value of r. Thus, the increase in

Figure 14. Estimated relative "fitness" (r; see text) vs. seed dormancy capability ,for plants receiving all dispersal service from *Semnornis* (S.f.), *Phainoptila* (P.m.), *Myadestes* (M.m.), or having all seeds deposited within 10 m of the parent (none).


WITHERINGIA SOLANACEA
M.m., P.m.
S.f.
none
2
1
0
WITHERINGIA COCCOLOBOIDES
M.m., P.m.
S.f.
none
2
1
0
PHYTOLACCA RIVINOIDES
M.m., P.m.
S.f.
none
5
4
3
2
1
0
-1
-2
0
2
5
10
20
40
"RELATIVE FITNESS" (r)
MAXIMUM SEED DORMANCY CAPABILITY (years)

fitness with increasing dormancy capability is not monotonically increasing and linear, as suggested by Fig. 13, but is in fact asymptotic.

Reproductive Consequences of Fruiting Phenology

Fruit ripening in all three plant species is concentrated in the wet season, although some fruits may be found at any time of the year (Fig. 10). In *P. rivinoides*, a single well-defined peak occurs early in the wet season, with 91% of all fruits ripening from April through June. In both *W. solanacea* and *W. coccoloboides*, two distinct ripening peaks occur in the wet season: one early (May-June), and one late (November-January). These distinct peaks were not due to individual plants within each population ripening at different times; nearly all individuals of each species produced two separate fruit crops each year, although these were not usually of the same size.

Fruiting in *W. solanacea* was somewhat less seasonal than in *W. coccoloboides*. Although peak ripening periods in both species coincided, the May-June and November-January peaks accounted for a greater proportion of the total fruit crop in *W. coccoloboides* than in *W. solanacea*. More importantly, the major ripening peak in *W. coccoloboides* was in the early wet season, while that in *W. solanacea* was in the late wet season.

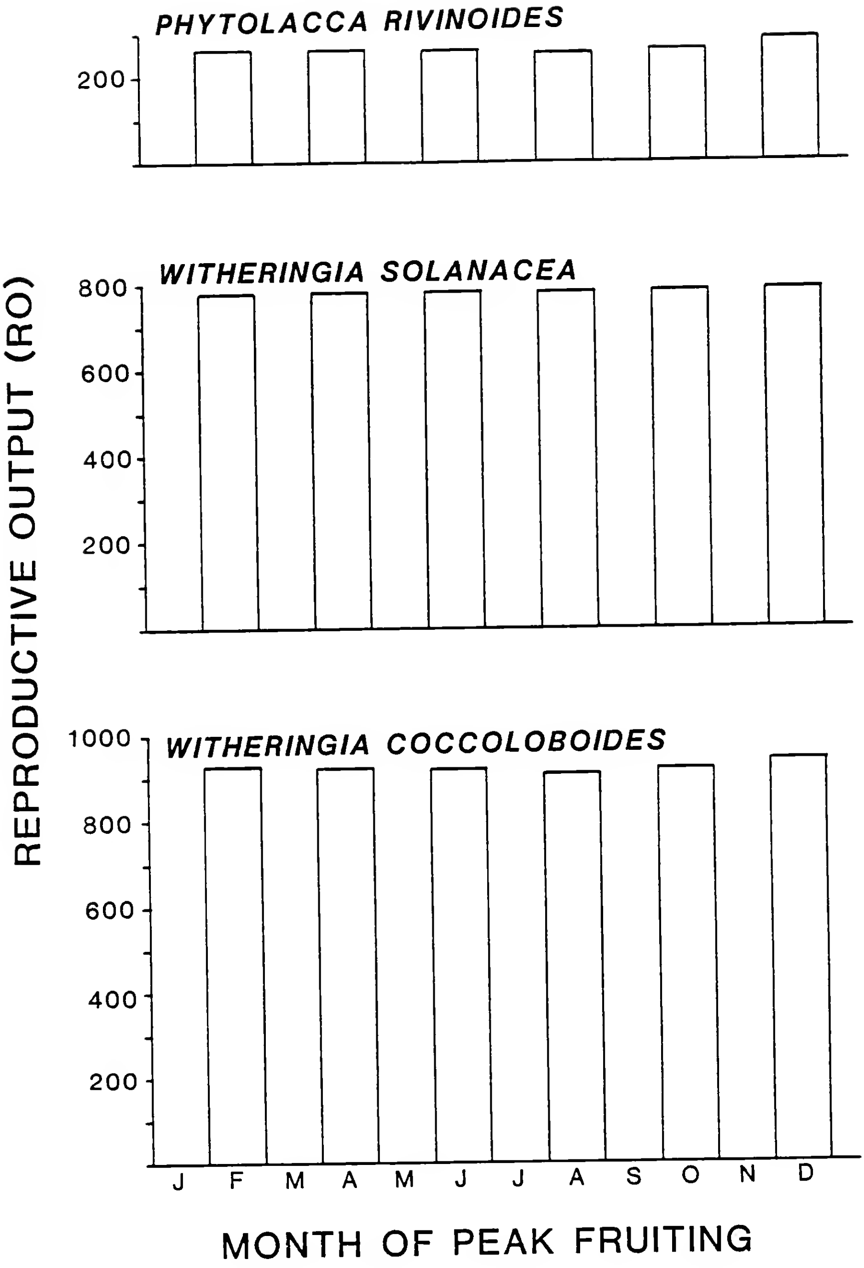
Because the major disperser for all three plant species, *Myadestes melanops*, is essentially absent from the Monteverde area from late October through December (Fig. 1), we might expect fruit removal rates to be depressed during the late wet season fruiting peak. To test the hypothesis that daily fruit removal rates are correlated with seasonal patterns of Myadestes abundance, I examined the relationship between Myadestes capture rate and daily fruit removal rate from May 1982 through April 1983. Daily fruit removal rate was computed as the proportion of marked ripe fruits on all plants that were removed. Because daily fruit removal rate is negatively correlated with the size of the fruit crop (Murray, in press), I computed partial correlations of removal rate with the monthly Myadestes capture rate, holding crop size constant.

In all three plant species, a significant partial correlation existed between Myadestes capture rate and daily fruit removal rate. Coefficients for P. rivinoides, W. solanacea, and W. coccoloboides were 0.74 ($P < .02$), 0.66 ($P < .05$), and 0.69 ($P < .05$), respectively. Thus, individual plants that ripen fruits during the season when Myadestes is absent should have, on average, lower reproductive success than those ripening fruits at other times.

Because the availability of suitable germination sites varies over the year (Fig. 7), plant reproductive success may be affected by seasonal fruiting patterns for reasons other than variation in fruit removal rate. To estimate the relative importance of this selective pressure on fruiting phenology, I compared the potential lifetime reproductive output of individuals that peak ripening in February, April, June, August, October, and December. For each plant species, I ran the simulation model described above six times, each time shifting the fruiting phenology curve temporally with respect to the estimated phenology of gap formation. For all runs, I used the estimated seed shadow produced by Myadestes, and allowed ungerminated seeds to remain dormant for two years. All other model parameters were the same for all runs on each species, as outlined above.

Somewhat surprisingly, estimates of reproductive output were very similar for plants that fruit at different times of year (Fig. 15): the highest estimates for each species are only 1% to 13% higher than the lowest estimates. Two factors account for this result. First, because treefall gaps sometimes remain open for germination for up to a year after formation, the temporal availability of suitable habitat patches is actually somewhat more constant than the highly seasonal nature of gap formation would suggest (e.g., Fig. 7). Second, and more importantly, enforced seed dormancy greatly reduces temporal variation in the number of seeds available for colonization of newly formed gaps. Even though fruit ripening is highly seasonal, the effective pool of seeds from a given parent remains much more constant over time. Had the estimates in Figure 15 been determined for plants with no seed dormancy capability, variation in reproductive output of plants that peak fruiting at different times would have been much greater.

Figure 15. Estimated lifetime reproductive output (RO) of plants that peak fruit ripening at different times of year (see text). All estimates assume a maximum seed dormancy capability of two years, and all dispersal service from *Myadestes melanops*.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WITHERINGIA SOLANACEA
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WITHERINGIA COCCOLOBOIDES
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REPRODUCTIVE OUTPUT (RO)
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MONTH OF PEAK FRUITING

DISCUSSION

Data presented here demonstrate that determining the consequences of seed dispersal ("dispersal quality", *sensu* McKey 1975) by different bird species is exceedingly difficult. Animal dispersers may influence plant reproductive success in three ways. First, animals may differ in the likelihood with which they ingest seeds of the fruits they remove from plants ("fruit handling"). Second, animals may differ in the chemical or mechanical effects exerted on seeds that are ingested ("seed treatment in the gut"). Third, animals can affect plant reproductive success through the seed shadows they produce, via colonization of patchily distributed microhabitats or escape from high density-dependent mortality near the parent plant.

Effects of Fruit Handling and Gut Treatment

Avian consumers of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* fruits differ in the "quality" of dispersal service they provide in all three of the above ways. Whereas *Myadestes melanops*, *Phainoptila melanoxantha*, and *Semnornis frantzii* invariably ingested fruits of these plants whole and ingested all of the seeds, the two tanagers (*Chlorospingus opthalmicus* and *Tangara dowii*) and the finch (*Pselliophorus tibialis*) discarded many or most seeds before swallowing the fruit pulp. Similar fruit-handling behavior in tanagers and finches has also been noted by several other investigators (Snow and Snow 1971, Moermond 1983, Moermond and Denslow 1985, Levey 1986). As with the species considered here, Levey (1986) also found that the probability of seed ingestion by tanagers and finches was inversely correlated with seed size within bird species, and positively correlated with seed size among bird species. Clearly, such differences in the ways that different birds handle fruits may result in different reproductive consequences to plants. In general, tanagers and finches are less likely to ingest seeds of any size than are birds that swallow fruits whole. Instead, most seeds will be dropped directly beneath the parent plant where they may be subject to high density-dependent mortality (e.g, Wilson and Janzen 1972, Howe and Primack 1975, Janzen et al. 1976, Platt 1976, Salmonson 1978, Clark and Clark 1981, Lemen 1981, Augspurger 1983a,b, 1984a,b, Howe et al. 1985). In addition, the lack of gut treatment may retard germination in such seeds (see below). Thus, not only does fruit size limit the number of potential consumer species for a given plant (e.g., Diamond 1973, Snow 1973, Moermond and Denslow 1985, Wheelwright 1985a), seed size may also impose constraints on the quality of dispersal service rendered by those animals that actually consume fruits.

Reproductive consequences of fruit removal by different birds may also vary due to different treatment effects of gut passage. Among the bird species considered here, all except the finch P. tibialis passed all ingested seeds intact (Table 2). Furthermore, germination success of these seeds (Table 3) did not differ from that of seeds carefully removed from fruits by hand (test for equality of percentages, Sokal and Rohlf 1969: 608; P>0.3 for all comparisons). In contrast, the one P. tibialis tested destroyed 98% of the W. solanacea seeds it ingested, and the remaining 2% that emerged intact were inviable. The implications of these differences in gut treatment effects for plant reproductive success are obvious: seeds ingested by P. tibialis are likely to be destroyed, hence these finches (but not all finches; e.g., see Jenkins 1969, Levey 1986), like most parrots (e.g., Forshaw 1978, Janzen 1981) and many doves (Snow 1971, Moermond and Denslow 1985), act primarily as seed predators.

Although gut treatment in some animals may have negative effects on germination, the opposite is often true. Germination success of many plant species is enhanced by gut treatment (Krefting and Rowe 1949, Rick and Bowman 1961, Olson and Blum 1968, Hladik and Hladik 1969, Nobel 1975, McDiarmid et al. 1977, Applegate et al. 1979, Lieberman et al. 1979, Fleming and Heithaus 1981, Glyphis et al. 1981), and is even absolutely required by some (e.g., Calvaria major; Temple 1977). In addition, gut passage may affect germination in ways more subtle than merely altering the proportion of seeds that eventually germinate. Data on germination rates of seeds with and without gut treatment (Table 3) indicate that in all cases except one (W. solanacea passed by Phainoptila), seeds processed through bird guts germinated more rapidly than those receiving no gut treatment. Similar results were obtained by Hladik and Hladik (1969) for seeds of some, but not all, plant species passed by monkeys. This response may be due to mild chemical and mechanical abrasion of the seed coat, facilitating perception of germination cues (e.g., light) and/or water imbibition. Whatever the mechanism, rapidly germinating seeds may enjoy a competitive advantage over those that take longer, especially among seedlings of rapidly growing pioneer species. Patches of soil disturbed by uprooting trees commonly contain more than 100 seedlings of P. rivinoides alone within one month, yet only one to three of these will survive to maturity (K. G. Murray, personal observation). In the face of such competition, even subtle treatment effects on germination rate may have important fitness consequences. While the data on germination rates shown in Table 3 are for seeds treated by a single individual of each bird species, and therefore do not allow statistical comparisons between bird species, the data suggest that gut treatment by some species (e.g., Semnornis) may result in more rapid germination than that resulting from treatment by other species.

Effects of Dispersal

Seed Shadows

Variation among the "seed shadows" produced by different birds can also produce differences in the quality of dispersal service rendered. The seed shadow estimates presented in Fig. 9 are, to my knowledge, the first such estimates for free-ranging birds in a natural habitat. Although estimates of the "seed rain" produced over the landscape by frugivorous animals are available from seed trapping studies and assesments of soil seed banks (e.g., Burtt 1929, Smythe 1970, Guevarra and Gomez-Pompa 1972, Foster 1973, Smith 1975, Vazquez-Yanes et al. 1975, Brunner et al. 1976, Lieberman et al. 1979, Thompson 1980, Bullock 1978, Janzen 1978), neither the sources of seeds sampled nor the identity of their dispersers is generally known. Thus, measures of the seed rain within a forest tell us nothing about the seed shadows produced by particular disperser species around individual plants. In contrast, the methods used in this study do allow estimation of individual plant seed shadows, albeit indirectly. Furthermore, the techniques are applicable to a wide variety of dispersal agents and habitats, and yield much additional information on temporal patterns of foraging, home range size, and digestive physiology of particular disperser species.

The estimated seed shadows in Figure 9 are remarkable in several respects. First, they are not, as is sometimes suggested (e.g., Harper 1977, Levin 1979, Fleming and Heithaus 1981), highly leptokurtic, with the great majority of seeds being deposited within a few meters of the parent plant. Instead, a large proportion of seeds may be moved for considerable distances. Median dispersal distances vary from 35 to 60 meters among the 9 bird species/plant species combinations, and maximum dispersal distances exceed 500 meters. Second, the range of estimated dispersal distances presented here exceeds that suggested for most other bird-dispersed plants. Longer dispersal distances have been suggested for seeds cached by Clark's Nutcrackers (Vander Wall and Balda 1977) and for some species dispersed by bats (e.g., Janzen et al. 1976, Fleming 1981), however. Dispersal distances of 70 m, 25 m, and "up to several hundreds of meters" were suggested for seeds of Casearea nitida (Howe and Primack 1975), Prunus mahaleb (Herrera and Jordano 1981), and Virola surinamensis (Howe and Vande Kerchove 1981), respectively. These authors' estimates, however, were based on relatively few visual observations of birds leaving fruiting trees. Because only short bird movements could be observed, their data may be biased in favor of short distances. This bias notwithstanding, it is unlikely that the large (5 to 20 mm) seeds of the trees studied by Howe and Primack (1975), Herrera and Jordano (1981), and Howe and Vande Kerchove (1981) are dispersed as far as the much smaller (ca. 1-3 mm) seeds of P. rivinoides, W.

solanacea, and W. coccoloboides. Large seeds are voided more rapidly by birds (often by regurgitation; Levey 1986, and personal observation), and the large fruit crops produced by trees encourage more sedentary behavior by frugivores (Pratt and Stiles, 1983). Thus, small seeds are probably dispersed farther, on the average, than large ones, especially when produced by plants with small fruit crops that do not encourage long or frequently repeated visits by individual frugivores.

Do the data suggest any tendency for non-random or "directed dispersal" (sensu Howe and Smallwood 1982) of seeds to gaps? Direct dispersal to gaps has been suggested by the common observations (e.g., Blake and Hoppes 1986, D. Levey, personal communication) that (1) herb- and shrub-layer fruit resources are often more concentrated within gaps than in surrounding forest understory, and that (2) mist net captures of frugivorous birds often reflect this concentration. At Monteverde, however, none of the bird species for which I have adequate data was captured most frequently in gaps (Table 1). In fact, the major understory frugivore at Monteverde, Myadestes melanops, was captured significantly less often in gaps than in forest understory. Furthermore, data from individual birds fitted with transmitters suggest no tendency for non-random gap-to-gap movement.

The lack of any preference for gaps in Myadestes, Phainoptila, and Semnornis reflects the fact that their fruit resources are not highly concentrated there. Individuals of these species forage from the lowest levels of the forest understory to subcanopy and even canopy levels (K. G. Murray, personal observation). In fact, most of the fecal specimens from captured individuals contained seeds of canopy and subcanopy trees and epiphytes. Although fruit resources within a few meters of the ground may be more concentrated in gaps at Monteverde as in other forests (Blake and Hoppes 1986, D. Levey, personal communication), fruits used by *Myadestes*, *Phainoptila*, and *Semnornis* are not concentrated in gaps if the entire vertical foraging ranges of birds are considered.

Distribution of "Safe Sites"

Although dispersal may result in decreased density-dependent mortality of seeds and seedlings near the parent plant, the advantage of dispersal for gap-dependent plants more likely results from two other factors: (1) an increased probability of encountering spatially and temporally unpredictable habitat patches (i.e., treefall gaps), and (2) reduced density-dependent mortality within those patches.

Tropical forests are often characterized as mosaics of mature-phase and gap-phase patches that differ in size, intensity of disturbance, and time elapsed since last disturbance (Richards 1952, Richards and Williamson 1975, Whitmore 1975, 1978, 1982, Oldeman 1978, Hartshorn 1978, 1980, Hladik 1982, Brokaw 1985). The Monteverde cloud forest also represents such a disturbance mosaic. Approximately 1.5% of the total land area at Monteverde is subjected to canopy disturbances each year, and the average density of new gaps (including even those as small as 1.6 m^2) over the landscape is approximately 17.5 per hectare per year. The 1.5% per year canopy disturbance rate reported here is similar to that reported for "elfin" forest along the continental divide at Monteverde (1.1%; Lawton and Putz, unpublished ms), as well as for other tropical forests (Leigh 1975, Hartshorn 1978, Brokaw 1982a, Foster and Brokaw 1982, Uhl 1982), and many temperate ones (Heinselman 1973, Abrell and Jackson 1977, Runkle 1982, Zackrisson 1977, Naka 1982, Platt et al. unpublished ms). Furthermore, the gap size distribution at Monteverde (Fig. 5) is similar to that determined for several other tropical and temperate forests (Runkle 1979, Brokaw 1982b, Lawton and Putz, unpublished ms). For seeds of gap-dependent plants, then, suitable patches for colonization are similarly rare in most forests.

Detailed analyses of the germination requirements of *P. rivinoides*, *Witheringia solanacea*, and *W. coccoloboides* show that the landscape is even more complex than just a mosaic of "safe sites" (*sensu* Harper 1977) surrounded by unsuitable habitat. For each gap in the forest, there is an associated probability of germination for seeds of gap-dependent plants, which depends upon its size and age (e.g., Figs. 2 and 3). Furthermore, the suitability of a given gap differs among the three species studied here, and probably for other species as well. For plants such as these, it is more useful to think of the forest not as discrete patches of suitable habitat embedded in a matrix of hostile environment, but rather as a mosaic of patches of different sizes and ages, each of which has an associated suitability for seeds of particular gap-dependent plants. At any point in time, the great majority of land area ($\geq$98.5% for these three species) consists of patches in which the probability of germination and establishment is negligible, and the remainder of the land area is occupied by patches of varying, but higher suitability.

Reproductive Consequences of Dispersal and Dormancy

Because the germination requirements of gap-dependent plants are complex, determining the reproductive consequences of seed shadows produced by birds is exceedingly difficult. Results presented here clearly demonstrate that seed dispersal increases both reproductive output and relative "fitness" of gap-dependent plants. However, the underlying cause of these increases has less to do with the number of seeds encountering suitable gaps than with the number of individual gaps they encounter. Assuming that gaps are formed randomly in space, any location has an equal probability of being within a gap. Consequently, the probability that a given seed will encounter a gap does not depend upon the distance it is dispersed. A major advantage of dispersal for gap-dependent plants is that it serves to spread seeds over a greater number of gaps, so that each germinating seed is faced with fewer potential competitors (i.e., siblings). Thus, even though seeds of these plants can germinate only in ephemeral habitat patches that occur unpredictably in space, one of the primary advantages of seed dispersal lies in avoiding density-dependent mortality within patches near the parent plant. This does not mean that avoidance of density-dependent mortality is the only advantage of dispersal in these plants, however. On average, widely dispersed seeds will encounter suitable germination sites after shorter periods of dormancy, and thus contribute more to the population gene pool, than those deposited closer to the parent plant. As a result, more extensive dispersal increases relative "fitness" (but not reproductive output) for reasons unrelated to density-dependent mortality. Results presented for these gap-dependent plants therefore support both the "escape" and "colonization" hypotheses proposed by Howe and Estabrook (1977).

The ability of seeds to remain dormant in the soil for long periods does not preclude the necessity for effective seed dispersal. Because undispersed dormant seeds could survive until the next canopy disturbance occurs on a particular site, it might be argued that dispersal is unimportant if seeds remain viable sufficiently long, and if mortality in the soil is low. Nevertheless, more effective dispersal mechanisms will always be favored; plants that disperse seeds always have higher reproductive success than those without dispersal, regardless of dormancy capability (Figs. 13 and 14).

Three factors account for this result. First, because the probability of germination in the gap of origin is negligible by the time a parent plant produces seeds (Fig. 3), the next germination opportunity for seeds deposited there will occur when the next disturbance occurs on that site. The 1.5% per year canopy disturbance rate at Monteverde suggests a "turnover rate" (i.e., the "mean time between successive creations of gap area at any one point in the forest"; Brokaw 1985) of 67 years. Thus, undispersed seeds of a gap-dependent plant should encounter new treefall gaps only once every 67 years, on the average. By dispersing its seeds, a plant greatly increases the number of suitable patches encountered by its seeds at any point in time (cf. Green 1983, Geritz et al. 1984). Second, because seeds germinating after a long period of dormancy contribute less to the population gene pool than those that germinate soon after dispersal, plant "fitness" is always increased by mechanisms (e.g., dispersal) that promote earlier encounter of suitable patches. Third, intense density-dependent mortality (due to intraspecific competition and/or predation) among seeds deposited very near the parent should always favor more effective dispersal, regardless of when seeds germinate. Thus, although enforced seed dormancy greatly increases reproductive success of gap-dependent plants, it can in no way be thought of as a "substitute" for effective dispersal.

Although none of the birds considered here is likely to transport seeds directly to gaps, the quality of dispersal service provided by different bird species to gap-dependent plants may vary considerably, as a function of the seed shadows they produce. The degree to which different seed shadows are selectively advantageous depends upon how we estimate relative plant fitness. On the one hand, the model described by equation 1 predicts that the number of seeds potentially germinating during the month dispersed (RO, assuming no seed dormancy) is quite similar following dispersal by Semnornis, Phainoptila, or Myadestes (Fig. 12). When reproduction from dormant seeds is also considered, however, differences between effects of dispersal by different birds on lifetime reproductive output are greatly accentuated (e.g., Figure 13). In fact, Fig. 13 shows that the number of offspring produced is a monotonically increasing linear function of dormancy, at least over most of the range of dormancy capability. This result suggests that (1) a given increment in the capacity for seed dormancy always has the same selective advantage, and (2) differences in the selective advantages of different seed shadows are greatly magnified by increasing seed dormancy capability. If seeds can remain dormant for just two years, for example, the increment to lifetime reproductive output resulting from dispersal by Semnornis is only 65-85% as great as that resulting from dispersal by Myadestes or Phainoptila, and these differences are further accentuated if seeds can remain dormant for even longer periods of time. Thus, even small increases in mean or extreme dispersal distances might result in substantial differences in lifetime reproductive success for plants that exhibit enforced seed dormancy.

In contrast, if we use r (equation 2) as an estimator of fitness, the effect of dormancy is less pronounced. Because seeds germinating after a long period of dormancy contribute less to plant fitness than those germinating sooner, r is greatly increased by the ability of seeds to remain dormant for a few years, but is increased only slightly by further increases in dormancy capability (Fig. 14). This result suggests that (1) seed dormancy beyond a few years may have no selective value, (2) differences among the fitness increments associated with different seed shadows are not as great as is suggested by comparison of the total numbers of offspring produced, and (3) these differences do not increase appreciably with increasing dormancy capability.

As used here, however, equation 2 also has important sources of bias. For example, the value of r is especially sensitive to the magnitudes of values for l_x and m_x. When values of m_x are large, estimates of r reach an asymptote quickly as x increases. When values of m_x are lower, but still retain the same proportional relationships to one another, values for r do not reach an asymptote until much higher values of x. This property of equation 2 is very important for its use as a fitness estimator here. Because the simulation model used to generate m_x values does not consider most sources of pre- or post-germination mortality, the m_x values estimated are artificially high. If we choose more realistic values for m_x while retaining the same proportional relationships between them (e.g., by multiplying each value by 0.001), r increases appreciably over much more of the range of values of x. In addition, differences among the increments in r associated with different seed shadows are larger, and become even larger as dormancy capability increases.

Because solutions for r in equation 2 are highly sensitive to the magnitude of values of m_x, and because I lack information on exact values, Figure 14 conservatively estimates the influence of both seed dormancy and different seed shadows on plant fitness. On the other hand, estimates of lifetime reproductive output derived from equation 1 (Fig. 13) present an inflated estimate of the influence of these factors on plant fitness. Thus, neither approach yields an unbiased estimator of fitness, and the real effects of dispersal and dormancy on plant fitness lie somewhere between the extremes presented here. Thus, (1) seed dormancy does increase plant fitness (to an unknown degree) over a wide range of dormancy capabilities, but especially over the short term. (2) Because seeds germinating soon after dispersal contribute more to plant fitness than those germinating later, dispersal by bird species whose seed shadows result in a greater probability of deposition in currently (or imminently) suitable sites confers a large fitness advantage on the parent. (3) Increasing dormancy capability magnifies (also to an unknown degree) differences between the fitness increments associated with different seed shadows, such that relatively minor differences between seed shadows may result in important differences in the increments to plant fitness associated with each.

Limitations of the Model

Results of the model runs for reproductive success presented in Figs. 12-15 should be interpreted with some caution. All values of reproductive success computed by the model are maximum possible values, for several reasons. First, my measures of the proportion of land area in gaps of different sizes probably overestimate the proportion of land area actually available for colonization. I measured germination success with respect to gap size at the approximate center of each gap, above any herb-layer vegetation that might obstruct sunlight. All other locations within gaps are subject to a greater degree of shading, both from trees bordering the gap and from existing vegetation within it. In addition, I conducted my experiments on exposed mineral soil, without an intact humus and leaf litter layer that may inhibit germination and seedling establishment of some plants (Putz 1983). Most of the soil surface in treefall gaps is covered by an intact litter layer; exposed mineral soil generally occurs only on the "mound" and "pit" created by uprooted trees. Second, the model assumes no mortality of dormant seeds other than that set by physiological limits on the maximum amount of time seeds can remain dormant but viable. In reality, many dormant seeds may be removed from the soil by predators and pathogens. Third, the model assumes that all dormant seeds are equally likely to germinate in response to a given canopy disturbance. However, seeds present in the soil for longer periods may be moved into successively lower soil horizons (by the actions of soil organisms such as earthworms), so that individual seeds become less and less likely to germinate in response to a given disturbance with increasing time in the seed bank. Fourth, the model assumes homogeneous dispersion of seeds within each distance interval, which minimizes seedling mortality due to interspecific competition. Actual seed shadows produced by birds are undoubtedly more heterogeneous, and mortality among seedlings in clumps should result in lower reproductive success than indicated by the model presented here.

Undoubtedly, most of the model's assumptions are often violated in nature, so that actual reproductive output and relative fitness are much lower than the estimates presented here. Nevertheless, the estimates are useful for comparing the consequences of different seed shadows, germination requirements, seed dormancy capabilities, and fruiting phenologies for potential reproductive success of individual plants.

Seasonal Constraints on Reproductive Success

In the sections above, I have discussed how plant reproductive success is influenced by interacting characteristics of the dispersal service rendered by birds, the landscape-level disturbance regime, and the physiological and life historical attributes of the plants themselves. Another plant characteristic that may influence reproductive success is the timing of seed dispersal in relation to seasonal patterns of patch formation and disperser abundance. Results presented in Fig. 15 suggest that even short-term seed dormancy effectively uncouples dispersal and germination; estimated reproductive output varies only slightly among plants that ripen fruits at widely different times of year. Thus, plant reproductive success should not suffer appreciably if fruit ripening does not coincide closely with peak periods of gap formation, even though gap formation is highly seasonal, and although gaps remain open for colonization for only short periods of time.

On the other hand, fruit removal rates, hence possibly plant reproductive success, do vary seasonally as a positive function of the abundance of *Myadestes melanops*, the primary dispersal agent. That many species of tropical frugivores undertake seasonal migrations is well known (e.g., Fogden 1972; Crome 1975a,b; Karr et al. 1982, Wheelwright 1983), and these are generally correlated with depressed fruit resource levels in some seasons. For plant species that are highly dependent upon such seasonal migrants for dispersal, seasonal variation in disperser abundance may be an important constraint on seasonal fruiting patterns. The relationship between *Myadestes* abundance and fruit removal rates at Monteverde may explain, in part, the observed seasonality of fruit ripening in *P. rivinoides*, *W. solanacea* and *W. coccoloboides*. The positive relationship between *Myadestes* abundance and fruit removal rates reported above is not a strong one, however; removal rates are only slightly depressed during the months when *Myadestes* is entirely absent from the Monteverde area. The highly seasonal fruiting patterns in these plants thus beg an additional adaptive explanation.

Such patterns might also result from (1) phylogenetic constraints on phenological plasticity, (2) seasonal constraints on seed or seedling survival, or (3) competition with other plant species for dispersal (e.g., Wheelwright 1985b). First, fruiting phenology in these plants may not be a very plastic character. All three species are both altitudinally and geographically widespread throughout Central America, and even northern South America. Populations in different locations face different selection pressures on fruiting phenology, because seasonal patterns of both gap formation and frugivore availiability vary among sites. The phenological patterns observed at Monteverde may actually have evolved in other populations, under different selection pressures.

Second, strong seasonal variation in seedling survival might impose more significant constraints on fruiting phenology than seasonal variation in fruit removal or seed germination. Garwood (1983) studied temporal patterns of seed germination in a seasonal rainforest on Barro Colorado Island, Panama. She found that germination in most gap-dependent tree species occurred early in the wet season, and that older seedlings were better able to survive through the first dry season than younger seedlings. She concluded that seedlings of gap-dependent species that emerge during the early wet season would have higher survival through their first dry season, especially at sites where the density of competing seedlings is high. The same may be true at Monteverde. Although forest soil at Monteverde does not dry out during the "dry season", the surface layer of soil in large gaps does, and seedlings in gaps commonly die from water stress during the height of the dry season (Murray, unpubl. data). Seeds that germinate during the early dry season may die before the rains begin. Thus, even though the early dry season (January - March) is quite favorable with respect to the availability of suitable colonization sites (Fig. 7) and *Myadestes* abundance (Fig. 1), it may actually be the worst season to ripen fruits. The timing of fruit ripening may be of little consequence for survival of most seeds, which germinate only after some period of dormancy. For those dispersed by chance to currently suitable sites (where they germinate immediately), however, dispersal during the early wet season (beginning in mid- to late May) may result in much higher survival.

Conclusions

The wide variation in dispersal quality provided by different birds at Monteverde suggests the potential for close coevolution between the three plant species and those dispersers providing high quality dispersal service. That potential appears even stronger when we also consider another important aspect of the plant-frugivore interaction, that of dispersal quantity. At Monteverde, *Myadestes* is by far the predominant understory frugivore: over 50% of all understory frugivores captured during an intensive (ca. 4100 total mist-net hours) study were of this species (Murray, unpubl. data). *Phainoptila* and *Semnornis* comprised only 2.0% and 1.2% of the total, respectively. Furthermore, of all *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* seeds recovered in fecal samples from mist-netted birds, the majority were from *Myadestes*. Thus, although *Phainoptila* and *Myadestes* may provide similar dispersal quality for some plants (e.g., *P. rivinoides*), *Myadestes* probably disperses a far greater quantity of seeds, and therefore is probably responsible for a greater proportion of successful reproduction in all three plant species at Monteverde.

Does the fact that only three bird species are responsible for most dispersal of *P. rivinoides*, *W. solanacea* and *W. coccoloboides* seeds at Monteverde indicate a specialized dispersal system? Furthermore, does the overwhelming importance of *Myadestes* indicate the potential for a tight coevolutionary relationship? The answer to both of these questions is probably no. All three plant species are geographically and altitudinally widespread in Central and South America (Standley 1937, Raeder 1961, D'Arcy 1973). In contrast, *Myadestes melanops*, *Phainoptila melanoxantha*, and *Semnornis frantzii* are limited to Costa

Rica and western Panama, and are generally restricted to middle and high elevations (Ridgely 1976). These plants, like many others (e.g., see Howe and Primack 1975, Howe 1977), are thus confronted by different disperser assemblages in different parts of their ranges. In fact, disperser assemblages may change markedly over very short distances. For example, although *Myadestes* is the major disperser of *W. solanacea* at elevations above 1500 m, at lower elevations on the Pacific slope of the Cordillera de Tilarán, the major dispersers may be Long-tailed Manakins (*Chiroxiphia linearis*, Wheelwright et al. 1984). During the breeding season, male manakins spend most of their time (and deposit most seeds) at their display perches. Dispersal by male manakins may thus have very different consequences for individual *W. solanacea* from dispersal by *Myadestes* just a few kilometers away. And although adaptation for dispersal by particular bird species is conceivable within single plant populations, gene flow between closely adjacent plant populations may swamp any such local adaptation.

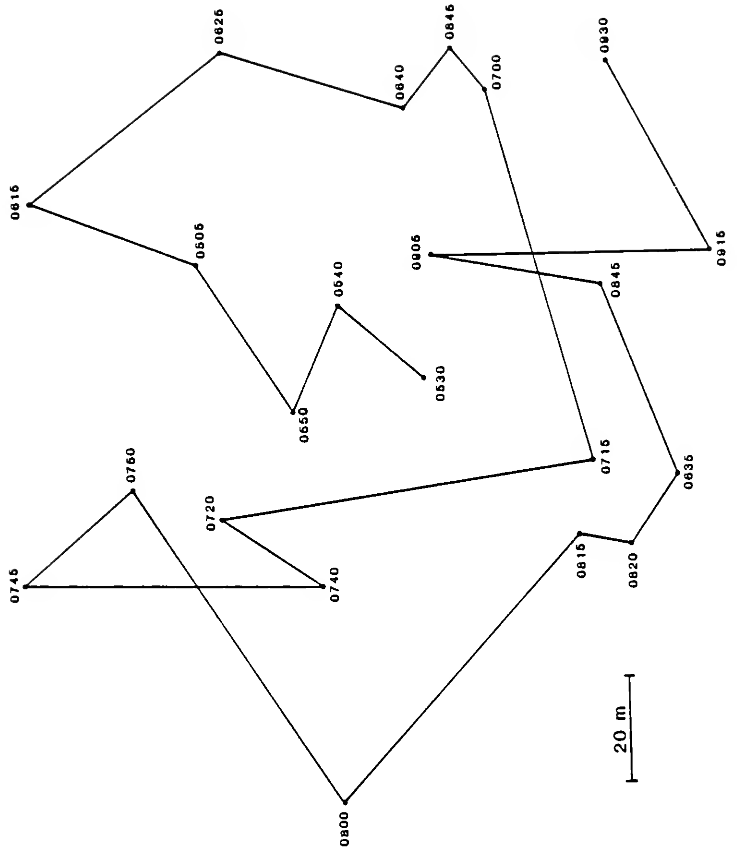
Furthermore, the relationships between *P. rivinoides*, *W. solanacea*, *W. coccoloboides* and their major dispersal agents at Monteverde are exceedingly asymmetrical. Although virtually all dispersal of these plants in the Monteverde Cloud Forest Preserve is performed by *Myadestes*, *Phainoptila*, and *Semnornis*, fruits of the three plant species comprise only a small proportion of the diets of the three bird species. Thus it is unlikely that any specialization of these birds for feeding on fruits of *P. rivinoides*, *W. solanacea*, and *W. coccoloboides* would be selectively advantageous. Such "diffuse" (*sensu* Janzen 1980) and asymmetrical ecological relationships between plants and their animal seed dispersers likely preclude tight coevolution between them (see also Wheelwright and Orians 1982, Janzen 1983b, Howe 1984).

APPENDIX

ESTIMATION OF "SEED SHADOWS" FROM DATA ON SEED PASSAGE RATES AND BIRD MOVEMENT PATTERNS: A HYPOTHETICAL EXAMPLE

The distribution of seed dispersal distances away from a particular plant was estimated from data on seed retention times and bird movement patterns. The data in Figure A-1 allow relatively precise measurement of the distances between all mapped locations, each of which is treated as a potential source plant, and the time spent at each. Figure A-2 shows, for each location, the bird's distance away from that location for each minute following the midpoint of the time interval spent there. Such data from many initial locations (source plants) are then combined to produce a probability matrix of distance versus time. The elements of this matrix (shown graphically in Figure A-3) represent the probabilities that the bird will be at a particular distance from the source plant at a particular time after the midpoint of the interval spent there. Multiplying this matrix by the probability distribution of seed passage times (Fig. A-4), and then summing the results for each distance interval over all 12 time intervals, yields a probability distribution of seed movement distances, or the probable "seed shadow" produced by one individual around one plant (Fig. A-5). Data from many individuals are combined (weighting the seed shadow computed for each individual equally) to estimate the overall seed shadow produced by particular frugivore species around individual plants.

Figure A-1. Foraging movements of a single frugivorous bird for a period of four hours. Times of arrival are shown for each location. See text for methods.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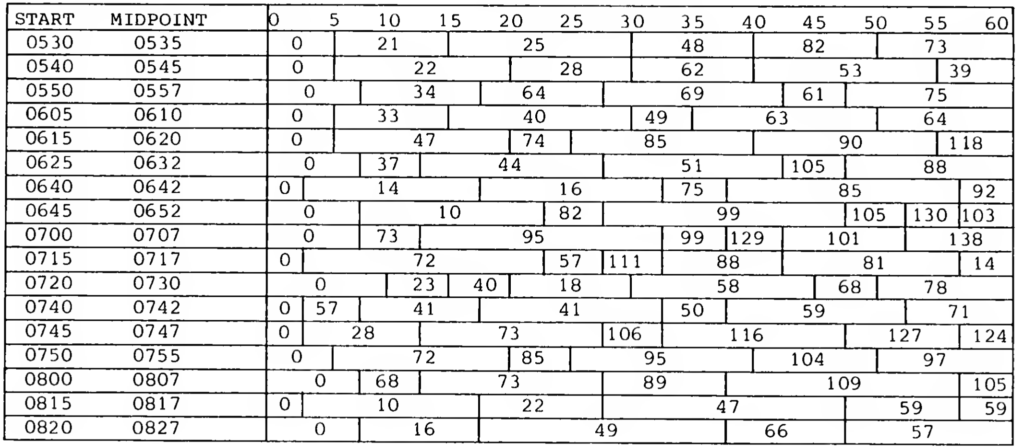
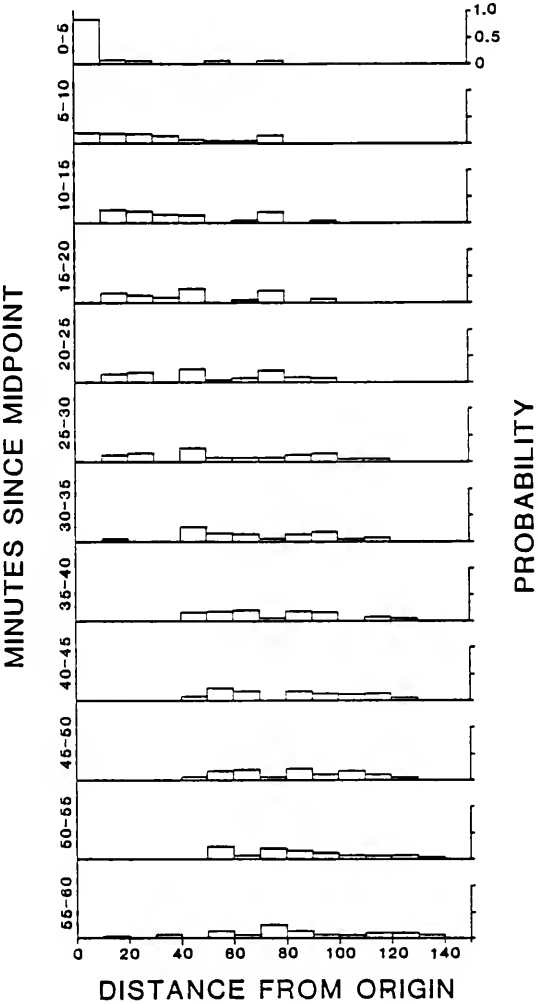
0815
0820
0745
0740
20 m
0800



TIME START	TIME MIDPOINT	MINUTES SINCE MIDPOINT (0 5 10 15 20 25 30 35 40 45 50 55 60)
0530	0535	0 21 25 48 82 73
0540	0545	0 22 28 62 53 39
0550	0557	0 34 64 69 61 75
0605	0610	0 33 40 49 63 64
0615	0620	0 47 74 85 90 118
0625	0632	0 37 44 51 105 88
0640	0642	0 14 16 75 85 92
0645	0652	0 10 82 99 105 130 103
0700	0707	0 73 95 99 129 101 138
0715	0717	0 72 57 111 88 81 14
0720	0730	0 23 40 18 58 68 78
0740	0742	0 57 41 41 50 59 71
0745	0747	0 28 73 106 116 127 124
0750	0755	0 72 85 95 104 97
0800	0807	0 68 73 89 109 105
0815	0817	0 10 22 47 59 59
0820	0827	0 16 49 66 57

Figure A-2. Bird distance from seed source plant vs. time. For each sequence of foraging movements beginning with a visit to a fruiting plant, numbers given indicate the bird's distance (in meters) from that plant during the following hour. Each sequence begins (time 0) at the midpoint of the time interval spent in the source plant.

Figure A-3. Probability distributions of bird movement vs. distance and time. For each successive 5 minute time interval following the midpoint of the interval spent at the source plant (see Fig. A-2), the figure shows the probability that a bird will be in each of 14 distance intervals (10 m each) away from the source plant.


MINUTES SINCE MIDPOINT
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
50-55
55-60
PROBABILITY
1.0
0.5
0
0
20
40
60
80
100
120
140
DISTANCE FROM ORIGIN

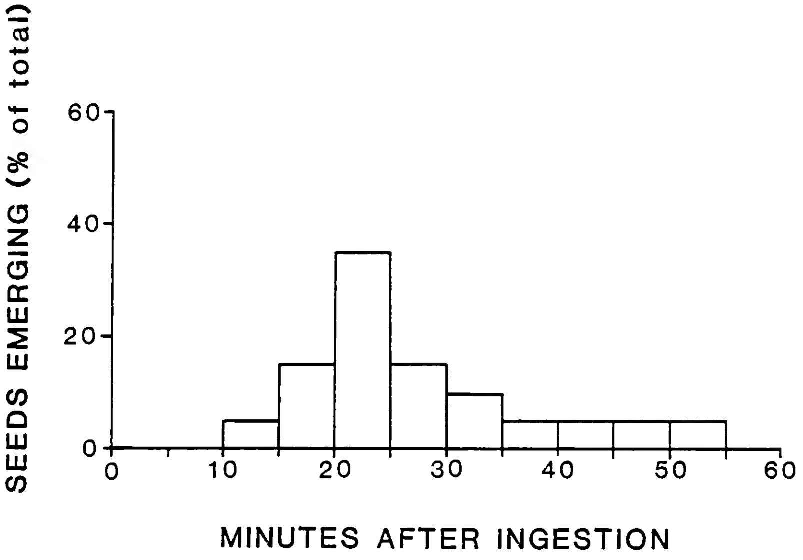
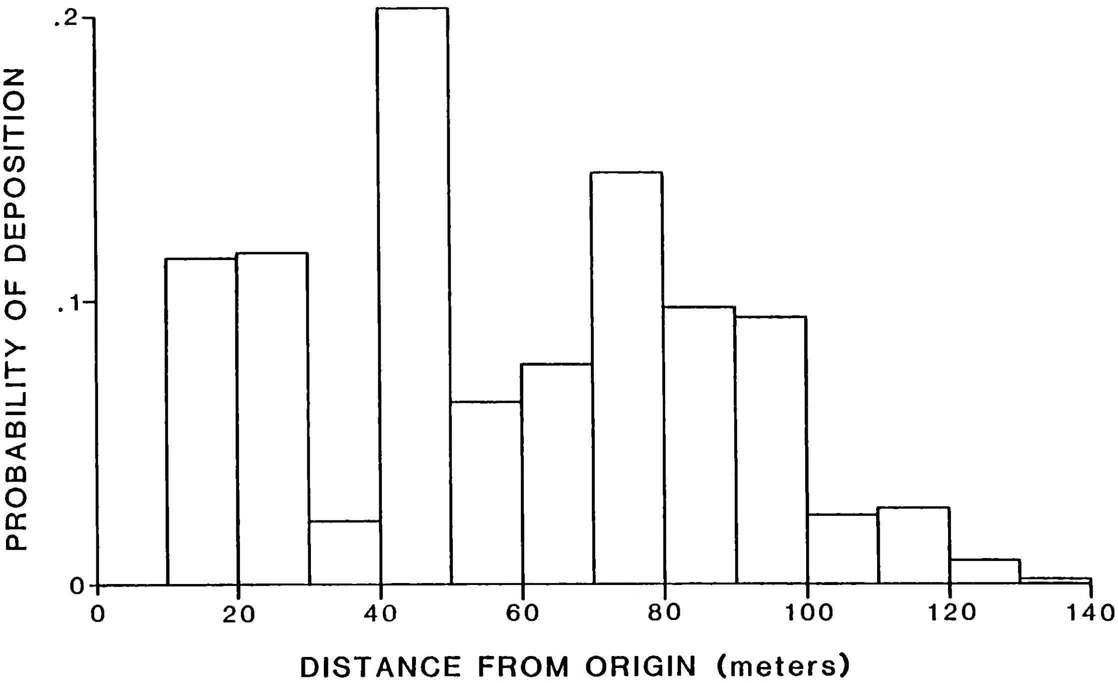


Figure A-4. Retention time distribution for seeds of the source plant species in a particular bird species' gut. See text for methods.

Figure A-5. Probability distribution of dispersal distances, or the probable "seed shadow" produced as a result of the 17 foraging movement sequences in Figure A-2. For each 5 minute time interval, the probability of seed emergence (Fig. A-4) is multiplied by the probability distributions of bird movement in Fig. A-3. For each distance interval, these products are then summed over all time intervals to yield the seed shadow.


PROBABILITY OF DEPOSITION
.2
.1
0
0
20
40
60
80
100
120
140
DISTANCE FROM ORIGIN (meters)

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BIOGRAPHICAL SKETCH

Kelvin Gregory Murray was born to Max W. and Lorene M. Murray on August 8, 1954. Those who gleefully poke fun at his Southern California manner, dress, and habits of personal hygiene will be distressed to learn that he is actually a native of Chicago, Illinois. Despite brief forays into eastern religions, motorcycle racing, and particle physics, Greg knew that he wanted to be a biologist at least by the 8th grade, a fact much-lamented by the science faculties at his junior high and high schools. Following graduation from high school, Greg studied biology at California State University, Northridge. There, he received his B.S. in 1977, with an emphasis on marine invertebrate ecology. For the next two years, he studied seabird and deermouse ecology on the Southern California Channel Islands and on the Pribilof Islands, in the Bering Sea. He received the M.S. degree in 1980 for his studies of deermouse predation on Xantus' Murrelet eggs.

In 1979, Greg married his childhood sweetheart, Kathy Winnett, whom he had met three years previously in a class on population and community ecology. Later that year, they made their way to Gainesville, to further their graduate careers at the University of Florida. Following two years of course work on campus, they moved to Costa Rica for 27 months of intense fieldwork. Upon their return, they initiated a biological project involving a lifetime of intense homework. Their son, Dylan, was born on June 6, 1984.

Greg's interests are diverse. In addition to his professional pursuits, he dabbles in electronics, photography, physical fitness, and LEGO^{tm} building blocks. He enjoys almost all types of music and theater, and he is an avid devotee of the Firesign Theater. He is not now, nor has he ever been, a strict adaptationist.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Peter Feinsinger, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

H. Jane Brockmann
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas C. Emmel

Thomas C. Emmel
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Walter Judd
Associate Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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