

AVIAN SEED DISPERSAL OF NEOTROPICAL GAP-DEPENDENT PLANTS

By

KELVIN GREGORY MURRAY

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL  
OF THE UNIVERSITY OF FLORIDA IN  
PARTIAL FULFILLMENT OF THE REQUIREMENTS  
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1986

#### ACKNOWLEDGMENTS

I am greatly indebted to many individuals for support and assistance in completing this project. Kathy Winnett-Murray was intimately involved in every phase of the project, providing assistance in the field work as well as valuable advice on planning, data analysis, and writing. That she was able to do all that, complete her own dissertation work, and still be a wonderful wife in the face of both our frustrations over the difficulties of field research, is truly amazing. Peter Feinsinger likewise provided advice, assistance, and humane editorial criticism from the earliest planning stages of the work. Without several of his well-timed pep-talks, the study would surely have suffered greatly and might never have been completed at all. I cannot overestimate his positive influence on this work, or on my graduate career in general. For this and for his friendship, I will always be grateful.

I benefitted greatly from discussions with the other members of my supervisory committee, H. Jane Brockmann, Thomas Emmel, Walter Judd, and Francis Putz, who also provided valuable editorial advice on earlier drafts of the dissertation. Discussions with Nicholas Brokaw, Carmine Lanciani, Robert Lawton, Douglas Levey, Timothy O'Brien, Carlos Martinez del Rio, and Harry Tiebout III were also very helpful.

My colleagues at the University of Florida, and especially the other biologists who resided concurrently at Monteverde, were also invaluable. Willow Zuchowski-Pounds, Bill Busby, Rita Schuster, and Sarah Sargent

provided assistance with field work. Jennifer Shopland kindly shared mist-netting and feeding observation data on frugivores. Advice on field techniques and data analysis were provided by these individuals as well as by Jim Beach, Martha Crump, Eric Dinerstein, Sharon Kinsman, Yan Linhart, David McDonald, Alan Pounds, Francis Putz, and Nat Wheelwright. I am especially grateful to all of these Monteverde biologists, and to members of the Monteverde community in general, for making my 27-month tenure there one of the most enjoyable periods of my life.

Wolf Guindon, Gary Hartshorn, Joseph Tosi, Jr., Manuel Ramirez, and Giovanni Bello kindly facilitated my use of the Monteverde Cloud Forest Reserve. Logistical support in Costa Rica was provided by personnel of the Organization for Tropical Studies, especially Roxanna Diaz. Financial assistance was provided by the Jessie Smith Noyes Foundation (administered by the Organization for Tropical Studies), the University of Florida Department of Zoology, a Sigma Xi grant-in-aid, and NSF grants DEB 80-11008 and 80-11023 to Peter Feinsinger and Yan Linhart, respectively.

Finally, I thank my family. My parents, Max W. Murray and Lorene M. Murray, and my sister, Gayle Fitchner, provided understanding and unwaivering encouragement throughout my educational career. My wife, Kathy, and my son, Dylan Winnett Murray, have taught me what is truly important, and help me to keep the various aspects of my life in their proper perspective.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS.....	ii
ABSTRACT.....	v
INTRODUCTION.....	1
STUDY AREA.....	5
METHODS.....	7
Crop Size, Fruiting Phenology, and Fruit Removal Rates.....	7
Seed Germination Experiments.....	8
Seed Dormancy Experiments.....	10
Gap Dynamics of the Monteverde Cloud Forest.....	11
Mist Netting and Analysis of Fecal Specimens.....	12
Fruit Handling, Seed Treatment, and Seed Passage Rates.....	13
Movement Patterns of Frugivores.....	14
RESULTS.....	16
Natural History of the Plants.....	16
Fruit Consumers.....	17
Fruit Handling and Seed Treatment in the Gut.....	23
Spatial and Temporal Distribution of Suitable Colonization Sites.....	27
Seed Shadows Produced by Birds.....	41
Mediation of Plant Reproductive Success by Birds.....	59
DISCUSSION.....	80
Effects of Fruit Handling and Gut Treatment.....	80
Effects of Dispersal.....	83
Limitations of the Model.....	92
Seasonal Constraints on Reproductive Success.....	94
Conclusions.....	97
APPENDIX ESTIMATION OF "SEED SHADOWS" FROM DATA ON SEED PASSAGE RATES AND BIRD MOVEMENT PATTERNS: A HYPOTHETICAL EXAMPLE.....	100
LITERATURE CITED.....	109
BIOGRAPHICAL SKETCH.....	119

Abstract of Dissertation Presented to the Graduate School  
of the University of Florida in Partial Fulfillment of the  
Requirements for the Degree of Doctor of Philosophy

AVIAN SEED DISPERSAL OF NEOTROPICAL GAP-DEPENDENT PLANTS

By

Kelvin Gregory Murray

December 1986

Chairman: Peter Feinsinger  
Major Department: Zoology

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 (Ptilonidae), 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<sup>2</sup> or as old as 6 months, whereas P. rivinoides germinates well only in gaps > 70 m<sup>2</sup> 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°18'N, 84°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<sup>2</sup>) 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<sup>2</sup>) 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<sup>tm</sup>. 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<sup>2</sup> 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 ( $\bar{x}=9.4$ ,  $n=20$ ) 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 ( $\bar{x}$ =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 ( $\bar{x}$ =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 ophthalmicus 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.

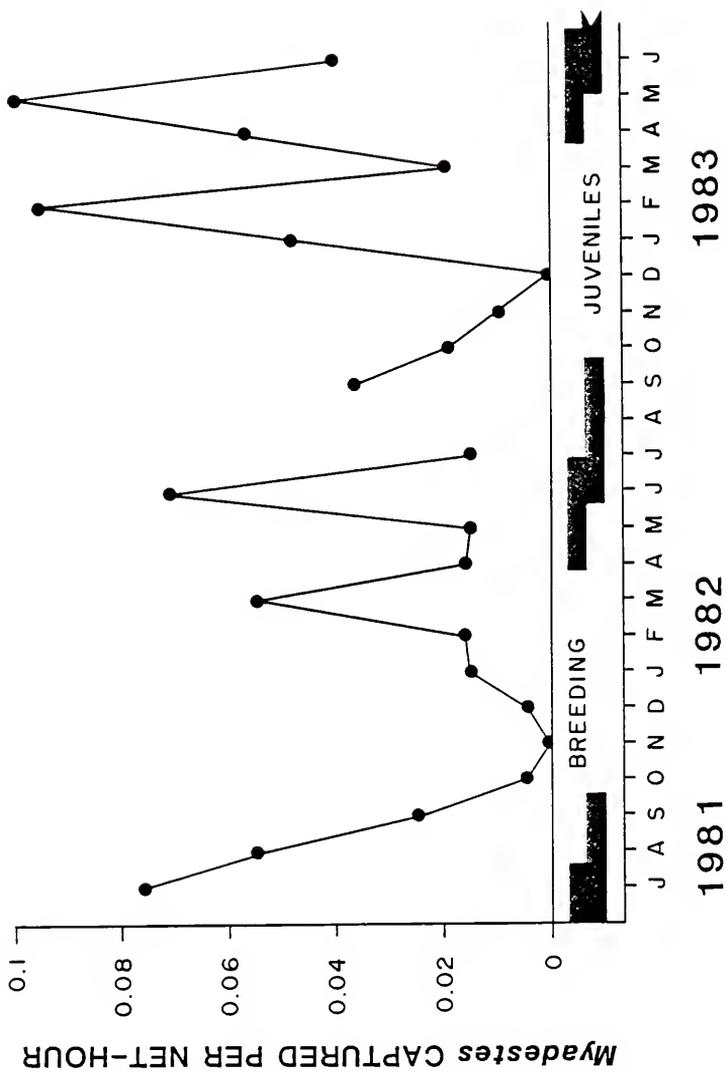
Capture rates for Myadestes were highly variable over time, however (Fig. 1). While usually very common in the reserve from February through August, they were all but absent from late October through early January. The seasonal decline in capture rate was due to emigration of both adults and young following 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" <sup>a</sup>
<u>Myadestes melanops</u>	66	30	33
<u>Phainoptila melanoxantha</u>	1	0	4
<u>Semnornis frantzii</u>	0	0	3
<u>Chlorospingus ophthalmicus</u>	10	9	5
<u>Tangara dowii</u>	0	0	1
<u>Pselliophorus tibialis</u>	1	0	2

<sup>a</sup> Capture data from these unusually large (1155-2442 m<sup>2</sup>) 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.



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 ophthalmicus and Tangara dowii, and the finch Pseliophorus 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 Pseliophorus, 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 Pseliophorus. 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. ophthalmicus (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 <sup>a</sup>	Plant species <sup>b</sup>	seed diameter (mm)	fruits eaten	seeds dropped	seeds ingested	voided intact <sup>c</sup>
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	-

<sup>a</sup> M.m. = Myadestes melanops, P.m. = Phainoptila melanoxantha, S.f. = Semnornis frantzii, C.o. = Chlorospingus ophthalmicus, T.d. = Tangara dowii, P.t. = Pselliophorus tibialis

<sup>b</sup> P.r. = Phytolacca rivinoides, W.s. = Witheringia solanacea, W.c. = Witheringia coccoloboides

<sup>c</sup> Of seeds ingested

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

Bird species <sup>a</sup>	Plant species <sup>b</sup>	percent germination (n)		days to 95% germination <sup>c</sup>	
		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

<sup>a</sup> M.m. = Myadestes melanops, P.m. = Phainoptila melanoxantha,  
S.f. = Semnornis frantzii, C.o. = Chlorospingus ophthalmicus,  
T.d. = Tangara dowii, P.t. = Pselliophorus tibialis

<sup>b</sup> P.r. = Phytolacca rivinoides, W.s. = Witheringia solanacea,  
W.c. = Witheringia coccoloboides

<sup>c</sup> Of those that germinated

<sup>d</sup> 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 ( $F_g=1.550$  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 ( $F_g=0.07$  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 ( $F_g=12.82$  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).

	<u>gap</u>	<u>forest</u>	<u>p</u>
	<u>after 60 days</u>		
<u>Phytolacca rivinoides</u>	89	0	<.001
<u>Witheringia solanacea</u>	86	14	<.001
<u>Witheringia coccoloboides</u>	86	2	<.001
	<u>after 410 days</u>		
<u>Phytolacca rivinoides</u>	89	0	<.001
<u>Witheringia solanacea</u>	86	61	<.001
<u>Witheringia coccoloboides</u>	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  $\ln(\text{gap area} + 1)$ . 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.

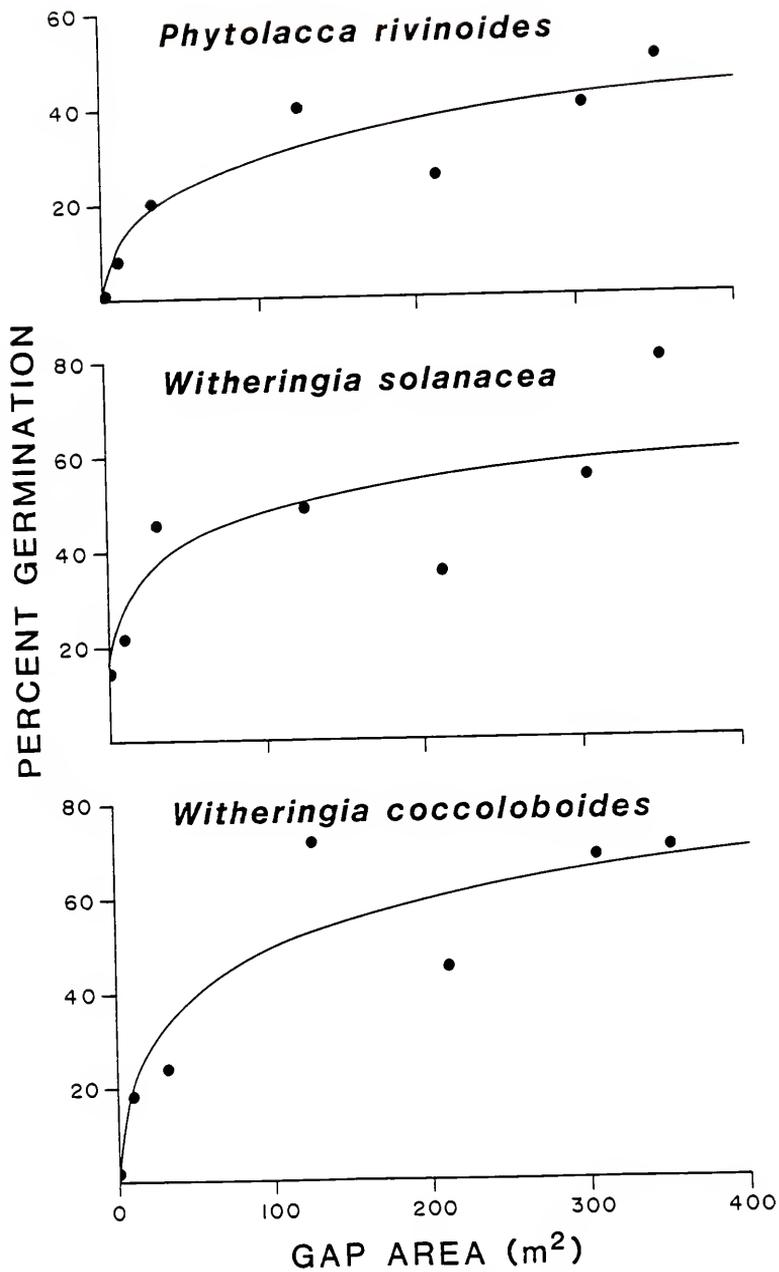
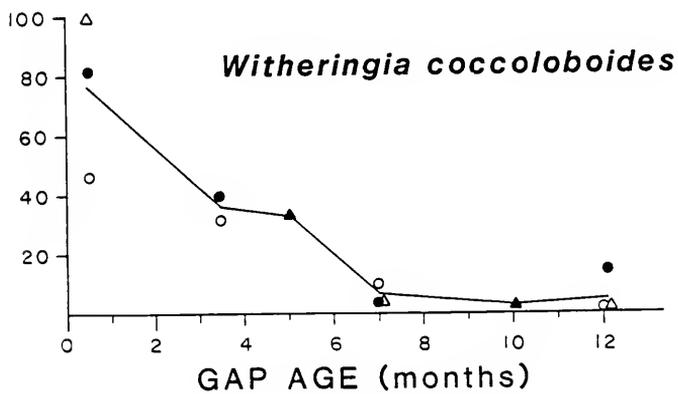
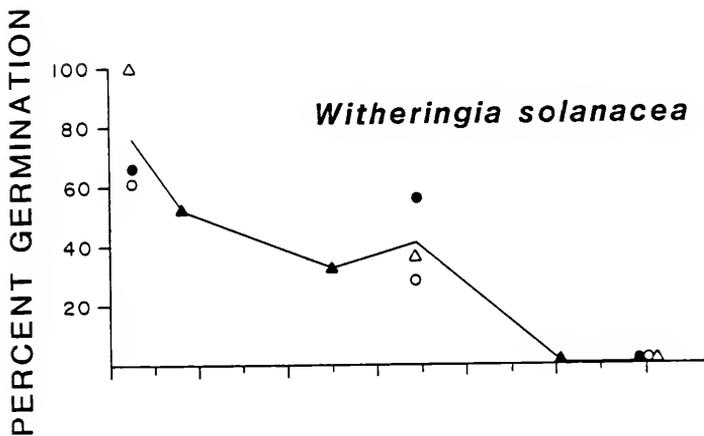
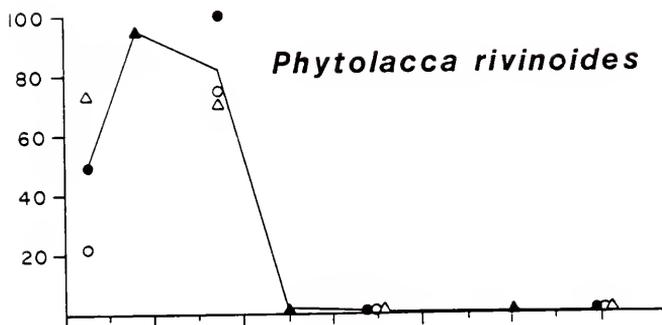


Figure 3. Germination success vs. gap age. Results from germination experiments in 4 gaps as they aged naturally (see text). Missing data for W. solanacea at 3.5 months and for W. coccoloboides at 1.5 and 3.5 months are due to a lack of sufficient seeds for those experiments. Different symbols indicate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



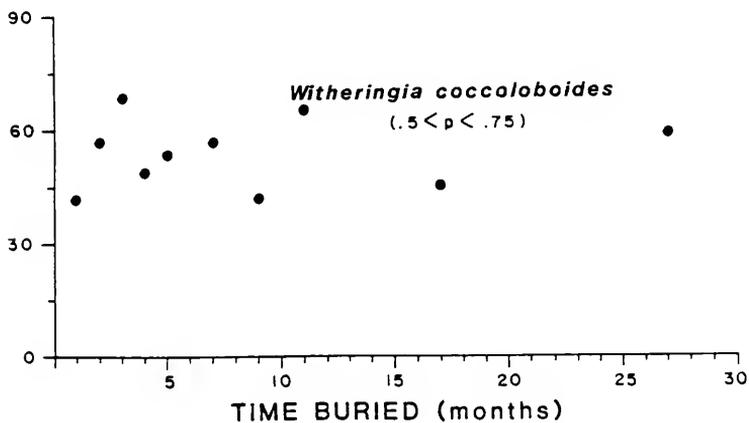
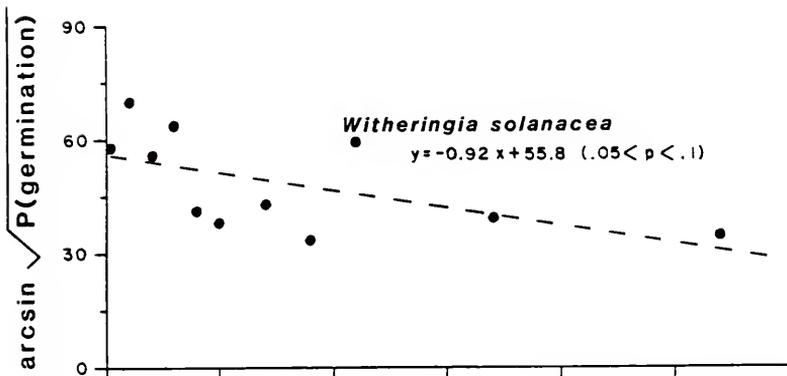
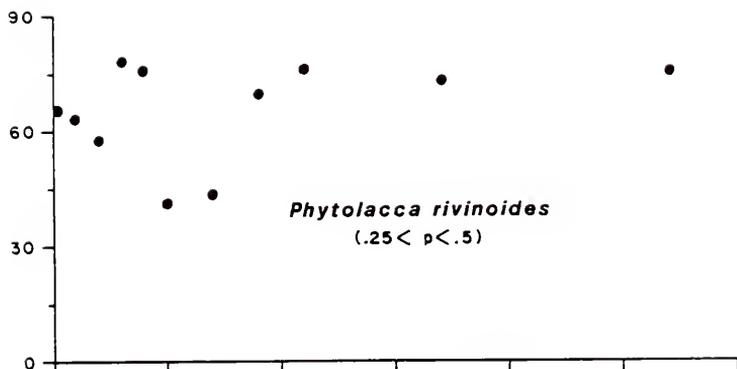
Following the initial increase in P. rivinoides, germination success decreased with increasing gap age much more rapidly than in either species of Witheringia. In fact, germination success in P. rivinoides was negligible by 7 months after gap formation, whereas some W. coccoloboides seeds germinated 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.



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  $10 \text{ m}^2$  were formed by one or more branches falling from the canopy, although entire trees occasionally formed gaps as small as  $5 \text{ m}^2$ .

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

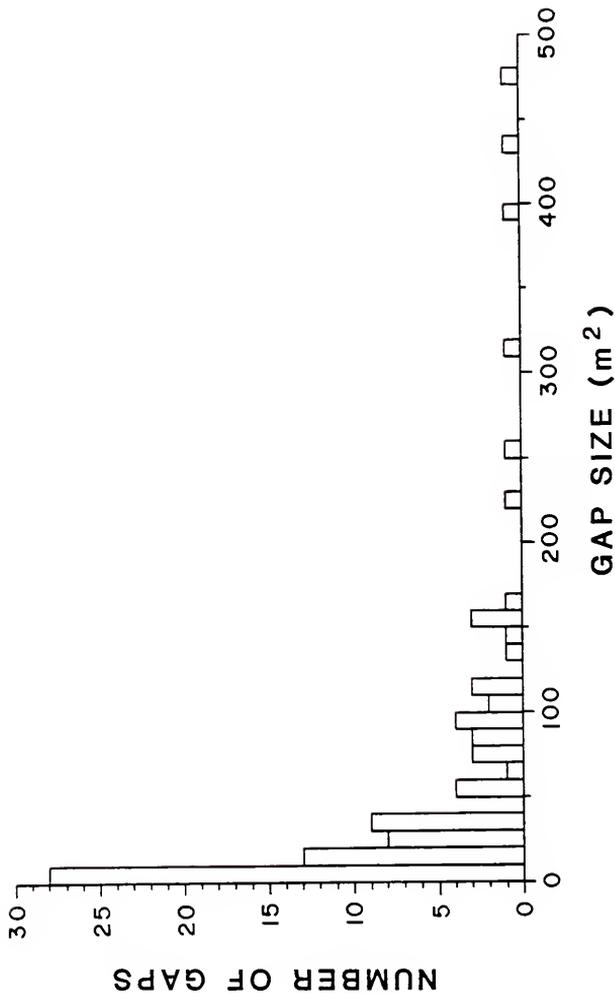


Figure 5. Size distribution of 90 canopy gaps formed over a 2-year period from ca. March 1982 - March 1984.

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  $> 400 \text{ m}^2$ . 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  $100 \text{ m}^2$  (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  $10 \text{ m}^2$  (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<sup>2</sup> 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.

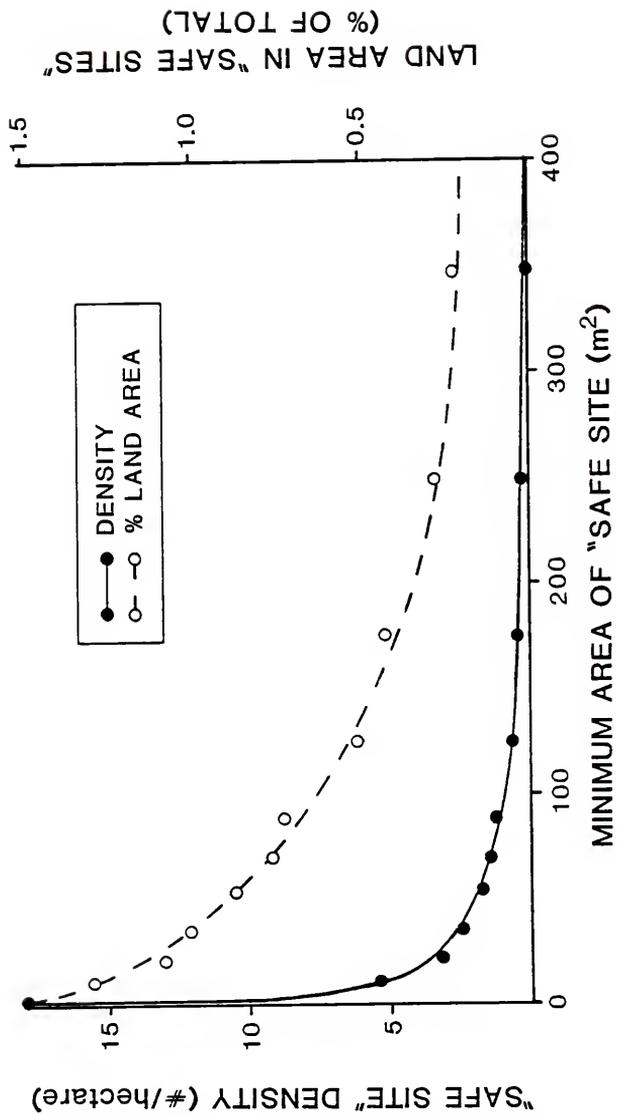
Although these analyses are useful for gaining a qualitative impression of the relationship between germination requirements and the availability of suitable habitat patches over the landscape, data presented in Figures 6 and 7 clearly show that applying the concept of "safe site" to treefall gaps oversimplifies 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.



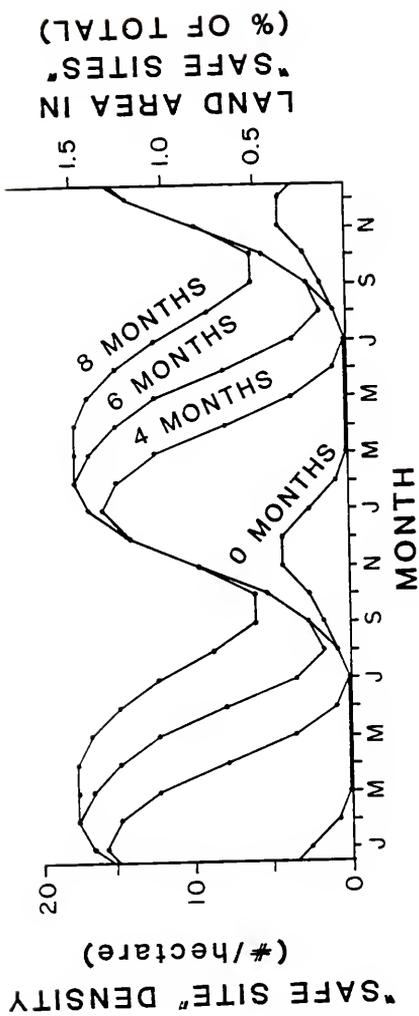


Figure 7. Density and areal coverage of "safe sites" as a function of time of year. Lines labelled 0, 4, 6, and 8 months show the density and coverage of gaps 0, < 4, < 6, and < 8 months old.

(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

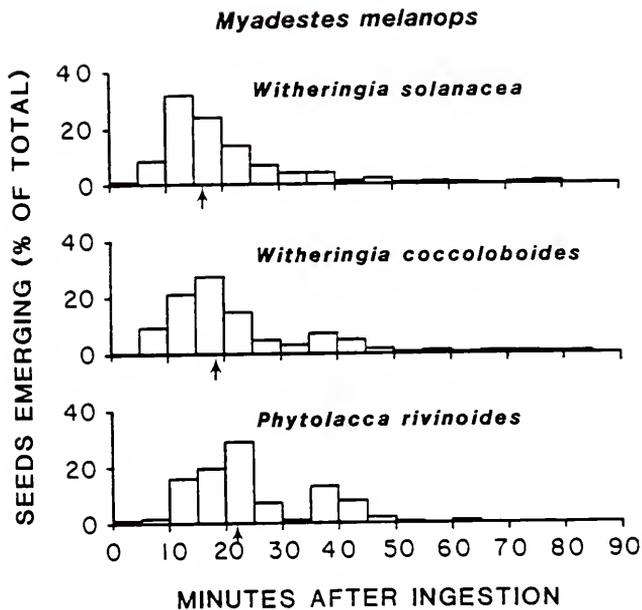


Figure 8. Seed passage rates for the three plant species in *Myadestes melanops*, *Phainoptila melanoxantha*, and *Semnornis frantzii*. Arrows indicate median passage times.

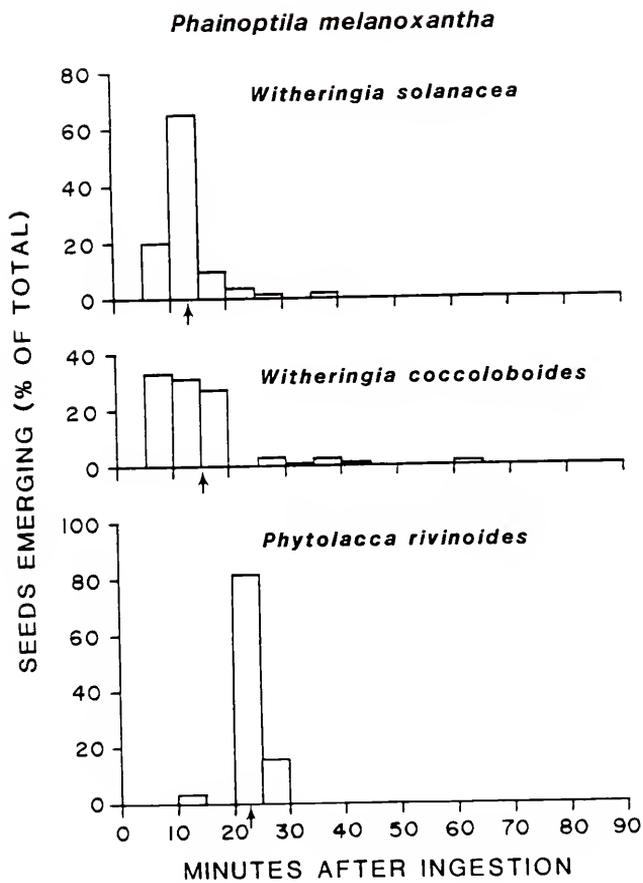


Figure 8 -- continued

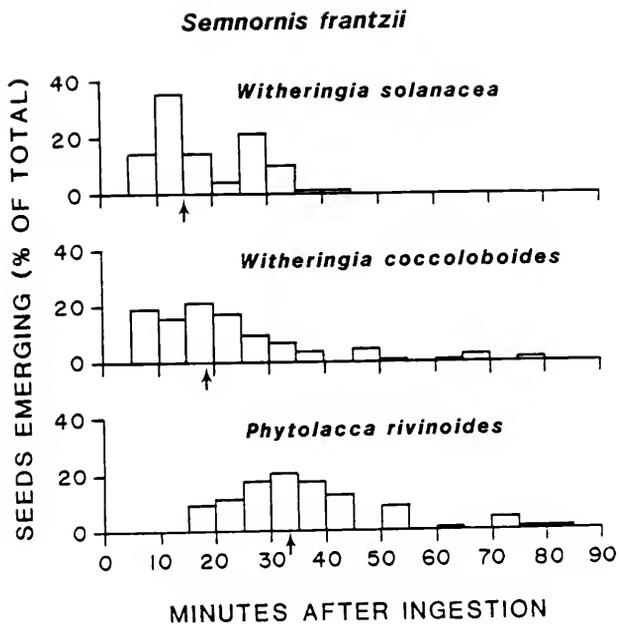


Figure 8 -- continued

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.	<u>plant species</u>	<u>comparisons</u>			
	<u>Phytolacca rivinoides</u>	Sf	> **	Mm	= Pm
	<u>Witheringia solanacea</u>	Sf	=	Mm	> ** Pm
	<u>Witheringia coccoloboides</u>	Sf	=	Mm	> ** Pm

B.	<u>bird species</u>	<u>comparisons</u>			
	<u>Phainoptila melanoxantha</u>	Pr	> **	Wc	> ** Ws
	<u>Myadestes melanops</u>	Pr	> **	Wc	> ** Ws
	<u>Semnornis frantzii</u>	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 preferential 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 ( $\chi^2 = 12.942$ ,  $p < .001$ ; 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		individual movements	recorded movements	time interval (min)		movement distance (meters)
bird species	df			between	within	
<u>Myadestes melanops</u>	KN/rt	258	9.1 (4.94)		106.9 (90.67)	
	KB/lr	21	7.2 (4.58)		59.7 (64.29)	
	BO/rt	158	10.3 (6.90)		51.8 (37.18)	
	OG/lr	178	7.7 (7.47)		16.4 (17.16)	
<u>Phainoptila melanoxantha</u>	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)	
<u>Semnornis frantzii</u>		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

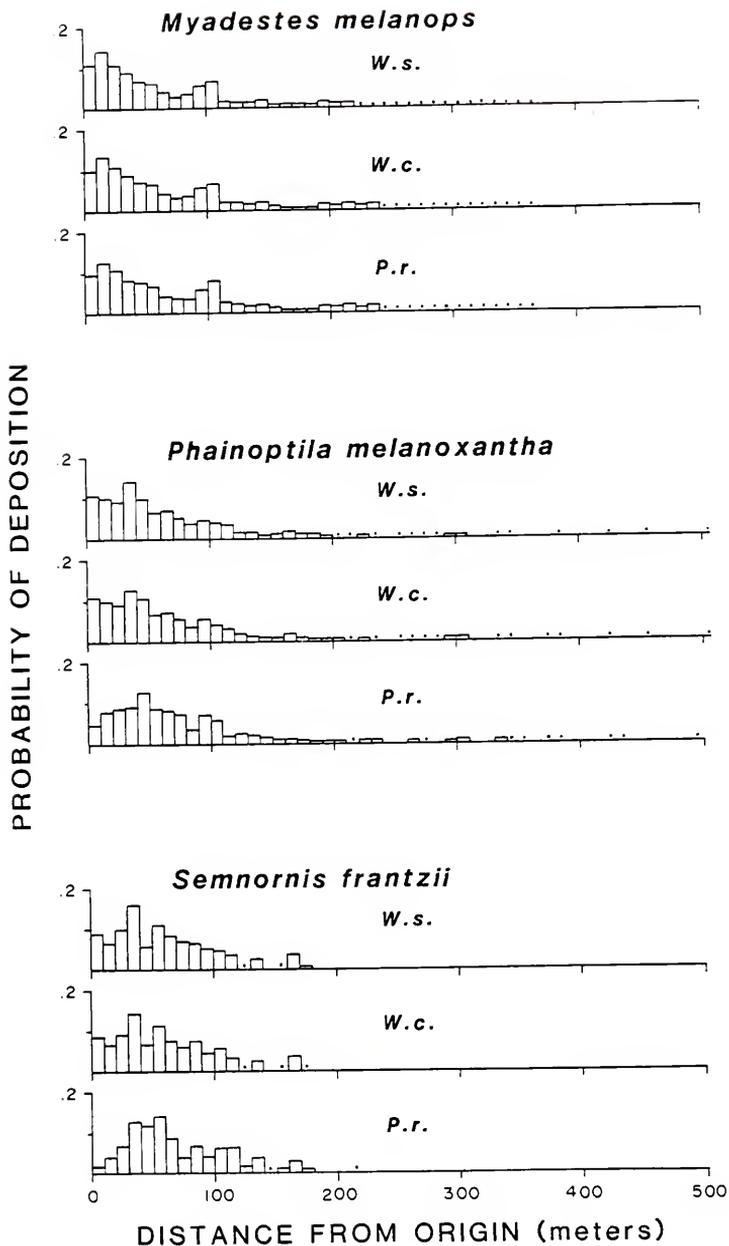
source	df	SS	MS	F
among species	1	7080	7080	0.029 (ns)
within species	5	1236278	247256	60.101 (p < .001)
error	991	4076727	4114	
total	997	5320085	5336	

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.



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 assume 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<sup>2</sup> 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

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

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,  $R_0$ . 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.

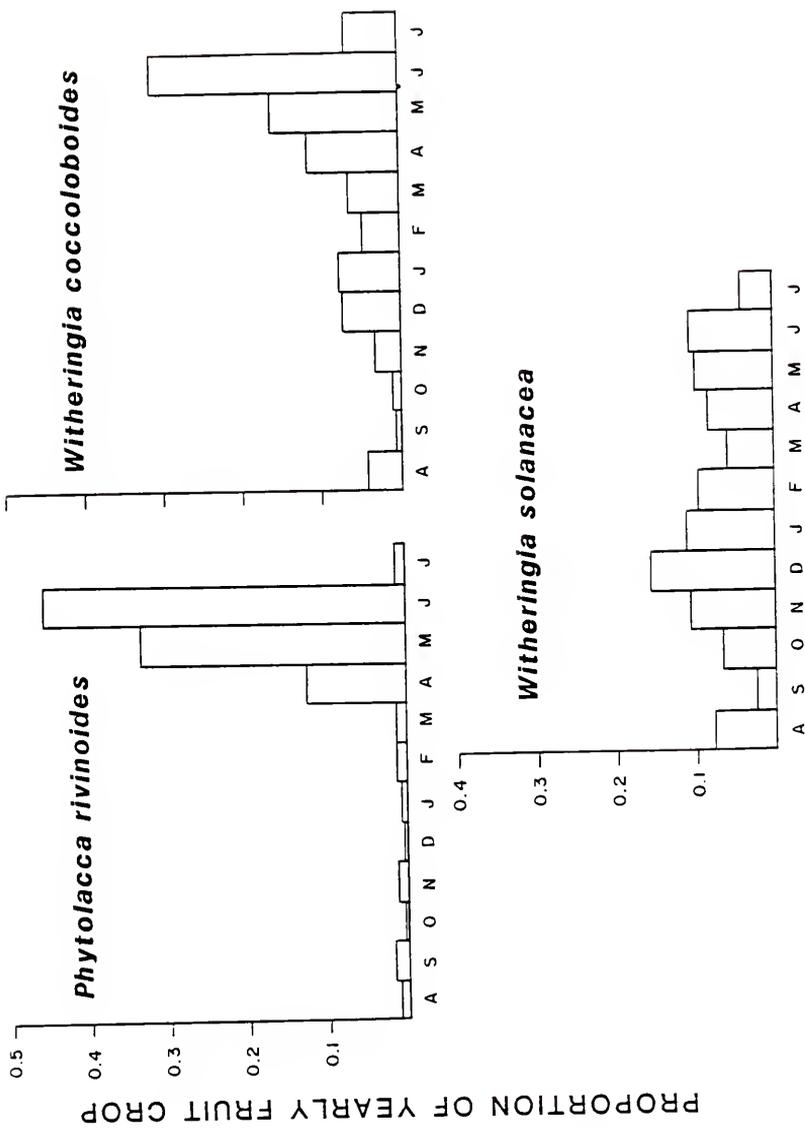
#### Dispersal Effects on Reproductive Output (RO), Assuming No Seed Dormancy

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. coccolobooides at Monteverde. Values given are for the "average" individual of each species (see text).



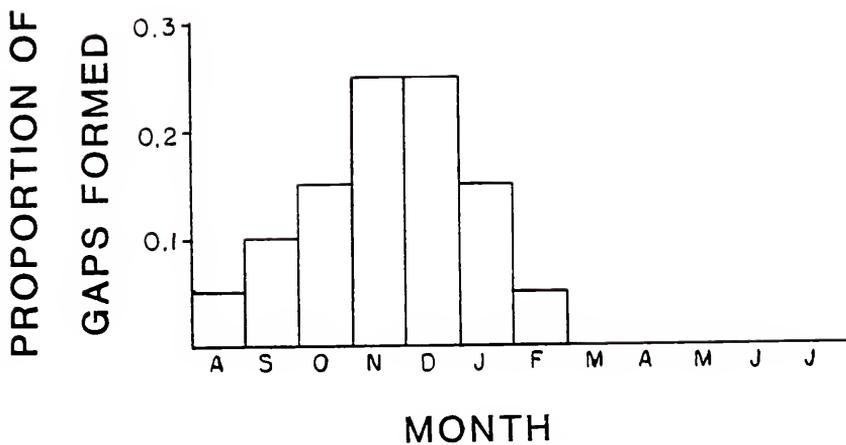
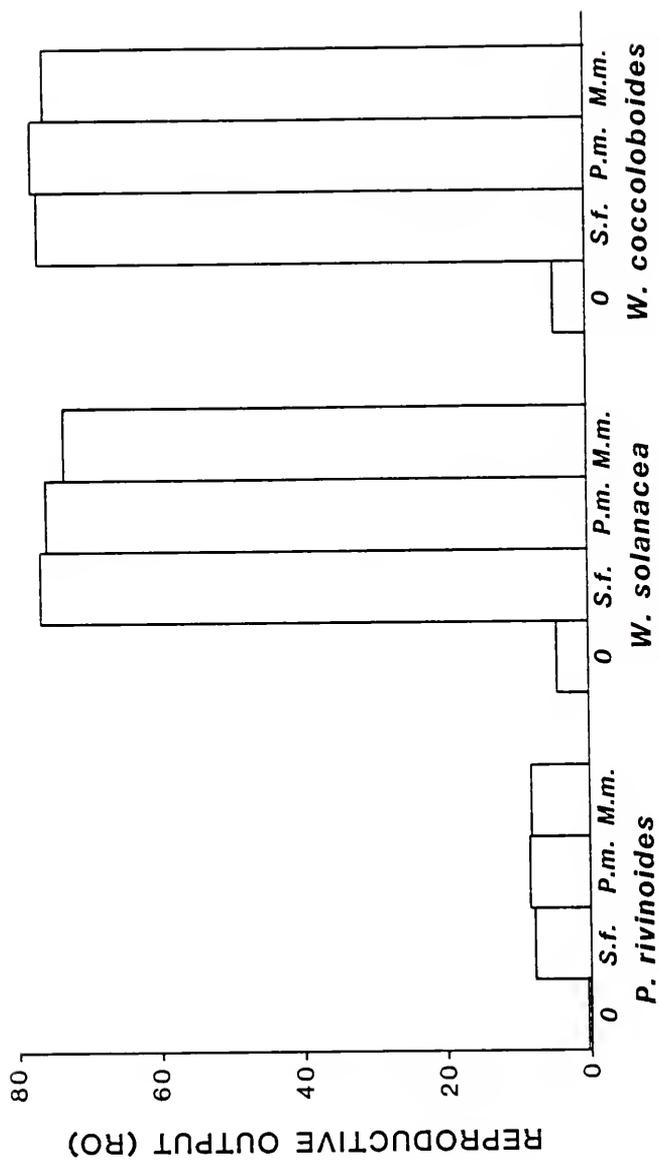


Figure 11. Estimated phenology of gap formation at Monteverde. Values given are the proportions of all gaps formed in a particular year that occur each month.

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

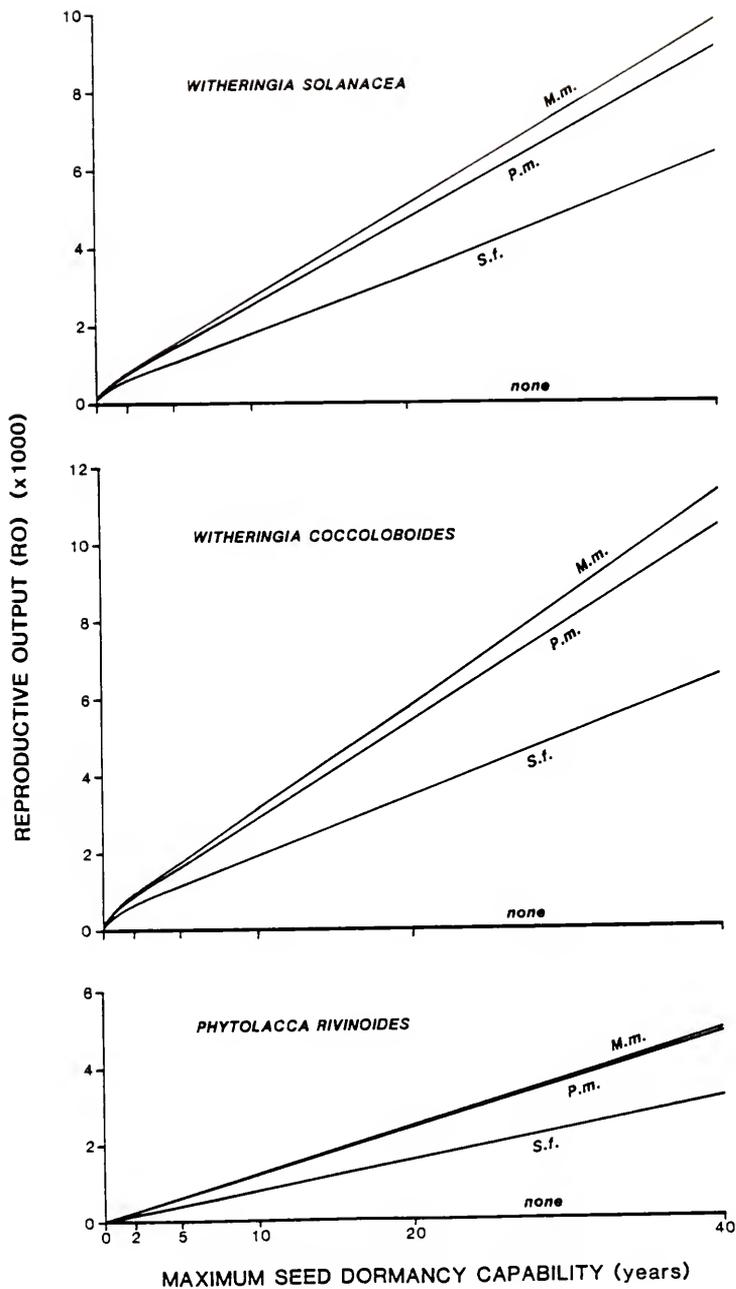


dispersed to sites currently suitable for germination, and thus germinate in the same month they are dispersed. These estimates do not include later reproduction from dormant seeds that germinate after a new canopy gap occurs overhead. Yet seeds of P. rivinoides, W. solanacea, and W. coccoloboides exhibit "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 output (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).



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.

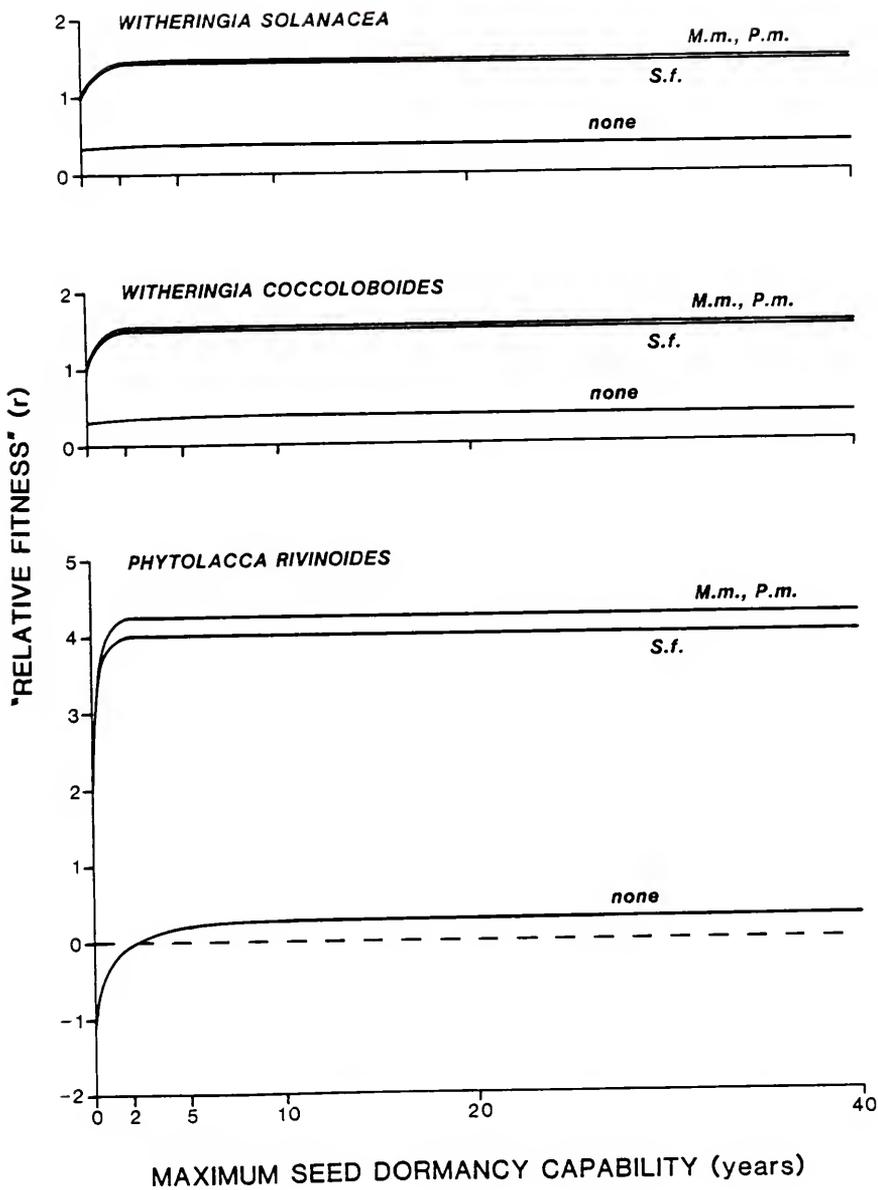
Effects on relative fitness. Although Figure 13 clearly shows that the total number of potential offspring is greatly increased by seed dormancy, it gives a misleading impression of the influence of seed dormancy on relative fitness. The estimator of reproductive output computed by equation 1 is most 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

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

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  $R_0$  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).



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.

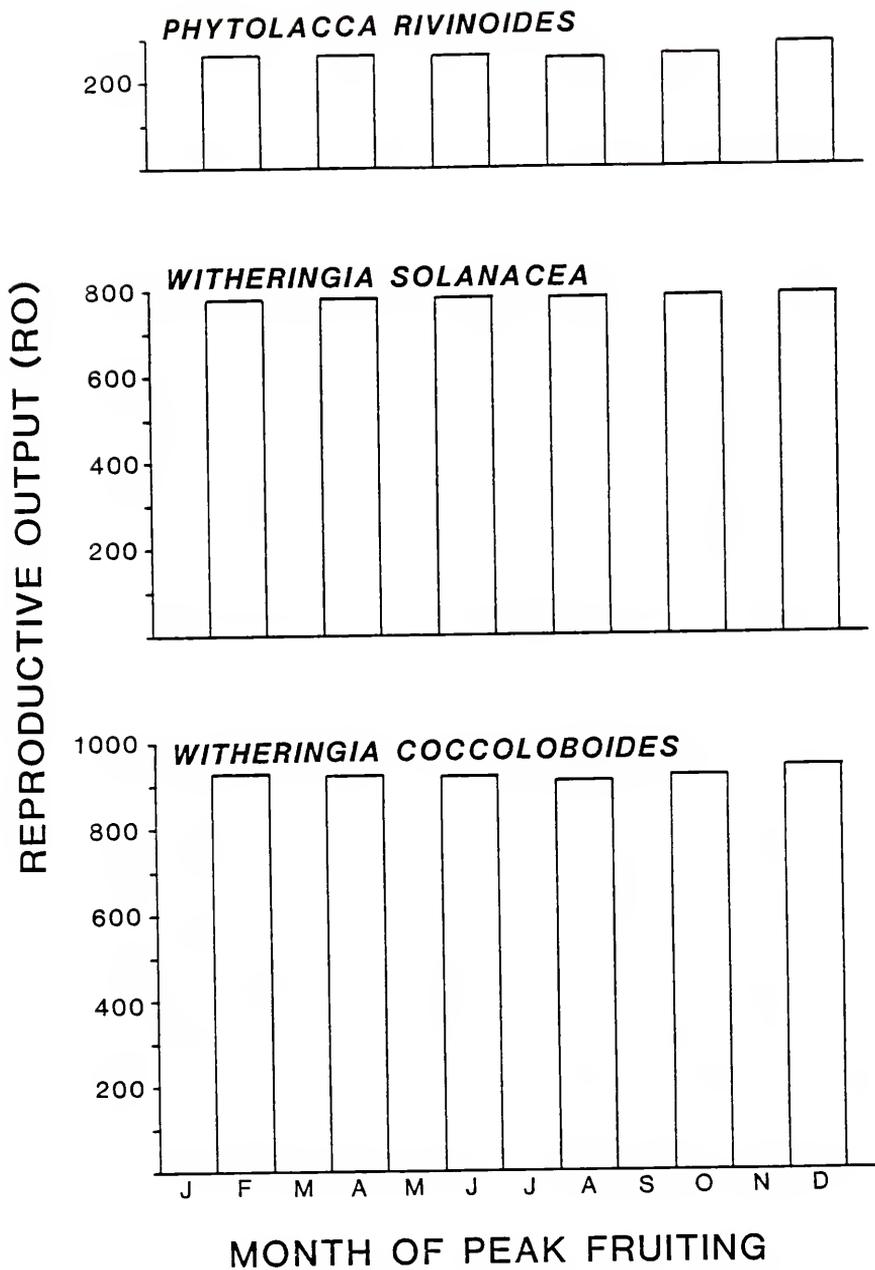
In all three plant species, a significant partial correlation existed between Myadestes capture rate and daily fruit removal rate. Coefficients for P. rivinoides, W. solanacea, and W. coccoloboides were 0.74 ( $P < .02$ ), 0.66 ( $P < .05$ ), and 0.69 ( $P < .05$ ), respectively. Thus, individual plants 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.



## 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 ophthalmicus 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 assessments of soil seed banks (e.g., Burt 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  $1.6 \text{ m}^2$ ) 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 (>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 availability 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

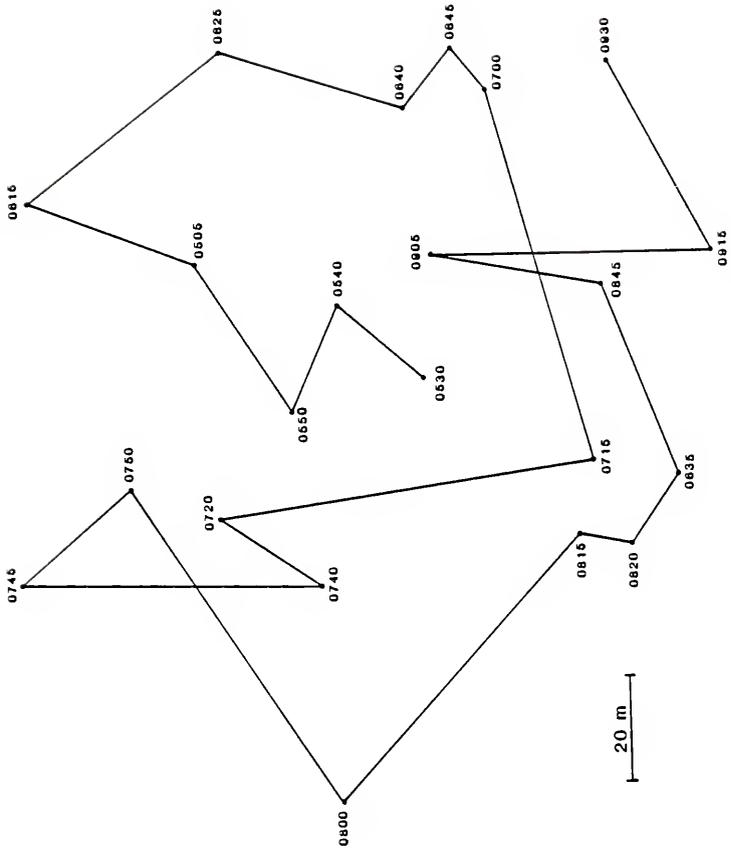
seed dispersers likely preclude tight coevolution between them (see also Wheelwright and Orians 1982, Janzen 1983b, Howe 1984).

## 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.

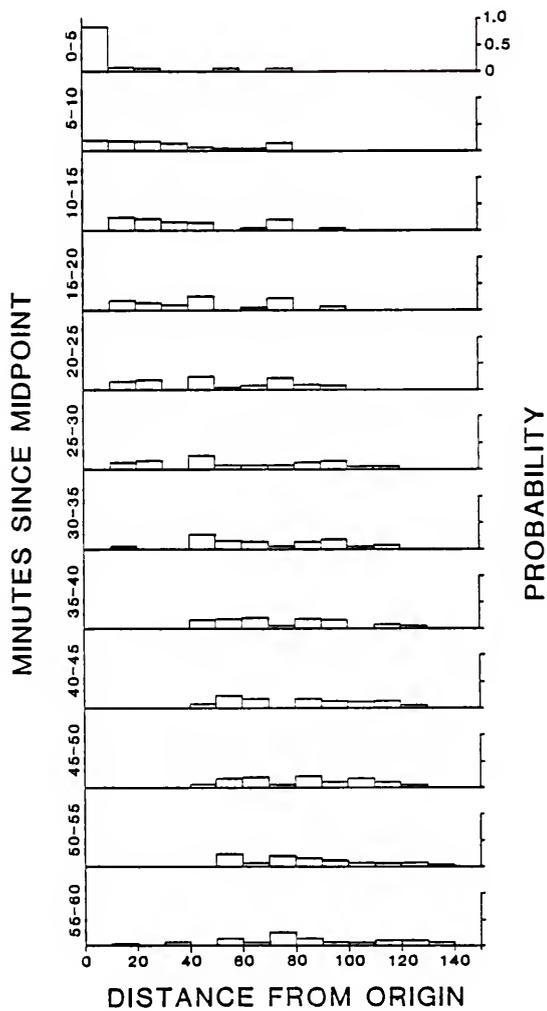
Figure A-1. Foraging movements of a single frugivorous bird for a period of four hours. Times of arrival are shown for each location. See text for methods.



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



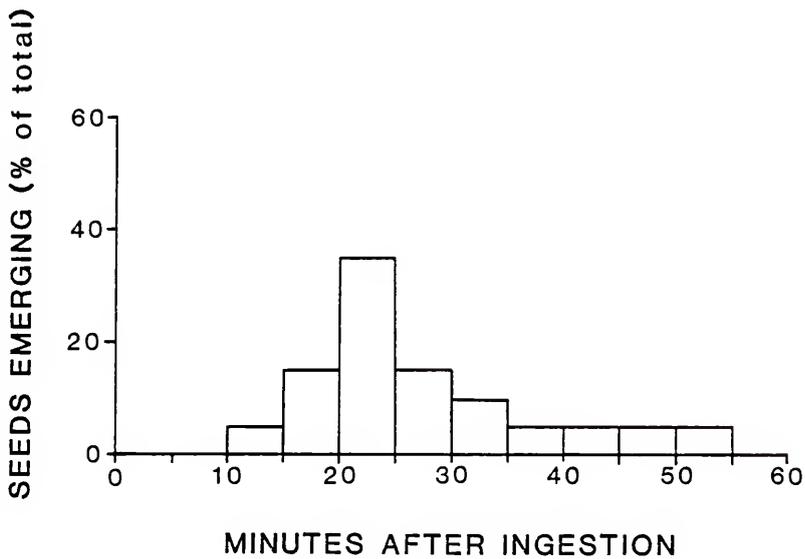
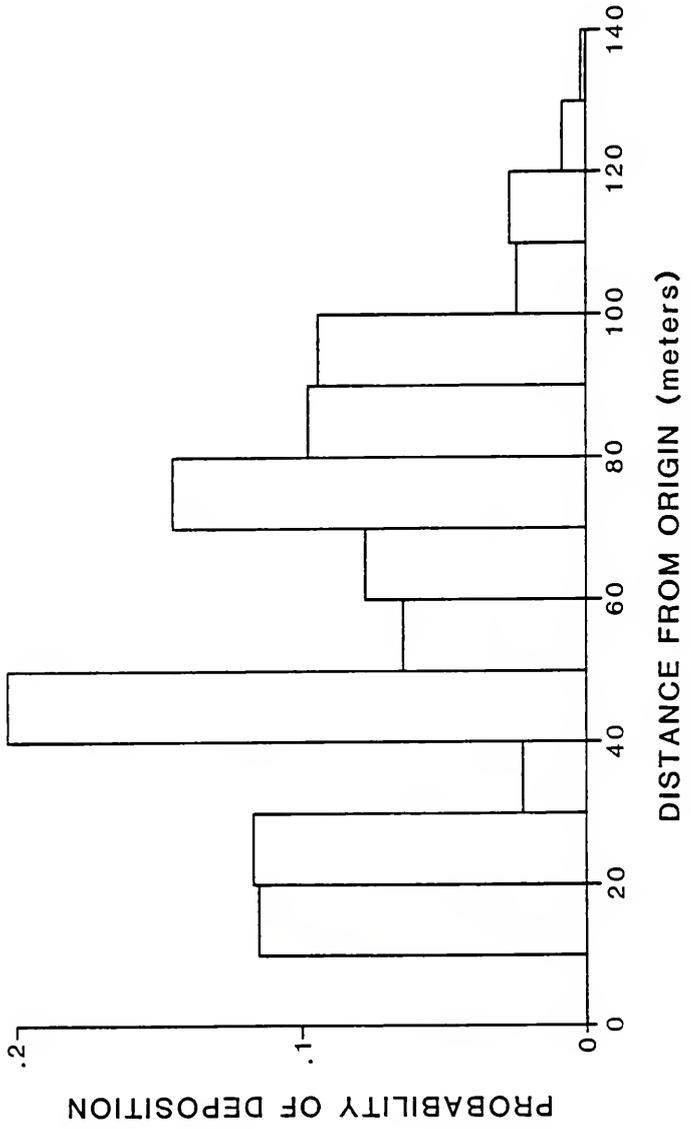


Figure A-4. Retention time distribution for seeds of the source plant species in a particular bird species' gut. See text for methods.

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.



LITERATURE CITED

- Abrell, D. B., and M. T. Jackson. 1977. A decade of change in an oldgrowth beech-maple forest in Indiana. *American Midland Naturalist* 98: 22-32.
- Applegate, R. D., L. L. Rogers, D. A. Casteel, and J. M. Novak. 1979. Germination of cow parsnip seeds from grizzly bear feces. *Journal of Mammalogy* 60: 655.
- Aubreville, A., and J. F. Leroy. 1970. Contribution a L'etude biologique d'une Araliaceae d'America tropicale: Didymopanax morotoni. *Adansonia* 10: 383-407.
- Augspurger, C. K. 1983a. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40: 189-196.
- \_\_\_\_\_. 1983b. Seed dispersal by the tropical tree, Platypodium elegans, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759-771.
- \_\_\_\_\_. 1984a. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61: 211-217.
- \_\_\_\_\_. 1984b. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65: 1705-1712.
- Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103: 328-340.
- Brokaw, N. V. L. 1980. Gap phase regeneration in a neotropical forest. Dissertation. Univ. of Chicago, Chicago, Illinois, USA.
- \_\_\_\_\_. 1982a. Treefalls: frequency, timing, and consequences. Pages 101-108 in E. G. Leigh, A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- \_\_\_\_\_. 1982b. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158-160.
- \_\_\_\_\_. 1985. Treefalls, regrowth, and community structure in tropical forests. Pages 53-69 in S.T.A. Pickett and P.S. White, editors. *Natural disturbance: the patch dynamics perspective*. Academic Press, New York, New York, USA.

- Brunner, H., R. V. Harris, and R. L. Amor. 1976. A note on the dispersal of seeds of blackberry (Rubus procerus P. J. Muell.) by foxes and emus. *Weed Research* 16: 171-173.
- Bullock, S. H. 1978. Plant abundance and distribution in relation to types of seed dispersal in chaparral. *Madroño* 25: 104-105.
- Burt, B. D. 1929. A record of fruits and seeds dispersed by mammals and birds from the Singida district of Tanganyika territory. *Journal of Ecology* 17: 351-355.
- Clark, D. A., and D. B. Clark. 1981. Effects of seed dispersal by animals on the regeneration of Bursera graveolens (Burseraceae) on Santa Fe Island, Galápagos. *Oecologia* 49: 73-75.
- Crome, F. H. J. 1975a. The ecology of fruit pigeons in tropical northern Queensland. *Australian Wildlife Research* 2: 155-185.
- Crome, F. H. J. 1975b. Breeding, feeding, and status of the Torres Strait Pigeon on Low Isles, northeastern Queensland. *Emu* 75: 198-198.
- Culver, D. C., and A. J. Beattie. 1980. The fate of Viola seeds dispersed by ants. *American Journal of Botany* 67: 710-714.
- D'Arcy, W. G. 1973. Solanaceae. Pages 573-780 in R. E. Woodson, Jr. and R. W. Schery, editors. *Flora of Panama*. Annals of the Missouri Botanical Garden, volume 60.
- Davidson, D. W., and S. R. Morton. 1981a. Competition for dispersal in ant-dispersed plants. *Science* 213: 1259-1261.
- \_\_\_\_\_. 1981b. Myrmecochory in some plants (F. Chenopodiaceae) of the Australian arid zone. *Oecologia* 50: 357-366.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12 (supplement on tropical succession): 47-55.
- \_\_\_\_\_, and T. C. Moermond. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: an experimental study. *Oecologia* 54: 170-176.
- Diamond, J. M. 1973. Distributional ecology of New Guinea birds. *Science* 179: 759-769.
- Docters van Leeuwen, W. M. 1954. On the biology of some Loranthaceae and the role birds play in their life-history. *Beaufortia* 4: 105-208.
- Estrada, A., and T. H. Fleming, editors. 1986. *Frugivores and seed dispersal*. W. Junk, Dordrecht, The Netherlands.
- Feinsinger, P. 1983. Coevolution and pollination. Pages 282-310 in D. J. Futuyma and M. Slatkin, editors. *Coevolution*. Sinauer Associates, Sunderland, Massachusetts, USA.

- \_\_\_\_\_, J. H. Beach, Y. B. Linhart, W. H. Busby, and K. Greg Murray. Disturbance, pollinator predictability, and pollination success among Costa Rican cloud forest plants. Ecology, in review.
- Fleming, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in Piper amalago (Piperaceae), a bat-dispersed tropical shrub. Oecologia 51: 42-46.
- \_\_\_\_\_, and E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropica 13 (Supplement on reproductive botany): 45-53.
- Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-343.
- Forshaw, J. M. 1978. Parrots of the world. David and Charles, London, England.
- Foster, R. 1973. Seasonality of fruit production and seed fall in a tropical forest ecosystem. Dissertation. Duke University, Durham, North Carolina, USA.
- \_\_\_\_\_, and N. V. L. Brokaw. 1982. Structure and history of the vegetation of Barro Colorado Island. Pages 67-81 in E. G. Leigh, A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C., USA.
- Garwood, N. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. Ecological Monographs 53: 159-181.
- Geritz, S. A. H., T. J. de Jong, and P. G. L. Klinkhamer. 1984. The efficacy of dispersal in relation to safe site area and seed production. Oecologia 62: 219-221.
- Glyphis, J. P., S. J. Milton, and W. R. Siegfried. 1981. Dispersal of Acacia cyclops by birds. Oecologia 48: 138-141.
- Green, D. S. 1983. The efficacy of dispersal in relation to safe site density. Oecologia 56: 356-358.
- Greenberg, R. 1981. Frugivory in some migrant tropical forest wood warblers. Biotropica 13: 215-223.
- Guevara, S., and A. Gomez-Pompa. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. Journal of the Arnold Arboretum 53:312-335.
- Handel, S. N. 1978. The competitive relationship of three woodland sedges and its bearing on the evolution of ant dispersal of Carex pedunculata. Evolution 32: 151-163.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, England.

- Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617-638 in P. B. Tomlinson and M. H. Zimmerman, editors. Tropical trees as living systems. Cambridge Univ. Press, London, England.
- \_\_\_\_\_. 1980. Neotropical forest dynamics. Biotropica 12 (supplement on tropical succession): 23-30.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3: 329-382.
- Herrera, C. M. 1981. Fruit variation and competition for dispersers in natural populations of Smilax aspera. Oikos 36: 51-58.
- \_\_\_\_\_. 1984. Adaptation to frugivory of Mediterranean avian seed dispersers. Ecology 65: 609-617.
- \_\_\_\_\_, and P. Jordano. 1981. Prunus mahaleb and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. Ecological Monographs 51: 203-218.
- Hilty, S. L. 1980. Relative abundance of north temperate zone breeding migrants in western Colombia and their impact at fruiting trees. Pages 265-271 in A. Keast and E.S. Morton, editors. Migrant birds in the neotropics. Smithsonian Institution Press, Washington D.C., USA.
- Hladik, A. 1982. Dynamique d'une foret equatoriale africaine: mesures en temps reel et comparaison du potential de croissance des differentes especies. Acta Oecologica Oecologia Generalis 3: 373-392.
- \_\_\_\_\_, and C. M. Hladik. 1969. Rapports trophiques entre vegetation et primates dans la foret de Barro Colorado (Panama). Terre et la Vie 116: 25-117.
- Holdridge, L. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- Holthuijzen, A. M. A., and C. S. Adkisson. 1984. Passage rate, energetics, and utilization efficiency of the cedar waxwing. Wilson Bulletin 96: 680-684.
- Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58: 539-550.
- \_\_\_\_\_. 1980. Monkey dispersal and waste of a neotropical fruit. Ecology 61: 944-959.
- \_\_\_\_\_. 1982. Fruit production and animal activity at two tropical trees. Pages 189-200 in E. Leigh, Jr., A. S. Rand, and D. Windsor, editors. The ecology of a tropical rainforest. Smithsonian Institution Press, Washington D.C., USA.
- \_\_\_\_\_. 1984. Constraints on the evolution of mutualisms. American Naturalist 123: 764-777.

- \_\_\_\_\_, and D. De Steven. 1979. Fruit production, migrant bird visitation, and seed dispersal of Guarea glabra in Panama. *Oecologia* 39: 185-196.
- \_\_\_\_\_, and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111: 817-832.
- \_\_\_\_\_, and R. B. Primack. 1975. Differential seed dispersal by birds of the tree Casearia nitida (Flacourtiaceae). *Biotropica* 7: 278-283.
- \_\_\_\_\_, E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (Virola surinamensis). *Ecology* 66: 781-791.
- \_\_\_\_\_, and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- \_\_\_\_\_, and G. A. Vande Kerchove. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60: 180-189.
- \_\_\_\_\_, and G. A. Vande Kerchove. 1980. Nutmeg dispersal by tropical birds. *Science* 210: 925-927.
- \_\_\_\_\_, and G. A. Vande Kerchove. 1981. Removal of wild nutmeg (Virola surinamensis) crops by birds. *Ecology* 62: 1093-1106.
- Janzen, D. H. 1978. The size of a local peak in a seed shadow. *Biotropica* 10: 78.
- \_\_\_\_\_. 1980. When is it coevolution? *Evolution* 34: 611-612.
- \_\_\_\_\_. 1981. Ficus ovalis seed predation by an orange-chinned parakeet (Brotogeris jugularis) in Costa Rica. *Auk* 98: 841-844.
- \_\_\_\_\_. 1983a. Dispersal of seeds by vertebrate guts. Pages 232-262 in D. J. Futuyma and M. Slatkin, editors. *Coevolution*. Sinauer Associates, Sunderland, Massachusetts, USA.
- \_\_\_\_\_. 1983b. Seed and pollen dispersal by animals: convergence in the ecology of contamination and sloppy harvest. *Biological Journal of the Linnaean Society* 20: 103-113.
- \_\_\_\_\_, G. A. Miller, J. Hackforth-Jones, C. M. Pond, D. Hooper, and D. P. Janos. 1976. Two Costa Rican bat generated seed shadows of Andira inermis (Leguminosae). *Ecology* 56: 1068-1075.
- Jenkins, R. 1969. Ecology of three species of saltators in Costa Rica with special reference to their frugivorous diet. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
- Jones, C. E., and R. J. Little. 1983. *Handbook of experimental pollination biology*. Van Nostrand, New York, New York, USA.

- Karr, J. R., D. W. Schemske, and N. Brokaw. 1982. Temporal variation in the undergrowth bird community of a tropical forest. Pages 441-453 in E. G. Leigh, Jr., A. S. Rand, and D. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- Krefting, L. W., and E. L. Roe. 1949. The role of some birds and mammals in seed germination. *Ecological Monographs* 19: 269-286.
- Lawton, R., and V. Dryer. 1980. The vegetation of the Monteverde cloud forest reserve. *Brenesia* 18: 101-116.
- Lawton, R. O., and F. E. Putz. Elfin forest dynamics in Monteverde, Costa Rica. Unpublished manuscript.
- Leck, C. F. 1972. The impact of some North American migrants at fruiting trees in Panama. *Auk* 89: 842-850.
- Leigh, E. G., Jr. 1975. Structure and climate in tropical rain forest. *Annual Review of Ecology and Systematics* 6: 67-86.
- Lemen, C. 1981. Elm trees and elf leaf beetles: patterns of herbivory. *Oikos* 36: 65-67.
- Levey, D. J., 1986. Methods of seed processing by birds and seed deposition patterns. In A. Estrada and T. H. Fleming, editors. *Frugivory and seed dispersal*. W. Junk, Dordrecht, The Netherlands.
- Levin, D. A. 1979. The nature of plant species. *Science* 204: 381-384.
- Lieberman, D., J. B. Hall, M. D. Swaine, and M. Lieberman. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.
- Lucas, H. A., and G. A. F. Seber. 1977. Estimating coverage and particle density using the line intercept method. *Biometrika* 64: 618-622.
- McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of Stemmadenia donnell-smithii (Apocynaceae) by birds. *Biotropica* 9: 9-25.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159-191 in L. E. Gilbert and P. H. Raven, editors. *Coevolution of animals and plants*. University of Texas Press, Austin, Texas, USA.
- Moermond, T. C. 1983. Suction-drinking in tanagers Thraupidae and its relation to frugivory. *Ibis* 125: 545-549.
- \_\_\_\_\_, and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36: 865-897.
- Murray, K. G. In press. Selection for optimal fruit crop size in bird-dispersed plants. *American Naturalist*.

- Naka, K. 1982. Community dynamics of evergreen broadleaf forests in southwestern Japan. I. Wind damaged trees and canopy gaps in an evergreen oak forest. *The Botanical Magazine, Tokyo* 95: 385-399.
- Nobel, J. C. 1975. The effects of emus (*Dromaius novae-hollandiae* Latham) on the distribution of the nitre bush (*Nitraria billardieri* DC.). *Journal of Ecology* 63: 979-984.
- Oldeman, R. A. A. 1978. Architecture and energy exchange of dicotyledonous trees in the forest. Pages 535-560 in P. B. Tomlinson and M. H. Zimmermann, editors. *Tropical trees as living systems*. Cambridge Univ. Press, London, England.
- Olson, S. L., and K. E. Blum. 1968. Avian dispersal of plants in Panama. *Ecology* 49: 565-566.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45: 285-305.
- \_\_\_\_\_. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* (Pursh) MacM.). *Oecologia* 22: 399-409.
- \_\_\_\_\_, S. L. Rathbun, M. M. Platt, and D. W. Hirsh. Compostion and dynamics of a mixed-species forest dominated by Southern Magnolia (*Magnolia grandiflora*) and American Beech (*Fagus grandiflora*). Unpublished manuscript.
- Pratt, T. K., and E. W. Stiles. 1983. How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *American Naturalist* 122: 797-805.
- Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64: 1069-1074.
- Raeder, K. 1961. Phytolaccaceae. Pages 66-79 in R. E. Woodson, Jr. and R. W. Schery, editors. *Flora of Panama*. Annals of the Missouri Botanical Garden, volume 48.
- Real, L. 1983. *Pollination biology*. Academic Press, Orlando, Florida, USA.
- Richards, P. W. 1952. *The tropical rain forest*. Cambridge Univ. Press, London, England.
- \_\_\_\_\_, and G. B. Williamson. 1975. Treefalls and patterns of understory species in a wet lowland tropical forest. *Ecology* 56: 1226-1229.
- Rick, C. M., and R. I. Bowman. 1961. Galápagos tomatoes and tortoises. *Evolution* 15: 407-447.

- Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton Univ. Press, Princeton, New Jersey, USA.
- Runkle, J. R. 1979. Gap phase dynamics in climax mesic forests. Dissertation. Cornell University, Ithaca, New York, USA.
- \_\_\_\_\_. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.
- Salmonson, M. G. 1978. Adaptations for animal dispersal of one-seeded juniper seeds. *Oecologia* 32: 333-339.
- Schultz, J. P. 1960. Ecological studies on rain forest in Northern Surinam. N. V. Noord-Hollandsche VitGevers Maatshappij, Amsterdam, The Netherlands.
- Skeate, S. T. 1985. Mutualistic interactions between birds and fruits in a northern Florida hammock community. Dissertation. Univ. of Florida, Gainesville, Florida, USA.
- Smith, A. J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* 56: 19-34.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *American Naturalist* 104: 25-36.
- Snow, B. K., and D. W. Snow. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88: 291-322.
- Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos*. 15: 274-281.
- \_\_\_\_\_. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194-202.
- \_\_\_\_\_. 1973. Distribution, ecology and evolution of the bellbirds (*Procnias*, Cotingidae). *Bulletin of the British Museum of Natural History (Zoology)* 25: 369-391.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Sorensen, A. E. 1981. Interactions between birds and fruit in a temperate woodland. *Oecologia* 50: 242-249.
- \_\_\_\_\_. 1983. Taste aversion and frugivore preference. *Oecologia* 56: 117-120.
- \_\_\_\_\_. 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology* 53: 545-557.

- Standley, P. C. 1937. Flora of Costa Rica. Publications of the Field Museum of Natural History (Chicago, Illinois, USA), Botanical series, volume 18.
- Stapanian, M. A. 1982. A model for fruiting display: seed dispersal by birds for mulberry trees. *Ecology* 63: 1432-1443.
- Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* 116: 670-688.
- \_\_\_\_\_. 1982. Fruit flags: two hypotheses. *American Naturalist* 120: 500-509.
- Temple, S. A. 1975. Plant-animal mutualism: coevolution with dodo leads to near extinction of plant. *Science* 197: 885-886.
- Thompson, J. N. 1980. Treefalls and colonization patterns of temperate forest herbs. *American Midland Naturalist* 104: 176-184.
- \_\_\_\_\_. 1981. Elaisomes and fleshy fruits: phenology and selection pressures for ant-dispersed seeds. *American Naturalist* 117: 104-108.
- \_\_\_\_\_, and M. F. Willson. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* 33: 973-982.
- Uhl, C. 1982. Tree dynamics in a species rich tierra firme forest in Amazonia, Venezuela. *Acta Cientifica Venezolana* 33: 72-77.
- van der Pijl, L. 1972. Principles of dispersal in higher plants. Second edition. Springer-Verlag, Berlin.
- Van der Wall, S. B., and R. P. Balda. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. *Ecological Monographs* 47: 89-111.
- Vazquez-Yanes, C. 1976. Estudios sobre ecofisiologia de la germinacion en una zona calido-humeda de Mexico. Pages 279-387 in A. Gomez-Pompa, C. Vazquez-Yanes, S. Del Amo, and A. Butanda, editors. *Regeneracion de selvas*. Editorial Continental, Mexico.
- \_\_\_\_\_. 1977. Germination of a pioneer tree (Trema guineensis Ficahlo), from equatorial Africa. *Turrialba* 23(3): 301-302.
- \_\_\_\_\_. 1980. Light quality and seed germination in Cecropia obtusifolia and Piper auritum from tropical rain forest in Mexico. *Phyton* 38: 33-35.
- \_\_\_\_\_, and A. Orozco-Segovia. 1982. Seed germination of a tropical rain forest tree (Heliocarpus donnell smithii) in response to diurnal fluctuations of temperature. *Physiologia Plantarum* 56: 295-298.

- \_\_\_\_\_, and A. Orozco-Segovia. 1984. Ecophysiology of seed germination in the tropical humid forests of the world: a review. Pages 37-50 in E. Medina, H. A. Mooney, and C. Vazquez-Yanes, editors. Physiological ecology of plants in the wet tropics. W. Junk, Dordrecht, The Netherlands.
- \_\_\_\_\_, A. Orozco-Segovia, G. Francois, and L. Trejo. 1975. Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. *Biotropica* 7: 73-76.
- \_\_\_\_\_, and H. Smith. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees Cecropia obtusifolia and Piper auritum and its ecological significance. *New Phytologist* 92: 477-485.
- Walsberg, G. E. 1975. Digestive adaptations of Phainopepla nitens associated with the eating of mistletoe berries. *Condor* 77: 169-174.
- Wheelwright, N. T. 1983. Fruits and the ecology of Resplendant Quetzals. *Auk* 100: 286-301.
- \_\_\_\_\_. 1985a. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808-818.
- \_\_\_\_\_. 1985b. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44: 465-477.
- \_\_\_\_\_, W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16: 173-192.
- \_\_\_\_\_, and G. H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist* 119: 402-413.
- Whitmore, T. C. 1975. Tropical rain forests of the far east. Clarendon Press, Oxford, England.
- \_\_\_\_\_. 1978. Gaps in the forest canopy. Pages 639-655 in P. B. Tomlinson and M. H. Zimmermann, editors. Tropical trees as living systems. Cambridge Univ. Press, London, England.
- \_\_\_\_\_. 1982. On pattern and process in forests. Pages 45-57 in E. J. Newman, editor. The plant community as a working mechanism. Blackwell, Oxford, England.
- Wilson, D. E., and D. H. Janzen. 1972. Predation on Scheelea palm seeds by bruchid beetles: seed density and distance from the parent palm. *Ecology* 53: 954-959.
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29: 22-32.
- Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

#### 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 deer mouse 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 deer mouse 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<sup>™</sup> 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.

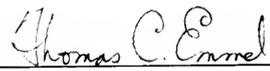
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Peter Feinsinger, Chairman  
Professor of Zoology

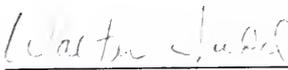
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
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  
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.

  
Francis E. Putz  
Assistant Professor of Botany

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.

December 1986

---

Dean, Graduate School

UNIVERSITY OF FLORIDA



3 1262 08553 4211