INTERACTIONS BETWEEN PASSERINES AND WOODY PLANTS AT A MIGRATORY STOP-OVER SITE: FRUIT CONSUMPTION AND THE POTENTIAL FOR SEED DISPERSAL

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ABSTRACT

Interactions between migratory passerines and woody plant fruiting patterns were studied at the eastern shore of Virginia. Migrants were collected daily from late August to late November, using standard mist nets. Gut contents of captured migrants were collected and analyzed for the presence of woody plant seeds. Nineteen bird species produced 1752 samples. Woody plant fruit production was sampled weekly. Fruit abundance, size, pulp water content, and relative nutritional value was measured for the 13 woody plant species which presented fruits. Differences in these fruit characteristics were analyzed using ANOVA statistical procedures. The fruits of *Myrica spp.* and *Juniperus virginiana* were significantly smaller, had lower water contents and higher relative energy yields than other fruits at the site (p=.05). The peak of avian migration numbers and ripe fruit production coincided. However, these events occurred one month later at this south temperate site compared with north temperate areas.

Two principal components anlayses were used to determine underlying patterns in bird-plant interactions. One analysis used average fruit consumption of each woody plant species by each bird species for a bird species-based analysis. The other analysis used total seed consumption of each plant species by each bird species for a plant species-based analysis. Three plant species accounted for the majority of the consumption by migratory birds. Four bird species were most important in the potential seed dispersal of woody plants. The presence of plant dispersal guilds is indicated by clustering of factor loadings in the principal component space describing total seed consumption. Interactions between the Yellow-rumped Warbler and *Myrica spp* .suggest a semi-specific mutualism. Other migrant-plant interactions follow models of diffuse coevolution.

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This thesis is dedicated to Bill Odum. His insights remain inspiring.

INTRODUCTION

In the United States, 75% of the individuals, and 62% of the bird species which breed in eastern temperate forests migrate to the neotropics annually for the winter season (MacArthur 1972). Neotropical migrants are dependent on a wide variety of habitats including breeding ground habitats, winter habitats and stopover sites along migration routes. The general decline in many neotropical migrant populations over the past decade has been attributed to deforestation and forest fragmentation in both temperate breeding grounds and tropical wintering grounds (Askins et al. 1990, Robbins et al. 1989). Forests in North America have been generally declining since the arrival of Europeans 500 years ago (Williams 1989). However, recent regional increases in forests are evident in the northeast (Williams 1989).

Understanding the interactions between avian migrants and the plant communities at stopover sites is critical to the development of migrant conservation programs. Because few migrant passerines carry enough fat to fuel an entire migration, they presumably must stop enroute to feed (Dawson et al. 1983). It is known that woody plant fruits are an important food source for many neotropical migrants (Bent 1953). Thrushes, flycatchers, orioles, tanagers, vireos and warblers all consume large quantities of fruits at their tropical wintering grounds (Howe and DeSteven 1979, Greenberg 1981). Many become frugivorous during their southward migration (Snow 1971, Thompson and Willson 1979, Stiles 1980, Sorenson 1981, Herrera 1985). However, despite recent interest in neotropical winter and breeding habitat requirements, there have been very few studies concerning the specific interactions between plants and avian frugivores at stopover sites (Willson 1983, Winker et al. 1990).

Frugivorous migrants may play a significant role in the potential seed dispersal of woody plants at stop-over sites. Fruit production and fall bird migrations have been correlated through regional overview studies in northern temperate areas (Thompson and Willson 1979, Snow 1971, Stiles 1980, Sorenson 1981, Herrera 1982, 1984, 1985,1986). Birds concentrate along migration pathways, maximizing both the availability of potential dispersers and the probability of dispersal to a wide variety of habitats for bird-dispersed plants (Thompson and Willson 1979, Stiles 1980, Herrera 1982). During the winter, potential bird dispersers are less common in northern temperate regions (Thompson and Willson 1979, Herrera 1984). Several researchers have proposed that where winter residents are plentiful, winter dispersal may be advantageous since there is minimal threat of microbial decay and reduced competition for dispersers with insect food sources (Thompson and Willson 1979, Herrera 1982, Stapanian 1986).

Studies concerned with the evolutionary basis for avian frugivory and seed dispersal have commonly concentrated on dispersal of individual plant species by a suite of avian dispersers (Snow 1971, Howe and DeSteven 1979, Howe and Vande Kerckhove 1980, Howe and Smallwood 1982, Herrera and Jordano 1982). These studies have provided an empirical understanding of specific dispersal strategies. However, avian dispersers are rarely specific to one plant (Herrera 1984). The importance of specific interactions from an evolutionary viewpoint probably corresponds to the degree of mutual dependence between two species (Herrera 1984). Almost all community level studies of avian frugivory and seed dispersal have been regional overviews, relying on coincidental phenomena for data (Thompson and Willson 1979, Stiles 1980, Herrera 1982). To truly understand the interrelationships between avian frugivores and fruit bearing woody plants, interactions should be studied at both the specific and community level. Very few researchers have undertaken such a perspective (Herrera 1984).

In one of the few community-level studies to date, Herrera (1984) established that substantial pairwise plant-bird reciprocity is not common in scrubland communities of Northern Spain. He concluded that actual reciprocity occurs in only a few bird-plant pairs, and that for the majority of cases, plants are much less important to dispersers than dispersers are to plants. Herrera described the existence of functional dispersal guilds, in which the Mediterranean scrub-plant dispersal system is maintained by a few strong bird-plant pairs, whose interactions inadvertently favor coexisting plants (Herrera 1984). The term guild is defined as a group of species that exploit the same class of environmental resources in a similar way (Root 1967). Originally, the presence of guilds was considered to be indicative of intense competition for the same resource. However, Herrera's use of guilds follows an alternative view which implies that guilds are groups of independent species sharing a resource, but not likely to be subject to much coevolution (Simberloff and Dayan 1991). The existence of plant dispersal guilds could have important implications for conservation programs if the dispersal of some plant species depends on the presence of other plant species. For example, to maintain plant diversity, stop-over sites should have at least one primary plant species which would serve to encourage dispersal of lower-ranking, meaning less abundant and/or less nutritionally rich, coexisting plants.

Declining passerine migrations may have a significant impact on the population ecology of plants that rely on migrant frugivores for dispersal. Very little attention has focused on the long term implications of changing frugivore populations and the impact on the population ecology of plants that depend on frugivores for dispersal.

The research presented here examines patterns of fruit presentation, passerine migrations and potential bird mediated dispersal on the Eastern Shore of Virginia at both the community and specific interaction levels. The majority of woody plants at this site, and on the nearby barrier islands, are bird-disseminated (van der Pijl 1972). Periodic storms and long term sea-level changes reset succession, making seed dispersal a critical factor in plant community structure (McCaffrey and Dueser 1990, Thompson and Willson 1978, and Wiens 1976). Historically, both the Eastern Shore and the barrier islands have been an important resource for migrating birds along one of the major migration routes (Figure 1). With rapid urbanization of the western shore of the Chesapeake Bay, the relatively undeveloped habitats of the Eastern shore have become increasingly important for migrating birds. The results of this study will be applied to the nearby barrier islands where possible. This extrapolation is supported by significant similarity in vegetation between the areas (McCaffrey and Dueser 1990), and similarity in migrant species assemblages (McCan pers. comm. 1993).

The study site represents a southern temperate region. No studies which I am aware of have examined migrant bird mediated dispersal in such a site. A suite of avian frugivores and plant seed dispersal interactions will be examined. Patterns in community level interactions may indicate the existence of dispersal guilds and/or may determine which plant species are most important as fuel sources for migrating passerines. The results of this study are compared with predictions from regional overviews in northern temperate regions, especially with regard to the effect of longer growing seasons and greater numbers of resident winter birds.

The specific objectives of this study are:

1. To gain an understanding of how migrant passerines utilize the woody plant fruit resources for refueling at a migratory stop-over site.
2. To explore the potential seed dispersal resulting from migrant frugivory.
3. To gain an understanding of the basis for differences in migrant utilization of woody plant fruits.
4. To compare observed patterns to the existing theoretical framework concerning seed dispersal by birds.

Literature Review

Evolution of Avian Seed Dispersal Mutualisms.

Almost all seed producing plants have developed some type of system for spreading their seeds. There is great variability in the efficiency and distance that seeds are dispersed (Willson 1983). Dispersal benefits plants by providing a mechanism to reach new habitats, escaping density dependent predation (Janzen 1970), and avoiding competition from siblings (Harper 1977).

The potential advantages of internal bird-mediated dispersal include longer dispersal distances, greater probability of deposition in a favorable site, and the possible benefits of manure applied at the time of deposition (Willson 1983). Compared with other dispersal mechanisms such as wind, and dispersal on animal exteriors, internal dispersal allows a parent plant to provision their offspring with large amounts of endosperm (Stapanian 1986). In return, plants must provide an edible reward to attract potential dispersal agents.

Birds species differ in their preference for various types of fruits and in their effectiveness as dispersal agents (Howe and Vande Kerckhove 1981). Passage through a bird's digestive tract improves germination for some seeds, has no effect in others, and has an adverse effect on some species (Willson 1983). Seeds must be protected from the harsh grinding and chemical conditions of the bird's gut (McKey 1975). Many fruits have cathartic properties which cause regurgitation. This limits the time that a seed stays in the digestive tract. Regurgitation usually means that seeds will be deposited relatively close to the parent plant.

Patterns in Nutritional Content of Temperate Fruits

General trends in the nutritional quality of temperate region fruits are evident. Fruits produced in the summer tend to be high in sugars and water, and to be produced in ephemeral, staggered abundances. Summer fruit staggering may be attributable to breeding season territoriality, which reduces the density of available frugivores, the presence of alternative insect foods, and potential fruit losses due to microbial decay (Janzen 1977, Stiles 1980). Fruits produced in the fall tend to be higher in carbohydrates and lipids. They can be either persistent, lasting into the winter season, or ephemeral (Stiles 1980, Johnson et al. 1985, Herrera 1985).

Tropical fruits tend to have fruit pulps richer in lipids than temperate fruits (Howe 1982). The rich pulp of tropical fruits is, in relative proportion to the large seed size, similar to the smaller nutritional rewards of most temperate fruits (Herrera 1985). Obtaining reliable results for fruit nutritional values has eluded researchers thus far, making it difficult to integrate nutritional value into theories of dispersal mutualisms (Johnson et al. 1985).

Fruits as Fuel for Migrations

It has been proposed that differences in nutritional composition of fruits may be associated with the seasonally changing metabolic demands of passerines (Thompson and Willson 1979, Stiles 1980, Sorenson 1981, 1983, Herrera 1985, Johnson et al. 1985), and the impact of microbial decay on fruit availability (Janzen 1977). During the breeding season, most migrant passerines are primarily insectivorous to meet the high protein demands of raising young (Stapanian 1986). Insects average 70% protein by dry weight in comparison with fruit pericarps, which average 5-10%, (Morton 1973, Johnson et al. 1985). During the fall and winter metabolic demands shift to higher carbohydrate and fat needs to build energy reserves for migration and for maintaining body temperatures in cold environments (Stiles 1980, Dawson et al. 1983). Although insects are generally abundant during the beginning of the migration season, it may still be advantageous for plants to display fruits at this time if potential dispersers are abundant (Thompson and Willson 1979). By the middle of the season, insect populations have generally become dormant, making migrants and resident birds more dependent on plant fruits and seeds (Kendeigh 1979).

Fruit Size and Display

Fruit size may be related to seed size (Willson 1983). Seeds contain the concentrated food which will sustain a young plant for the first stages of growth until leaves form. Small-seeded plants do not have to invest much energy in the production of seeds, but they must forego the advantages of having greater energy storage capabilities to aid the seedling in the first year of growth (Stapanian 1986).

In general, larger seeds require animal dispersal because of the physical constraints to wind dispersal. A nutritional reward is used to attract potential dispersers. Limits to fruit size are imposed by the size of the dispersal agent. Critical fruit size is defined as the maximum size a bird can effectively handle and consume. Smaller birds will be constrained by smaller critical fruit sizes (Martin 1985).

In general, plants which are dispersed by birds are red, blue or black in color, contrasting with green foliage. Fruits tend to be of an intermediate size, and to be located near the ends of branches where they are easily accessible (Van der Pijl 1972).

Mutualism Cost Benefit Ratios

Dispersal agents and energy for the accumulation of photosynthate are available year round in the tropics, possibly favoring specialist dispersal systems (Snow 1971). For plants, the efficiency of a disperser depends on the number of flights made by that disperser and the condition and destination of seeds dropped with each flight (Howe and Estabrook 1977). A specialized fruit or seed requiring specific sites for successful development relies on birds which frequent those sites. In order to encourage birds to specialize, large, high nutrient reward fruits are produced over a long time period. The greater investment of energy per fruit is offset by higher quality dispersal (Stapanian 1986).

In temperate regions it has been suggested that the seasonal nature of fruit production and dispersal favors opportunistic dispersal (Snow 1971, Howe and Estabrook 1977, Thompson and Willson 1979, Stiles 1980). Opportunists produce low quality fruits over relatively short time periods, attracting a variety of avian dispersers (Howe and Estabrook 1977). The benefits of an opportunistic strategy include relatively low energy investment per fruit, and a variety of dispersers. The cost is relatively low quality dispersal.

Variation in fruit size has been linked to specialist or opportunistic dispersal agents (Howe and Vande Kerckhove 1979). While it may be advantageous for plants to package many seeds per fruit since the pulp-to-seed ratio decreases with increasing number of seeds (Willson 1983), Herrera (1982) argues that relative pulp-to-seed ratio may be an important factor for birds because seeds occupy space in the digestive tract but provide no nutrition. Thus, birds favor low seediness.

Having similar fruits may benefit plants by increasing the general density of acceptable fruits in an area (Faaborg 1986). Optimal foraging models show that at low prey densities, alternative prey may be more profitable.

Howe and Estabrook (1977) developed a model for fruit crop size, nutritional value and duration of fruiting based on opportunistic or specialist dispersal systems. In this model, to be attractive to opportunistic dispersal agents, plants should have relatively small fruits displayed in large fruit crops and be in fruit for relatively short periods. Plants dispersed by specialist dispersal agents would have larger fruits, smaller fruit crops so as not to over supply dispersers, and longer fruiting seasons.

Study Site

One of the goals of this study was to gain an understanding of migratory bird use of woody plants on the barrier islands, with respect to frugivorous refueling. However it was not logistically possible to do the field work on the barrier islands. Nevertheless, the vegetation on the Eastern Shore is remarkably similar to that found on the barrier islands (McCaffrey and Dueser 1990). Field work was conducted at the Eastern Shore National Wildlife Refuge, located at the southern tip of the Delmarva Peninsula (Figure 1). The vegetation at the study site is characterized by dense shrubs, successional fields, and some canopy tree stands. The site is bordered by a salt marsh on the east, the Chesapeake Bay on the south, and large open grass fields on the west and north. Soils are sandy, and the general topography is flat. The majority of woody species both on the barrier islands and at the study site are primarily bird-dispersed (Van der Pijl 1972). Migrating birds, following the Atlantic coastline concentrate at the tip of the Delmarva Peninsula, waiting for favorable winds before crossing the Chesapeake Bay.

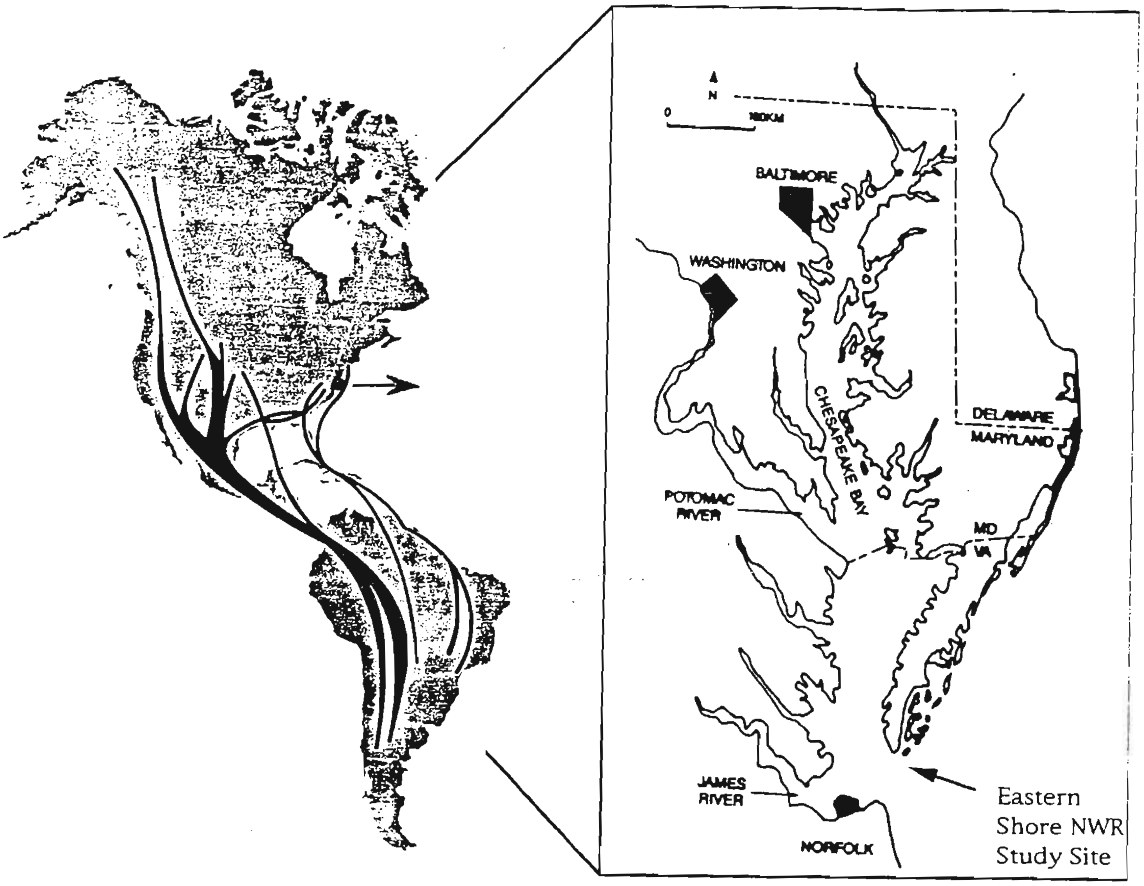


Figure 1. Study site location on the Delmarva peninsula.

METHODS

The study was conducted for 75 days, from August 29 until November 16, 1991. This time bracketed the fall passerine migration. Woody plant fruit production and migrant avian abundance were sampled along five transects, each approximately 400 m long. These transects were chosen to represent all available micro-habitats. Woody plants within 10 m of the transect center were considered representative of the woody plant community with which the migrants interacted (Herrera 1984).

Passerine Migration

Migration timing and abundance.

Five standard mist nets (12m x 2.6m of 30- and 36-mm mesh) were employed along the center of each transect (Figure 2). Most nets were oriented in an east-west direction, perpendicular to the north-south direction of migration, and spaced approximately 50 m apart. Nets were operated daily, from 0.5 hours before sunrise, to approximately 4:30 PM, and checked every 15 minutes, except on four days when nets were closed due to inclement weather.

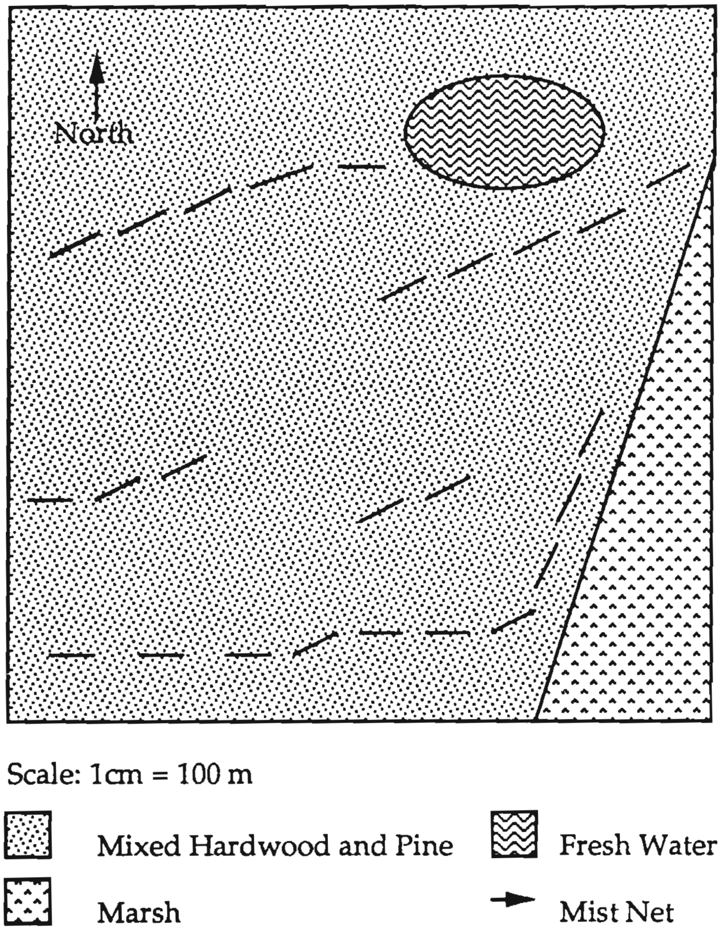


Figure 2. Detail of study site showing location of mist nets and banding station.

Diet

All captured birds were placed immediately into cloth bags and carried to a centrally located banding station. At the banding station, birds were kept, for approximately 40-60 minutes, in wooden holding cages, lined with paper.

The holding time was determined to be sufficient to allow for the passing, either through regurgitation or defecation, of most woody plant seeds (Johnson et al. 1985, Herrera 1982, Herrera 1984). The majority of birds produced samples within this time. Birds which did not produce samples within this time were held longer, or released if they appeared to be stressed. Voided gut contents were labeled and frozen until analysis. Samples were separated on the basis of whether they contained primarily insect remains, plant matter or both. The number and species of seeds was recorded for each sample using a voucher collection of woody plant seeds present at the site constructed to facilitate identification.

Woody Plant Fruits

Abundance Estimates

Most woody plants within 10 m of the mist nets were identified to species. *Smilax, Rosa* and *Myrica* species were identified to genus. Phenology and estimates of ripe fruit abundance were noted for all individuals along the transects. Ripeness was determined on the basis of color and firmness (Sherburne 1972, Herrera 1984). A fruiting index was developed to estimate relative fruit abundance. The number of ripe fruits on each plant was estimated as being less than 10, between 10 and 100, between 100 and 1000, or greater than 1000.

Size

Fifty fruits were taken from 5 different individuals of each species. These fruits were measured with calipers to determine size.

Nutritional Value

Differences in fruit nutritional value were estimated using the methods of Herrera (1982). Two equations were used to estimate the significance of both fruit design (i.e. size and seediness) and the nutritional value of the pulp (i.e. amount and substance). Relative Yield, hereafter RY, (Equation 1), is a measure of the ratio of pericarp mass to seed mass. Since seeds are not digested, they may represent liabilities to frugivores when they occupy space in the digestive tract that could otherwise be filled with nutritious material (Herrera 1982). To calculate RY, the percent dry pulp is divided by the fresh fruit mass. This incorporates seed mass and accounts for the 'cost' to the frugivore of consuming and not digesting seeds. Optimal profitability, hereafter OP, (Equation 2), integrates RY with a specific nutritional component of the pulp (Herrera 1982). Optimal profitability describes the relative yield for specific nutritional components, such as lipids, sugars and proteins. Relative yield and optimal profitability are descriptive evaluations of fruit nutritional characteristics. They are useful for comparisons between species. Protein, lipid and sugar contents were determined from the literature (see Stiles 1980 and Johnson et al. 1985).

Relative Yield $RY=\frac{(1-W)}{FM}$

FM=fresh mass of whole fruit
W=% water in pulp

Optimal Profitability $OP=RY(NC)$

NC=nutritional component in question.

(Equations based on Herrera 1982.)

Statistical Analysis of Fruits

Differences in seed size, percent water in the pulp and relative yield were compared using analysis of variance statistical procedures, p=0.05, (Snedecor and Cochran 1989). These three characteristics were regressed against migrant consumption to determine if correlations existed (Snedecor and Cochran 1989).

Statistical Analysis of Avian-Fruit Interactions

Chi-square Tests

Chi-square tests (p=0.05) were used to determine if there were differences in the number of fruits consumed of each plant species, the number of bird species consuming each plant species, and the number of fruit species consumed by each bird species (Snedecor and Cochran 1989).

Principal Components Analysis

One goal of this study is to understand how interactions between migrating passerines and woody plant fruits are important for migration refueling and potential seed dispersal. The nature of biological phenomena is such that there are often correlations among several variables. To determine what the functional relationships between variables are, it is clearly necessary to know what the variables to be related are. For example, to gain an understanding of the relationships between avian migrants and the dispersal of woody plant seeds, it is first necessary to determine which interactions between variables are most important. For this study, principal components analysis, which is one type of factor analysis, was used to elucidate the important interactions between migrants and woody plants at the study site.

Factor analysis is ideal for examining the interactions between the 19 frugivore species and the 13 woody plant species because it has the potential to reduce the dimensionality of the data set to reveal the principal components which explain most of the variance (Bulger et al. 1993). Principle components analysis can be considered as a way of generating hypotheses about such interrelated variables (Comrey and Lee 1992). By essentially restructuring a data set into smaller sets of components of the original variables, it may be possible to determine the fundamental relationships which drive the system.

The goal of factor analysis is to isolate constructs that have greater intrinsic value for the purpose of understanding the relationships between variables (Comrey and Lee 1992). An original data matrix is reorganized into a variance-covariance matrix, or a correlation matrix, and matrix algebra is used to reduce this data set into linear combinations that form orthogonal axes. These linear combinations account for more variation in the original data than any single variable alone. Each orthogonal axis represents a principal component. The perpendicular axes of the components describe a multidimensional space (Iezzoni and Pritts 1991, Bulger et al. 1993).

Components are extracted by examining variables simultaneously. Transformation equations are extracted that represent as much variation from the original data set as possible (Iezzoni and Pritts 1991). After the first component is extracted, the effect of this component is removed from the correlation matrix. The second component is then extracted from the matrix of the first components 'residual' correlations. Thus, transformation equations are extracted one at a time, with the condition that the values from each subsequent equation are uncorrelated, and that the axes are orthogonal to each other (Iezzoni and Pritts 1991, Comrey and Lee 1992).

In general, when there are two or more factors, unrotated factors are not considered to represent useful scientific factor constructs, and factor rotation is necessary (Comrey and Lee 1992). The axes may be rotated to maximize the variance explained along each axis. In orthogonal rotations, the components remain uncorrelated with each other, and the resulting loading matrix represents correlation coefficients between the original variables and the principal components (Bulger et al. 1993).

Variable sampling adequacy is a measure of the extent to which a composite of variables is logically homogenous. Variables with low sampling adequacy have an unpredictable influence on principle components analysis., Elimination of those variables results in a more appropriate data set for analysis (Cureton and Dangostino 1983).

Two principal components analyses were conducted. One, examines the bird-fruit interactions from the birds' perspective; the other examines the interactions from the plants' perspective.

Principle components analyses were calculated using Statview 512® computer software.

Principle Components Analysis of Frugivore Preferences

A matrix of bird-fruit interactions was established, where average consumption by frugivore species were considered as variables, and woody plant fruits were considered as the cases. The use of average fruit consumption explores the importance of each fruit species to the diet of each bird species. It was expected that principle components analysis of this matrix would extract the components which are most important in explaining fruit choice by frugivores at the study site. Five variables were identified in this data set which had very low sampling adequacies, presumably as a result of very low sample sizes (all had sample sizes of less than 10 birds). These variables were eliminated from the data matrix (Cureton and Dangostino 1983).

Principle Components Analysis of Potential Seed Dispersal

A matrix of bird-fruit interactions was established using the total seed consumption of each fruit species as the variables, and the migrant bird species as the cases. Using total seeds consumed examines the importance of each bird species to dispersal of each plant species. This analysis extracted the factors most important in explaining potential seed dispersal patterns. Two cases were deleted because of very low sample sizes.

RESULTS

Passerine Migration

A total of 2782 birds of 67 species were captured from late August to late November, 1991. Eighty percent of all birds captured produced samples containing woody plant seeds, resulting in 1752 samples. Fifteen percent produced samples containing only insect material, and 5 % did not produce samples. Nineteen species, representing six families, were frugivorous (Table 1). The abbreviations listed in Table 1 will be used in all the figures and tables which follow. Common names are from the American Union of Ornitholigist' checklist.

Results were combined for five day periods, hereafter referred to as 'pendays', to reduce the effects of weather fluctuations. The total number of migrants and frugivores peaked in the middle of the migration season (mid-October) (Figure 3). However, individual species varied in the time of peak abundance (Figure 4 a-e). The most abundant species was the Yellow-rumped Warbler, which was 11 times more abundant than the next most abundant species. Nets were closed for three days near the end of the season due to severe storm weather.

Table 1. Frugivorous migrants captured at the study site from August 31 through November 15, 1991.

Family	Species	Common Name	Abbreviation	#. Captured
Corvidae	*Cyanocitta cristata*	Blue Jay	Bjay	80
Mimidae	*Toxostoma rufum*	Brown Thrasher	Thrs	21
	Dunetella carolinensis	Gray Catbird	Gcat	141
	Mimus polyglottus	Northern Mockingbird	Mock	2
Turdidae	*Catharus minumus*	Gray-Cheeked Thrush	Gcth	10
	Catharus ustulatus	Swainsons Thrush	Swth	14
	Catharus guttatus	Hermit Thrush	Heth	37
	Catharus fuscescens	Veery	Veer	11
	Hylocichla mustelina	Wood Thrush	Woth	8
Vireonidae	*Vireo olivaceous*	Red-Eyed Vireo	Revi	5
	Vireo griseus	White-Eyed Vireo	Wevi	2
Parulidae	*Dendroica coronata*	Yellow-rumped Warbler	Yrwa	1676
	Dendroica magnolia	Magnolia Warbler	Mawa	15
	Setophaga ruticilla	American Redstart	Amre	45
	Dendroica castanea	Bay-Breasted Warbler	Bbwa	4
	Geothylpis trichas	Common Yellowthroat	Coye	125
	Seiurus noveborancensis	Northern Waterthrush	Nwth	91
	Seiurus aurocapillus	Ovenbird	Oven	17
Icteridae	*Ictera virens*	Yellow-Breasted Chat	Ybch	7
	Icterus galbula	Northern Oriole	Bori	2

* Abbreviations will be used hereafter in figures and tables.

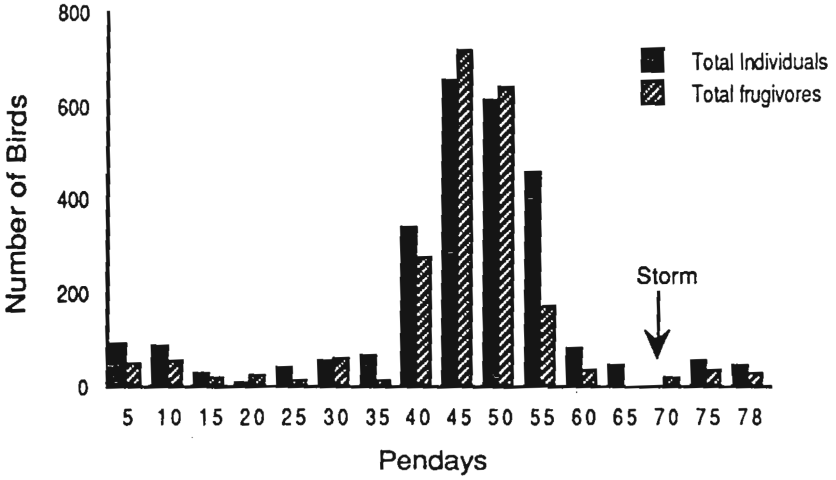


Figure 3. Timing and abundance of total migrants and total frugivores captured during the study period, August 31 through November 15, 1991. Data was compiled into five day periods (pendays) to reduce the effects of weather variability.

Figure 4. Figure 4 a-e. Timing and abundance of 19 frugivorous species found at the study site. Species were grouped according to overall abundance. Note: y axis scale changes from 4a-4e. Figure is continued on following pages.

Veer= Veery
Gcth=Gray Cheeked Thrush
Mawa=Magnolia Warbler
Heth=Hermit Thrush
Nwth=Northern Water Thrush
Gcat=Gray Catbird
Bbwa=Bay-breasted Warbler
Revi=Red eyed Vireo
Mock=Northern Mockingbird
Swth=Swainsons Thrush
Oven=Ovenbird
Amre=American Redstart
Thrs=Brown Thrasher
Coye=Common Yellowthroat
Bjay=Blue Jay
Bori=Baltimore Oriole
Wevi=White eyed Vireo
Yrwa=Yellow-rumped Warbler

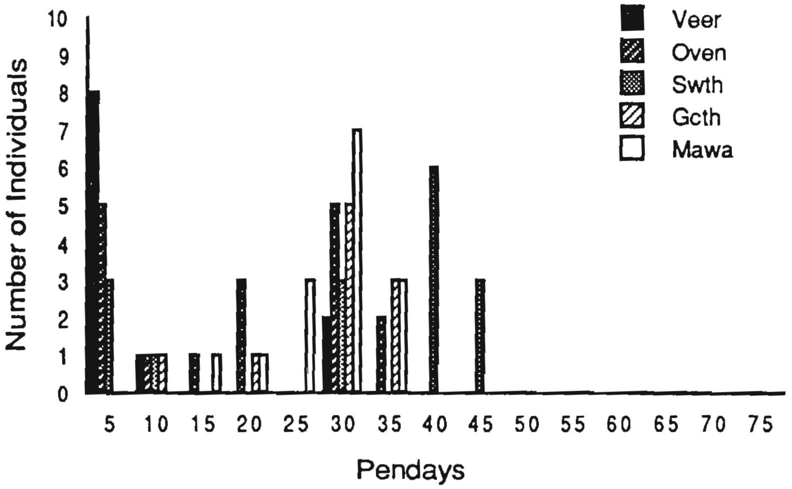


Figure 4a.

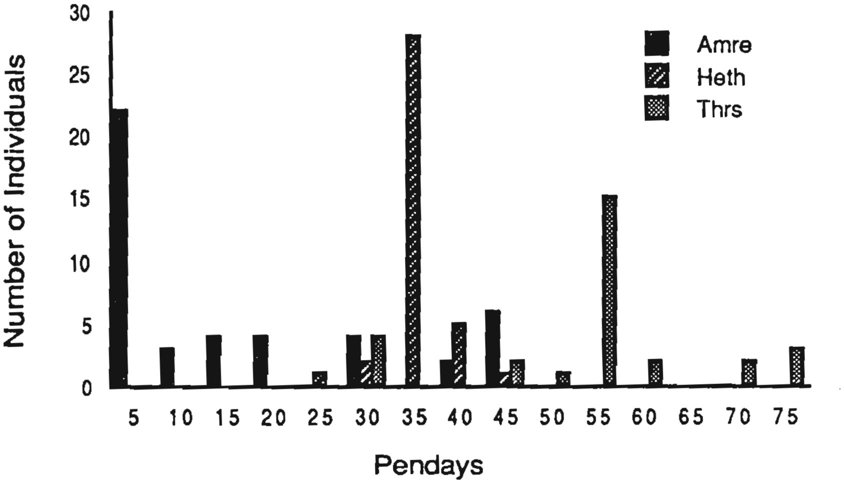
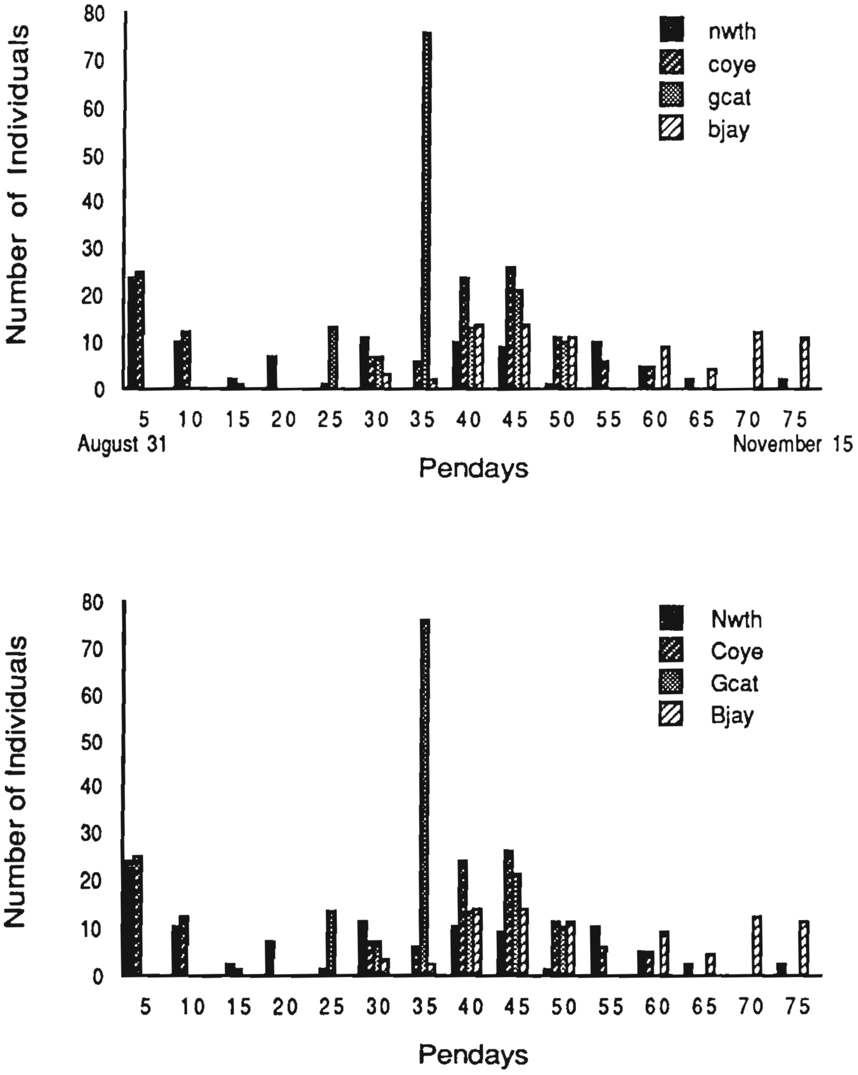


Figure 4b.


Number of Individuals
80
70
60
50
40
30
20
10
0
■ nwth
▨ coye
▩ gcat
▨ bjay
5
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45
50
55
60
65
70
75
August 31
November 15
Pendays
Number of Individuals
80
70
60
50
40
30
20
10
0
■ Nwth
▨ Coye
▩ Gcat
▨ Bjay
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60
65
70
75
Pendays

Figure 4c.

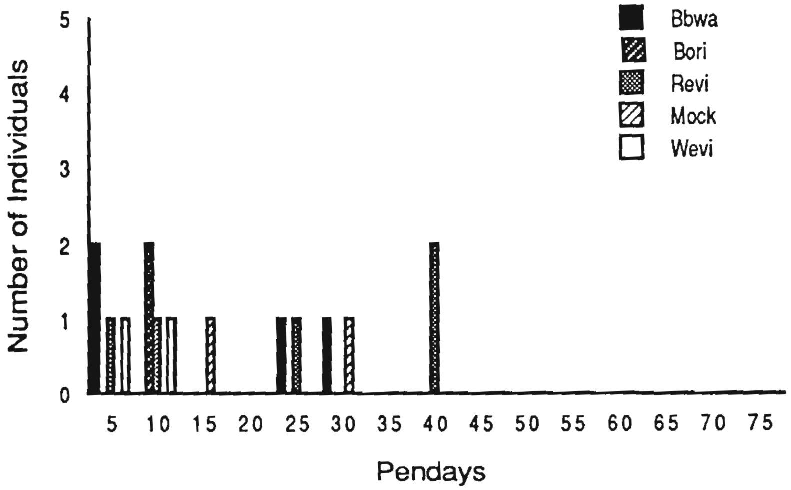


Figure 4d.

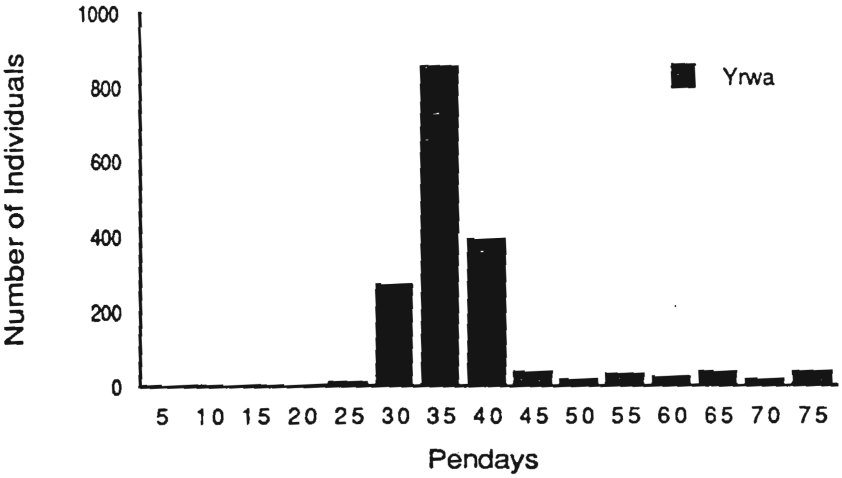


Figure 4e.

Woody plant Fruit Production

Thirteen woody plant species, representing 10 different families, produced fruits during the fall bird migration season which fit the characteristics of bird-dispersed fruits (Table 2). In general, plants which are dispersed by birds tend to be blue or red, contrasting with the plant's foliage and of a size that can be ingested and passed through a bird's digestive tract. Bird dispersed fruits also tend to be located near the tips of branches where they are easily accessed by birds, but not by mammals, which are often seed predators (Van der Pijl 1972). Total ripe fruit production peaked during the middle of the migration season. The number of species with ripe fruits peaked at the end of the migration season (Figure 5). Individual species varied in timing and abundance of ripe fruit production (Figure 6 a-e). The abbreviations listed in Table 2 will be used hereafter in figures and tables.

Table 2. Woody plant species producing fruits during the migration season.

Family	Species (Abbreviation)*		Common Name	Fruiting Time
Ulmaceae	*Celtis laevigata*	(CEL)	Hackberry	F
Cornaceae	*Cornus florida*	(COR)	Flowering Dogwood	F/P
Cupressaceae	*Juniperus virginiana*	(JUN)	Eastern Red Cedar	F/P
Rosaceae	*Rosa spp.*	(ROS)	Wild Rose	W/P
	Prunus serotina	(PRU)	Black Cherry	S
	Rubus idaeus	(RUB)	Red Raspberry	S
Caprifoliace	*Lonicera sempervirens*	(LON)	Wild Honeysuckle	F/P
Myricaceae	*Myrica spp.*	(MYR)	Bayberry	F/P
Aquifoliaceae	*Ilex opaca*	(ILE)	American Holly	W/P
Vitaceae	*Vitis aestivalis.*	(VIT)	Wild Grape	F
	Parthenocissus quinquefolia	(PAR)	Virginia Creeper	F
Liliaceae	*Smilax spp.*	(SMI)	Greenbriar	W/P
Anacardiaceae	*Toxicodendron radicans*	(TOX)	Poison Ivy	F

S=Summer Fruiting F=Fall fruiting
W=Winter Fruiting P=Persistent Fruits

*Abbreviations will be used hereafter in figures and tables.
Smilax spp.= either *S. bona-nox* or *S. rotundifolia.*
Myrica spp. =either *M. cerifera* or *M. pensylvanica*-could not distinguish seeds.
Rosa spp= could not be distinguished-many hybrids.

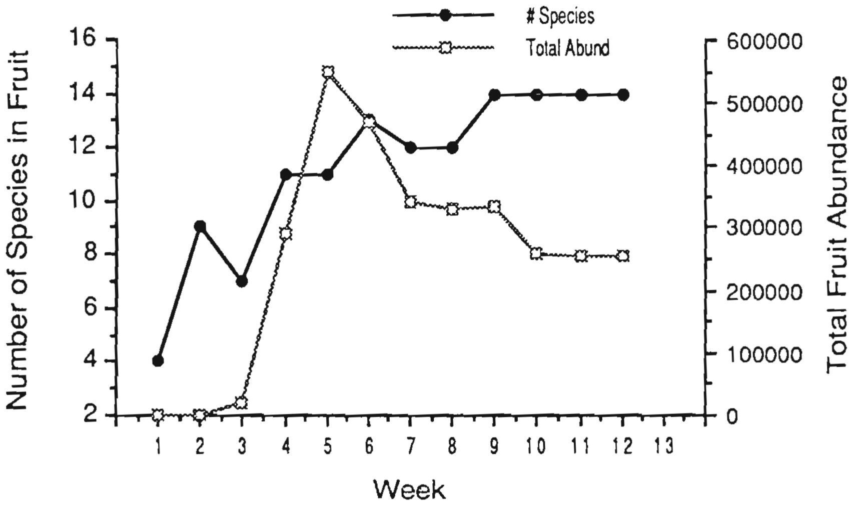


Figure 5. Timing of ripe fruit production and total fruit abundance for individuals of 13 woody plant species within 10m of mist nets.

Figure 6. Timing and abundance for fruit producing woody plants at the study site. The study season began August 31, 1991 and lasted through November 15, 1991. Fruit species were grouped according to abundance of fruit production. Note y axis changes from 6a-6b. Figure is continued on following pages.

PRU=*Prunus virginiana* (Black Cherry)
RUB= *Rubus idaeus* (Red Raspberry)
CEL= *Celtis occidenatlis* (Hackberry)
PAR= *Parthenocissus quenquefolia* (Virginia Creeper)
COR=*Cornus florida* (Flowering Dogwood)
MYR= *Myrica spp.* (Bayberry)
LON=*Lonicera sempivirens* (Wild Honeysuckle)
VIT= *Vitis aestivalis* (Wild Grape)
TOX=*Toxicodendron radicans* (Poison Ivy)
SMI=*Smilax spp.* (Greenbriar)
JUN=*Juniperus virginiana* (Eastern Red Cedar)
ROS=*Rosa spp.* (Wild Rose)
ILE=*Ilex aquifolia* (American Holly

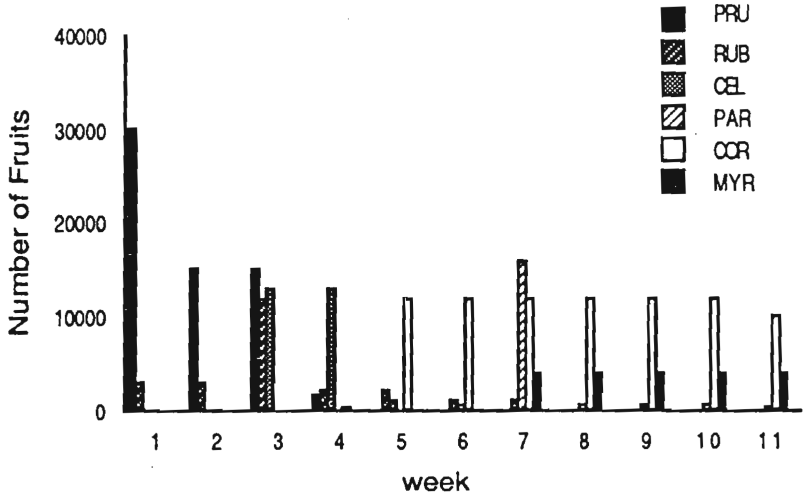


Figure 6a.

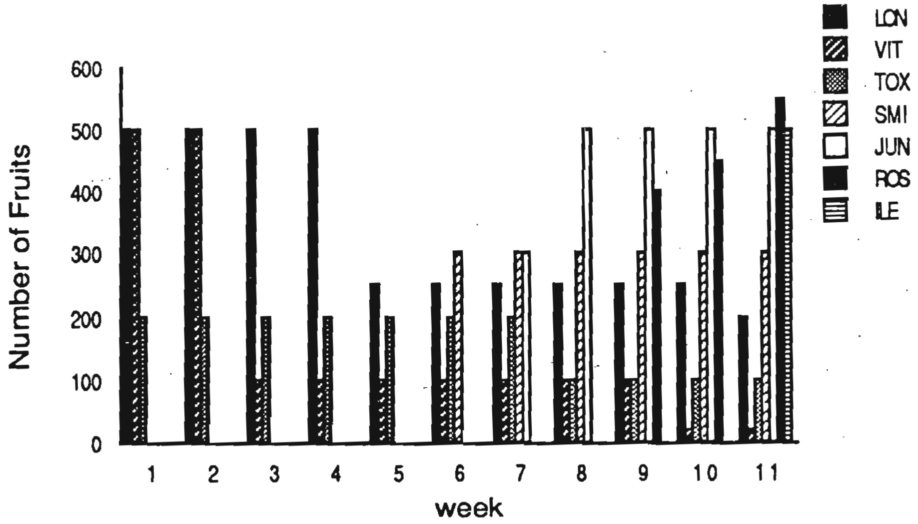


Figure 6b.

Data from the literature on the nutritional composition of fruits are inconsistent, however certain trends are evident (see appendix, Table 11). Woody plants that fruit in late summer and early fall have the highest sugar and water contents. All species of woody plants at the study site have fruits which are relatively low in protein content. *Juniperus virginiana* and *Myrica spp.* differ from the other woody plant species at the study site by producing fruits which have high lipid and low water contents. The other woody plant species are composed of 60-90% water (Table 3). Relative yield of most species is between .1 and .2. *Juniperus virginiana* and *Myrica spp.* have relative yields of .4 (Table 3). Optimal profitability was similar for all species except *J. virginiana* and *Myrica spp.* which had significantly higher optimal lipid profitability (Table 3). *J. virginiana* and *Myrica spp.* are significantly smaller in size than other fruits at the study site. *Celtis laevigata* is significantly larger than other fruits (Table 3). The majority of fruits are between 6-7mm in diameter. Correlations between fruit consumption and seed size, percent water content, relative yield, were poor.

Table 3. Seed size, water content, relative yield and optimal profitabilities of fruits at study site. Protein, sugar and lipid contents used to determine optimal profitability were taken from the literature (Stiles 1980, Johnson et al. 1985).

* indicate significant differences as determined by analysis of variance (p=.05).

Fruit Species	Seed Size (mm)	% water	Ave # Seeds/ Fruit	Relative Yield (mg)	Optimal Profitability Pro (mg)	Optimal Profitability Lip (mg)	Optimal Profitability Sug (mg)
Celtis laevigata	9.8*	.49	1	.101	.972	.972	3.24
Cornus florida	6.4	.91	4	.0647	.218	2.69	.669
Juniperus virginiana	3.5*	.43*	1.5	.400*	-	8.0	-
Rosa spp.	6.1	.58	6	.193	-	-	-
Prunus serotina	7.5	.84	1	.120	.243	.051	2.4
Rubus idaeus	7.17	.80	27	.183	1.01	.643	6.56
Lonicera sempivirens.	7.5	.73	3	.191	-	-	-
Myrica spp.	3.17*	.40*	1	.404*	-	9.38	-
Ilex opaca	7.2	.90	6	.044	-	.348	-
Vitis aestivalis	8.1	.88	4	.112	.251	.091	1.39
Parthenocissus quinquefolia	7.48	.90	3.5	.069	.265	1.77	.764
Smilax spp.	7.3	.81	3	.141	.562	.118	1.97
Toxicodendron radicans	5.8	.80	3	-	-	-	-

Rel. Yield=Relative Yield
OP=Optimal Profitability
OPpro=Protein content
OPlip=Lipid content
OPsug=Sugar content
See text for explanations of terms.

Patterns in Fruit Consumption

Fruits from the different woody plant species were consumed in significantly different quantities by migrating frugivores over the duration of the study (Chi-square, p=.0001, X^2=39.3, DF=12).

The timing of fruit consumption varied for different woody plant species (Figure 7a-c). *Rubus idaeus* (RUB), *Toxicodendron radicans* (TOX), *Vitis aestivalis* (VIT) and *Prunus serotina* (PRU) were all consumed early in the season. *Parthenocissus quinquefolia* (PAR), and *Ilex opaca* (ILE) were primarily consumed during the middle of the season. *Myrica spp.*(MYR), *Juniperus virginiana* (JUN), and *Lonicera sempivirens* (LON) were consumed in the greatest quantities in the middle of the season, with consumption continuing through the end of the migration season. *Cornus florida* (COR) was consumed throughout the season. *Rosa spp.* (ROS) and *Smilax spp.* (SMI) were primarily consumed late in the migration season.

Seeds of *Myrica spp.* accounted for 74% of all seeds consumed, *Parthenocissus quinquefolia* for 14%, *Cornus florida* for 3.5% and *Juniperus virginiana* for 2.5%. Each of the remaining woody plant species accounted for less than 2% of the total consumption (Figure 8). Relatively few samples contained more than one species of seed.

Figure 7. Fruits consumed during the migration season in large quantities (a), moderate quantities (b) and the lesser quantities (c). The study season began August 31, 1991 and lasted through November 15, 1991.

RUB=*Rubus idaeus.* (Wild Rose)
PAR=*Parthenocissus quinquefolia* (Virginia Creeper)
MYR=*Myrica spp.* (Bayberry)
PRU=*Prunus serotina* (Black Cherry)
VIT=*Vitis aestivalis* (Wild Grape)
JUN=*Juniperus virginiana* (Eastern Red Cedar)
COR=*Cornus florida* (Flowering Dogwood)
LON=*Lonicera sempivirens* (Wild Honeysuckle)
SMI=*Smilax spp.* (Greenbriar)
ROS=*Rosa spp.* (Wild Rose)
ILE=*Ilex aquifolia* (American Holly)
TOX= *Toxicodendron radicans* (Poison Ivy)

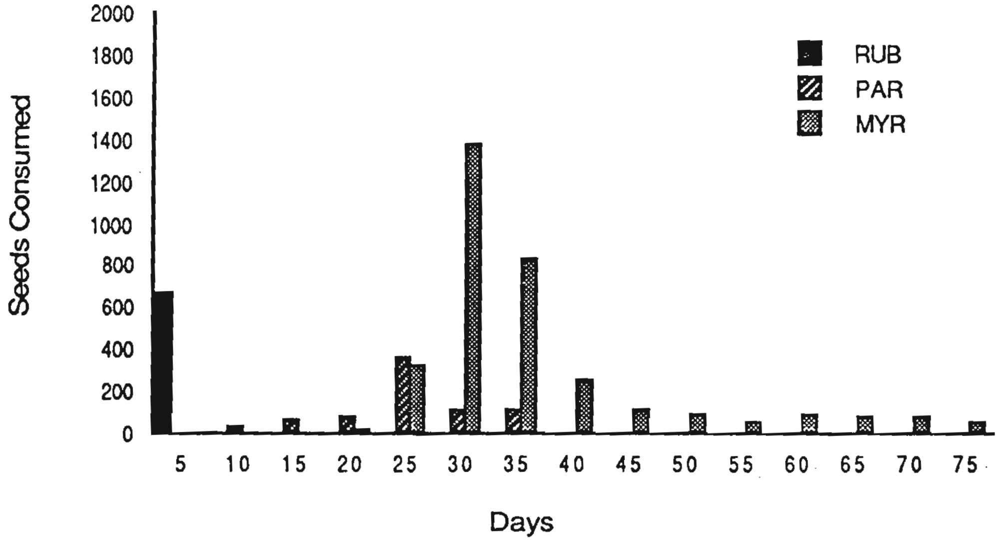


Figure 7a.

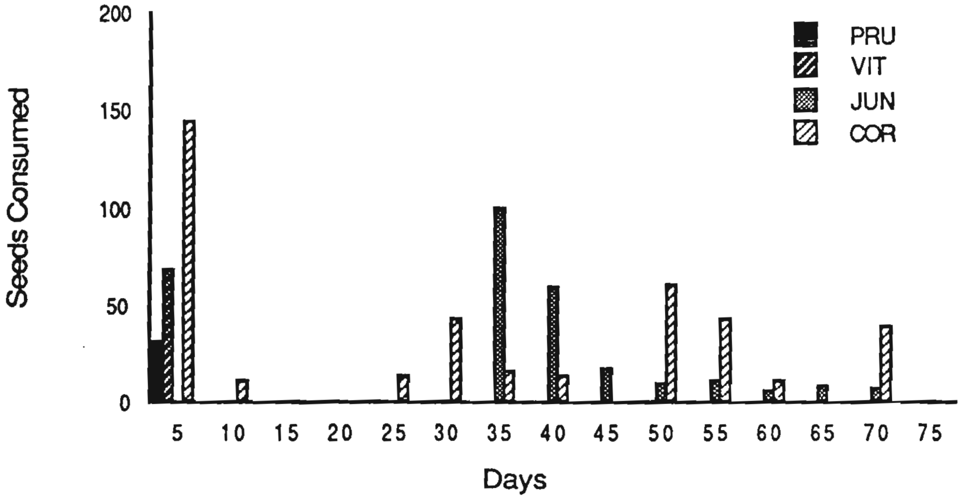


Figure 7b.

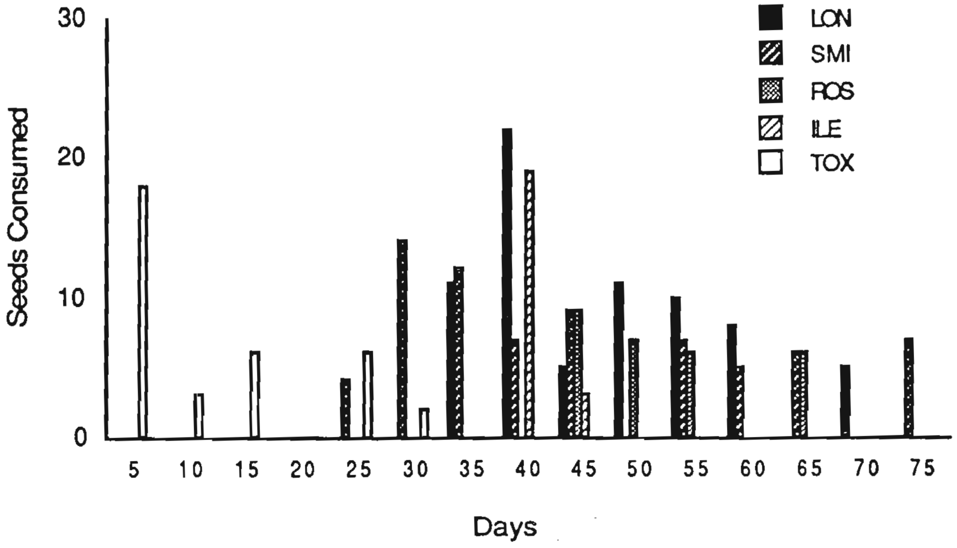

Seeds Consumed
30
20
10
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
Days
LON
SMI
ROS
ILE
TOX

Figure 7c.

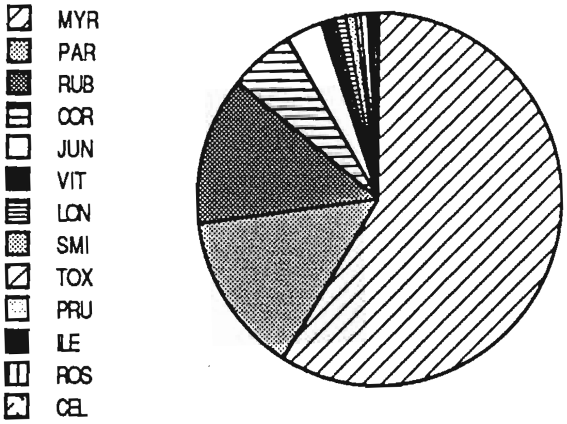


Figure 8a.

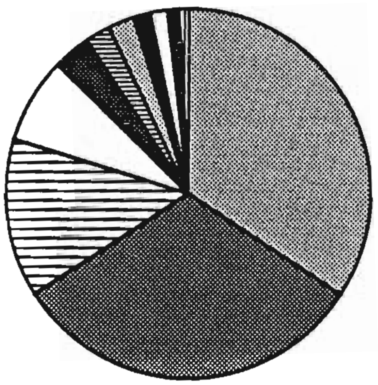


Figure 8b.

Figure 8. (a). Percentage of seeds from 13 woody plant species represented in stomach content samples of frugivorous migrants collected from August 31 through November 15, 1991. (b). Percentages excluding *Myrica* spp. A total of 6738 seeds were collected from 1780 samples.

Total fruit consumption for the entire study site was positively correlated with frugivore abundance (r squared =.75, DF=80). However, only specific interaction, that between Yellow-rumped Warbler and *Myrica spp.* showed a positive correlation between bird abundance and fruit consumption (Figure 9). When fruit abundance for each woody plant species was ranked, with the most abundant species being first, consumption by migrants was not related to ranking. The species which were consumed in the greatest quantities were ranked sixth and seventh (Table 4).

The number of bird species consuming the fruits of each woody plant species varied from 1 to 14, with the average being 4.7. There was a tendency for winter fruiting plants to be consumed by fewer species than fall or summer fruiters (Table 9). The number of woody plant species consumed by one bird species varied from a high of 10 (Nwth=Northern Waterthrush), to a low of 1 (Bbwa=Bay Breasted Warbler; Woth=Wood Thrush).

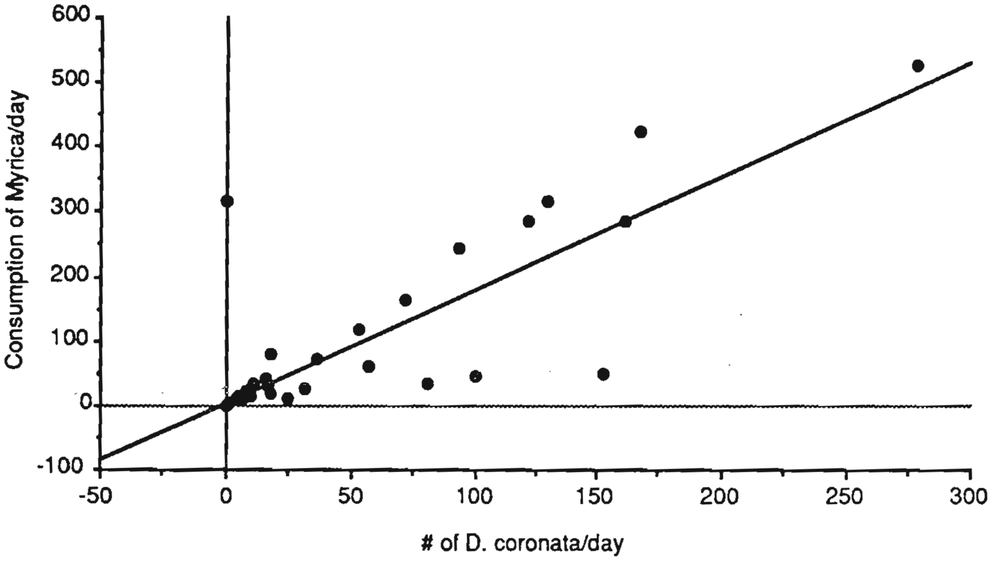


Figure 9. Correlation between consumption of *Myrica spp.* and the number of Yellow-rumped Warblers present from August 31, 1991 through November 15, 1991. R squared=.73, DF=74, Std. Error=55.12

Table 4. Comparison of abundance ranking and consumption. Rank was determined from total abundance for the entire study period. Rank 1 indicates greatest fruit production, rank 13 indicates lowest fruit production.

Species	Abundance Rank	Percentage of total consumption
COR	1	5.8
PRU	2	0.61
MYR	3	58.5
CEL	4	0.07
RUB	5	13.2
PAR	6	14.1
LON	7	0.99
ROS	8	0.31
JUN	9	3.1
SMI	10	0.91
ILE	11	0.43
TOX	12	0.69
VIT	13	1.3

Principal Components Analysis

Recall that the goal of the principal components analysis is to elucidate the biological meaning for variance in the data set by interpreting intercorrelations among the variables (Iezzoni and Pritts 1991). After orthogonal rotation, the factor loadings on each component represent correlation coefficients between the original variables and the principal components (Comrey 1973, Bulger et al. 1993). Variables that have large loadings of the same sign for the same component are positively intercorrelated; variables that have large loadings of the opposite sign for the same component are negatively intercorrelated (Bulger et al. 1993). The original matrices used for both the average fruit and total seed consumption principal components analyses are reported in the appendix (Tables 12 and 13, respectively).

Birds' Perspective

The principal components analysis of average consumption identified five components which explain nearly 100% of the variance associated with the original variables (Table 6). The first three components account for 77% of the proportionate variance. Each principal component represents an underlying relationship between the variables. For each component in this analysis, this relationship is most clearly explained by the "importance" of one woody plant species to frugivorous migrants. Importance is used here to describe a percentage of the total fruits consumed by each frugivore species.

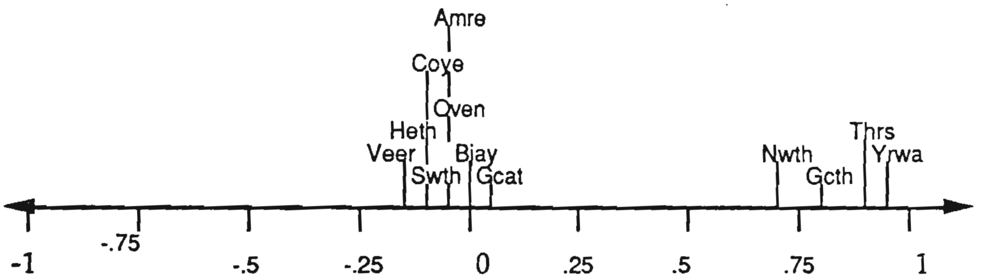
The first component isolates the importance of *Myrica spp.*, the second component isolates the importance of *Cornus florida*, and the third component isolates the importance of *Parthenocissus quinquefolia* in the diets of frugivorous migrants at the study site. Each component has been named after the interactions which it represents. Thus, Myrica/Frugivore, Cornus/Frugivore, and Parthenocissus/Frugivore are the names of the first, second and third components, respectively. No interaction, or set of interactions was found to explain the intercorrelations of the last two components. In a two-dimensional representation of the factor loadings on each component, high correlation with a component is related to high average consumption of a woody plant species by a bird species (Figure 10).

Table 5. Principle components analysis for average fruit consumption of 11 woody plant species by 12 frugivorous migrant species. Eigenvalues, with percent variance explained (rotated), and varimax rotated variable loadings (correlation coefficients) for frugivorous birds with respect to the five components extracted in the principal components analysis. The highest correlation coefficient for each variable is shown in bold face. Variables with high coefficients on the same component are intercorrelated.

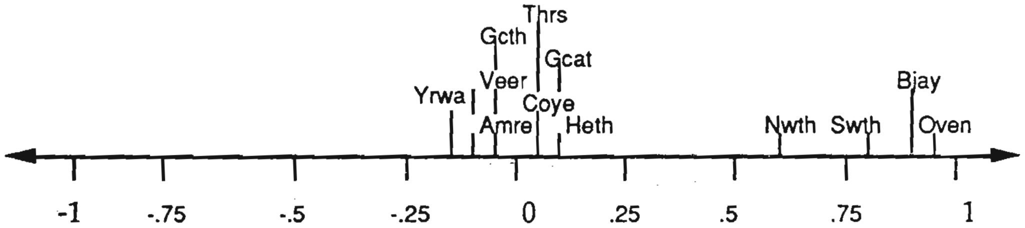
	Component					
Eigenvalue:	**1**	2	3	**4**	5	
% variance:	27.8	24.0	25.7	12.2	10.3	
Variable						Communality
Amre	-.183	-.113	-.028	**-.534**	**-.632**	.808
Nwth	**.729**	**.616**	.213	-.107	.049	.997
Coye	-.051	.115	**.983**	-.034	-.031	.993
Veer	-.163	-.061	-.039	-.292	**.821**	.806
Oven	-.046	**.848**	-.32	.008	-.045	.92
Heth	-.059	.061	-.11	**.88**	-.152	.79
Swth	-.073	**.779**	**.527**	-.108	.26	.968
Gcat	.396	.049	**.908**	-.054	-.039	.996
Gcth	**.71**	-.016	**.692**	-.087	-.031	.998
Thrs	**.963**	-.007	.133	-.177	-.066	.979
Bjay	-.002	**.852**	.295	.307	-.106	.964
Yrwa	**.985**	-.137	.004	-.093	-.005	1

Figure 10. One -dimensional representation of the principal components that describe the patterns of average fruit consumption of 11 woody plant species by 12 migrant species. Each component is represented by an arrow which intersects the middle of the component space at zero. The variable correlations with each component are indicated by their location along the principal component line. Correlation increases towards 1 and -1. The percent variance explained by each component is indicated in parentheses after the component number. Figure is continued on the following page.

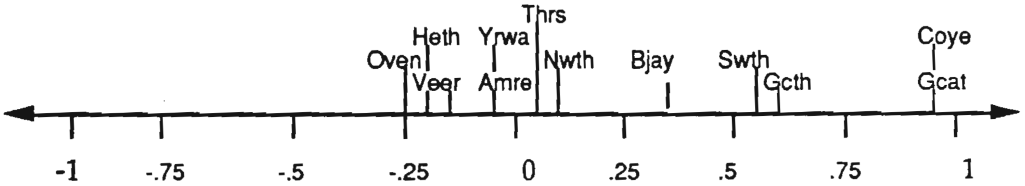
Amre=American Redstart
Nwth=Northern Waterthrush
Coye=Common Yellowthroat
Veer=Veery
Oven=Ovenbird
Heth=Hermit Thrush
Gcat=Gray Catbird
Gcth=Gray Cheeked Thrush
Thrs=Brown Thrasher
Bjay=Blue Jay
Yrwa=Yellow-rumped Warbler
Swth=Swainsons Thrush



Principal Component 1 (27.8%): Myrica/Frugivore component. Represents the importance of *Myrica spp.* in the diets of frugivorous migrants.



Principal Component 2 (24%): Cornus/Frugivore component. Represents the importance of *Cornus florida.* in the diets of frugivorous migrants.



Principal Component 3 (25.7%): Parthenocissus/Frugivore component. Represents the importance of *Parthenocissus quinquefolia.* in the diets of frugivorous migrants.

Plants' Perspective

Four principal components were extracted from the analysis of total seed consumption by migrating frugivores. Each factor explained approximately 25% of the variance (Table 7). Each component may be explained by the consumption pattern of one frugivore species. In a two-dimensional representation of each component, high correlation with a component is related to high total seed consumption (Figure 11).

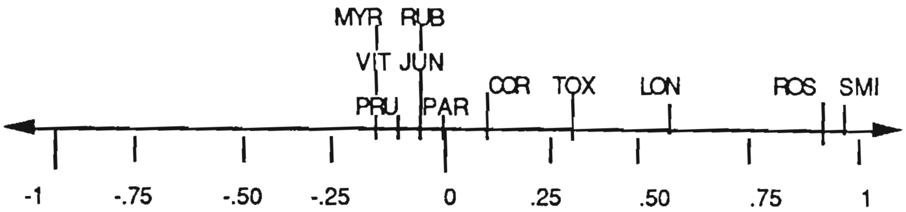
The components have been named to describe the interaction which they represent. For the first component, the factor loading's are related to the consumption pattern of The Brown Thrasher (Thrs). For the second component, they are related to the consumption pattern of the Northern Waterthrush (Nwth). For the third, they are related to the consumption pattern of the Common Yellowthroat (Coye). The factor loading patterns of the fourth component are related to the consumption pattern of the Yellow-rumped Warbler (Yrwa).

Table 6. Principle components analysis for total seed consumption of 11 woody plant species by 17 frugivorous migrant species. Eigenvalues, with percent variance explained (rotated), and varimax rotated variable loadings (correlation coefficients) for woody plant fruits with respect to the four components extracted in the principal components analysis. The highest correlation coefficient for each variable is shown in bold face. Variables with high coefficients on the same component are intercorrelated.

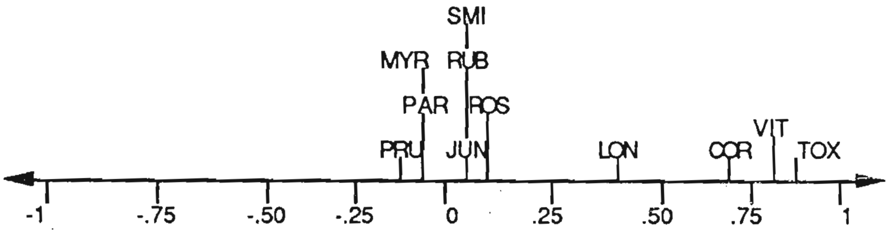
	Component				
Eigenvalue:	**1**	**2**	**3**	**4**	
% Variance:	27.0	24.5	23.7	24.8	
Variable					Communality
PRU	-.154	-.117	.135	-.183	.089
JUN	-.064	.092	-.003	**.988**	.989
ROS	**.957**	.159	-.011	-.016	.942
RUB	-.088	.112	**.959**	-.112	.953
PAR	-.023	-.088	**.949**	.055	.912
VIT	-.068	**.779**	.158	-.035	.637
MYR	-.057	-.088	-.001	**.984**	.99
LON	**.548**	.409	-.161	-.04	.496
COR	.136	**.715**	-.165	-.049	.559
SMI	**.953**	.027	-.017	-.03	.91
TOX	.27	**.792**	-.02	-.021	.62

Figure 11. One-dimensional representation of the principal components that describe the patterns of total seed consumption of 11 woody plant species by 17 migrants. Each component is represented by an arrow which intersects the middle of the component space at zero. Variable correlations with each component are indicated by their location along the principal component line. Correlations increase towards 1 and -1. The percent variance explained by each component is in parentheses after the component number. Figure is continued on following pages.

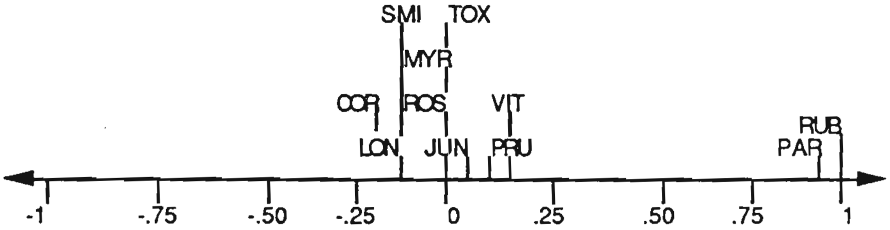
PRU=*Prunus serotina*	(Black Cherry)
COR=*Cornus florida*	(Flowering Dogwood)
JUN=*Juniperus virginiana*	(Eastern Red Cedar)
RUB=*Rubus idaeus*	(Red Raspberry)
LON=*Lonicera sempivirens*	(Wild Honeysuckle)
MYR=*Myrica spp.*	(Bayberry)
VIT=*Vitis aestivalis*	(Wild Grape)
PAR=*Parthenocissus quinquefolia*	(Virginia Creeper)
SMI=*Smilax spp.*	(Greenbriar)
TOX=*Toxicodendron radicans*	(Poison Ivy)



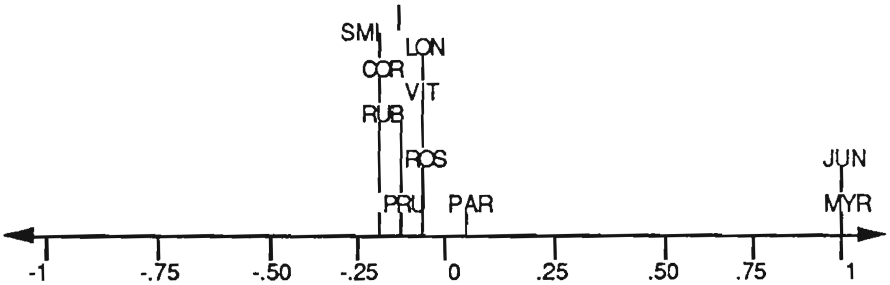
Principal Component 1 (27%): Thrs/ Seed Dispersal. Represents the importance of *Toxostoma rufum*, the Brown Thrasher (Thrs) in dispersing seeds of woody-plants.



Principal Component 2 (24.5%): Nwth/ Seed Dispersal. Represents the importance of *Seiurus novaborancensis*, the Northern Waterthrush (Nwth) in dispersing seeds of woody-plants.



Principal Component 3 (23.7): Coye/ Seed Dispersal. Represents the importance of *Geothylpis trichas*, the Common Yellowthroat (Coye) in dispersing seeds of woody-plants.



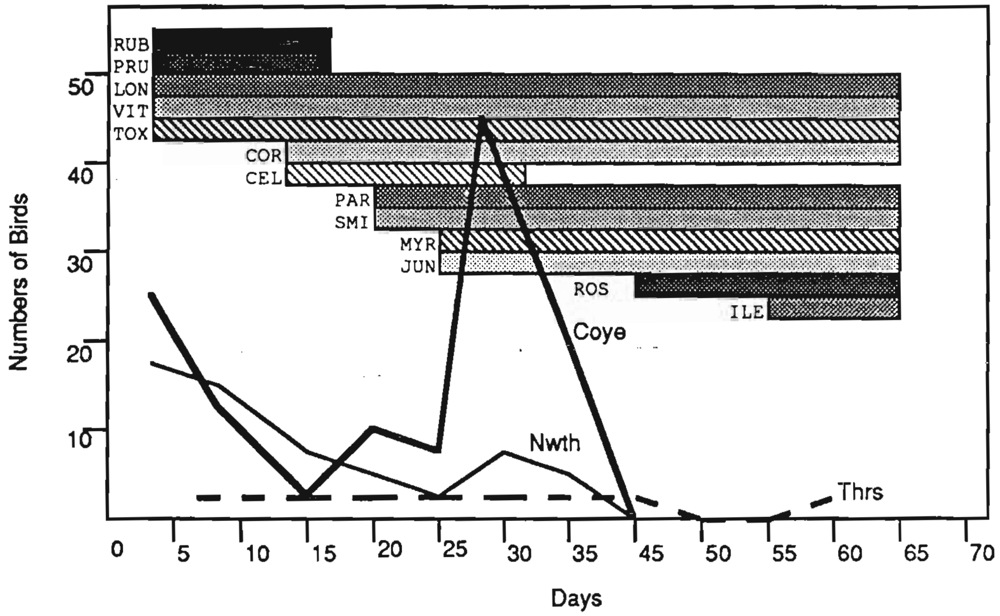
Principal Component 4 (24.8%):Yrwa/ Seed Dispersal. Represents the importance of *Dendroica coronata*, the Yellow-rumped Warbler (Yrwa) in dispersing seeds of woody-plants.

Each of the factors describing the total seed consumption patterns has at least two woody plant species which are strongly positively correlated (Figure 11). Factor loadings which are in close proximity may be described as being "grouped" or clustered (Iezzoni and Pritts 1991). One group includes *Myrica* (MYR) and *Juniperus virginiana* (JUN), one includes *Parthenocissus quinquefolia* (PAR) and *Rubus idaeus* (RUB), one includes *Vitis aestivalis* (VIT), *Toxicodendron radicans* (TOX) and *Cornus florida* (COR); and one group includes *Rosa* (ROS) and *Smilax* (SMI). These groupings may be an indication of dispersal guilds.

The coincidence of frugivore abundance and fruit abundance appears to be one of the most important factors determining potential seed dispersal. Excluding the Yellow-rumped Warbler, (Yrwa), the three bird species which were most important in explaining the principal component axes for total seed consumption had in common that they consumed relatively large quantities of the species which were in fruit when they were present. The Northern Waterthrush (Nwth) and The Common Yellowthroat (Coye) were not the most abundant frugivores during the early and middle of the migration season. However, they consumed relatively large quantities of several plant species which were in fruit during this time (Figure 14). Other frugivore species which were equally or slightly more abundant were not as important in the potential seed dispersal of the woody plant community. The Yellow-rumped Warbler was by far the most abundant frugivore from the middle to the end of the migration season, but primarily consumed *Myrica spp.* The Brown Thrasher (Thrs) was the most abundant frugivore at the end of the season, other than the Yellow-rumped Warbler. Figure 12 shows the timing of ripe fruit production for each species, in relationship to the timing and abundance for the three frugivores mentioned above.

Figure 12. Abundance and timing of the migrant frugivores associated with the principal component analysis describing total seed consumption (excluding Yrwa), in relationship to fruit availability. Figure continued on following page.

Coye=Common Yellowthroat
Nwth=Northern Waterthrush
Thrs=Brown Thrasher
RUB=*Rubus idaeus* (Red Raspberry)
PRU=*Prunus serotina* (Black Cherry)
LON=*Lonicera sempivirens* (Wild Honeysuckle)
VIT= *Vitis aestivalis* (Wild Grape)
TOX=*Toxicodendron radicans* (Poison Ivy)
PAR=*Parthenocissus quinquefolia* (Virginia Creeper)
SMI=*Smilax spp.* (Greenbriar)
MYR=*Myrica spp.* (Bayberry)
JUN=*Juniperus virginiana* (Eastern Red Cedar)
ROS= *Rosa spp.* (Wild Rose)
ILE=*Ilex aquifolia* (American Holly)


RUB
PRU
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Nwth
Thrs
Numbers of Birds
10
20
30
40
50
0
5
10
15
20
25
30
35
45
50
55
60
65
70
Days

DISCUSSION

Characteristics of migrant frugivores and fruit production in a south temperate location

In most temperate forests, bird dispersed plants typically have the greatest cover values in edges, gaps, riparian zones and early successional sites, and occupy much less space in mature forests (Herrera 1984). Keeping with this trend, the study site and the higher barrier islands have a greater percentage of plants which produce bird dispersed fruits than the more mature, inland forests (McCaffrey and Dueser 1990).

The widely reported pattern of the coincidental timing of ripe fruit production and southward bird migrations in temperate regions is supported by this study. However, the passerine migration through this south temperate area started later, lasted longer, and was not as abrupt as migrations through north temperate areas (Thompson and Willson 1979, Stiles 1980, Sorenson 1981). Although the migration at this site peaked approximately one month later than in north temperate regions, the peaks in abundance of both woody plant fruits and migrating birds still coincided. Considering the complexity of the factors determining migration timing, it is unlikely that there is direct selectional pressure between birds and plants to produce this coincidence. Weather conditions such as strong winds, high humidity, precipitation and solar radiation input have all been linked to variability in migration timing (Richardson 1978). The milder climate of south temperate areas may act as a proximal que for later fruit production, which by chance, coincides with the later timing of bird migrations.

Winter fruit production may be a more important dispersal strategy in south temperate areas. Both the timing and diversity of fruits produced at this south temperate location are unlike patterns observed in north temperate areas and more similar to observations from Mediterranean scrublands. In north temperate forests the greatest diversity and quantity of fruits are produced in late summer and early autumn (Thompson and Willson 1979, Stiles 1980, Sorenson 1981). In Mediterranean scrublands, fruit quantities and diversity are greatest in late autumn and winter (Herrera 1984). At this south temperate location total fruit abundance was greatest from middle to late autumn, and the greatest diversity of plant species in fruit was at the end of autumn. This indicates that fruit production begins and ends later at this south temperate location, with respect to north temperate areas.

It is not known whether phenological events such as germination, flowering and fruiting follow each other after fixed time intervals, or are independently controlled by environmental cues (Rathke and Lacey 1985). It seems likely that the time between flowering and fruit production is a function of both types of control (Willson 1983, Rathke and Lacey 1985). The fact that the same species of temperate woody plant species fruit later at more southern latitudes indicates that there is some degree of flexibility in the controls. Herrera (1984) suggests that the mild and wet climates of Mediterranean scrublands allows for persistent winter fruiting. It seems possible that milder climates induce later fruiting in North American south temperate locations as well.

Potentially flexible fruiting times produce several options based on the ratio of energy invested in fruit production to dispersal success. Fruit production is expensive energetically. Fruits which are not successfully dispersed represent an energetic loss to the parent, however successful seed dispersal results in potential germination. Spring fruit production is limited for most woody plants because flower pollinators are not available until the weather warms (Willson 1983). Fruits develop and mature during the summer. There is little incentive for early summer fruit ripening because most dispersers are spread out due to territoriality, and are more interested in obtaining high protein insect foods to feed their growing young (Thompson and Willson 1979, Willson 1983). Therefore, fall is the ideal time for fruit ripening of bird dispersed fruits. Photosynthate accumulates during the summer to support fruit ripening and potential dispersers are abundant. However, one potentially important disadvantage in moderate to warm temperatures is rapid microbial decay of fruits that are not consumed (Janzen 1977, Stiles 1980). Fruits produced later in the fall season are not as susceptible to microbial decay because temperatures are generally lower. The trade-off to later fruit ripening is lower frugivore abundance as migrations end. In south temperate areas, migrants are more likely to become winter residents. Indeed, it is likely that many of the birds caught during this study at the end of November will become winter residents (Christmas Count Surveys 1987, 1988, 1989). These resident winter frugivores are present for longer periods of time than fall migrants, which may impart advantage to the production of later ripening and/or persistent fruits.

Importance of fruit resources to migrants

This study indicates that the fruits of woody plants are an important resource for several species of passerine migrants, and that these migrants play a significant role in dispersing several woody plant species. Thirty percent of the migrant species, and 63% of migrant individuals, passing through the study area consumed fruits of woody plants in some quantity. Some of these species were highly frugivorous, while others consumed only a few fruits.

Three categories of fruit production are evident at the study site; primary, secondary and tertiary. Primary fruiters are generally considered to be species which produce nutrient rich pulps, relatively large fruit crops, and fruits that ripen during the peak time of fruit diversity and abundance (Herrera 1984). Primary fruits would be the most profitable to frugivores, and it may therefore be expected that they would be consumed in the greatest quantities. However, primary fruits would also be the most energetically expensive for plants to produce, and it would therefore be expected that fewer fruits would be produced. The only fruit species at the study site to have all the characteristics of a primary species were *Myrica spp* .(Bayberry). Consumption of *Myrica spp.* fruits represented 75% of all fruit consumption, and 98% of this consumption was by the frugivore the Yellow-rumped Warbler.

Secondary species may be described as those which produce abundant, but low nutritional quality fruits that coincide with migration timing. These low quality, abundant fruits may be equally attractive as high quality fruits to migrants if greater fruit quantities reduce time spent searching and foraging. Secondary fruits are consumed by many frugivores. Four woody plant species fit this description: *Parthenocissus quinquefolia* (Virginia Creeper), *Cornus florida* (Flowering Dogwood), and *Rubus idaeus* (Red Raspberry) and *Celtis occidentalis* (Hackberry). *Parthenocissus quinquefolia* was the most abundant fruit during the peak of the migration season. *Cornus florida,* was the most abundant fruit at the end of the migration season. Both *R. idaeus* and *P. serotina* produced very abundant fruits, but only at the beginning of the migration season. Despite the abundance of *Celtis occidentalis* fruits during the migration peak, they were not consumed by many migrants. The remaining fruit species are described here as "tertiary" fruit resources. These are species which produce few, low quality fruits, although they are consumed to some extent.

Timing of ripe fruit production and abundance of fruits appear to be more important factors than fruit nutritional value to migrating birds for the other woody plant species at the site. Most woody plants at the study site produced fruits which were similar with respect to nutritional value and size, with the exception of *Myrica spp.* and *J. virginiana* fruits, which were significantly smaller and had higher relative yields (Table 3). However, there was a substantial difference in the timing and abundance of fruits produced by different woody plant species. In general, more abundant fruits were more likely to be consumed, with the exception of *Myrica spp.,* which were not the most abundant fruits, but were consumed in very large numbers by the Yellow-rumped Warbler. For example, two secondary species, *Prunus serotina* and *Rubus idaeus,* could potentially be important to migrants, but they are generally finished fruiting before the majority of migrants arrive. In contrast, the fruits of *Parthenocissus quinquefolia* and *Cornus florida* were very abundant during the migration peak and their fruits were consumed in large quantities.

Importance of migrant frugivores to seed dispersal

In north temperate areas measures of fruit removal rates vary seasonally from 50-60% of the ripe crop per week for fall fruiters, 20-30% per week for summer fruiters and <20% per week for the winter crop (Thompson and Willson 1979, Sorenson 1981, Stapanian 1982). These studies indicate that dispersal may be fairly inefficient, considering the energy invested in fruit production, and that there may be competition for dispersers (Willson 1983, Herrera 1984).

Four groups of factor loadings in the principal component space describing total seed consumption are evident (Figure 12). Of the four groups, one included one secondary and two tertiary fruiters, one group included one primary fruiter and one tertiary fruiter, and one group included two tertiary fruiters. The fourth group included two secondary fruiters. (However, it is unlikely that they form a dispersal guild because they were in fruit at different times during the migration season.) These groups suggest the presence of dispersal guilds. The consumption of a higher-ranking plant in a group indirectly favors the consumption of lower-ranking, coexisting plants. The maintenance of these relationships is dependent on the varied diets of frugivores Herrera (1984).

Dispersal guilds are suggested when more than one plant is functionally dependent on the same frugivore species for dispersal. Dispersal guilds may allow primary or secondary fruiters to indirectly enhance the seed dispersal possibilities of lower-ranking plants, or allow species from the same fruiting category to enhance each others seed dispersal possibilities (Herrera 1984). Competition for dispersers may be clouded by the presence of disperser guilds, if enhanced production by one species also benefits another.

COR, VIT and TOX dispersal guild.

The Gray-cheeked Thrush (Gcth), the Northern Waterthrush (Nwth), and the Blue Jay (Bjay), all consumed large quantities of the secondary species *Cornus florida* (COR) Flowering Dogwood, but each also consumed smaller quantities of the tertiary species, *Vitis aestivalis* (VIT), Wild Grape and *Toxicodendron radicans* (TOX), Poison Ivy.

MYR, JUN guild.

Interactions between the Yellow-rumped Warbler and *Myrica spp.* (MYR), accounted for 75% of all frugivore-fruit interactions. The Yellow-rumped Warbler consumed large quantities of the primary fruiter *Myrica spp.* the Bayberry, and relatively small quantities of the tertiary fruiter *J. virginiana* (JUN), the Eastern Red Cedar.

SMI, ROS guild.

Brown Thrasher consumed two tertiary species; *Smilax spp.* (Greenbriar) and *Rosa spp.* (Wild Rose). Although total consumption of neither of these species was very high, the patterns of consumption and the agent, the Brown Thrasher are similar, suggesting a dispersal guild.

The Yellow-rumped Warbler is unique among frugivores at the study site because it is an abundant winter resident, and specifically consumes *Myrica spp.* regardless of the abundance of other fruits. The other frugivores exhibit less specific frugivory, consuming either small quantities, and/or fruits of several species. With the exception of the Yellow-rumped Warbler, the consumption of different woody plant fruits appears to be largely based on migration timing. Although there is considerable variation in yearly migration timing, certain species generally migrate early, whereas others tend to migrate later (Figure 4).

Three categories of important frugivores can be discriminated based on the number and diversity of fruits consumed. Frugivores in these categories share the characteristics of relatively high abundance and relatively large fruit consumption of some woody plant species. The three categories may be described as "high omni-consumption", "low omni- consumption" and "high specific-consumption". These categories represent refinements of the specialized/opportunistic models of Howe and Estabrook (1977). The refinements may be useful for modelling bird dispersal.

High Omni-Consumption.

This category includes abundant frugivores which consume fruits from at least five different woody plant species, and which consume large quantities of at least one fruit producing species. Two migrant species, the Northern Waterthrush (Nwth) and the Common Yellowthroat (Coye) fit into this category. Both these species migrate early in the season, arriving at the study site from early September through mid-October in relatively large numbers. These two species are exposed to a large diversity of fruits throughout their presence at the study site (Figure 14), and they consume large quantities of fruits of at least one species, and lesser quantities of many species. Although other frugivores may be equally, or slightly more abundant at the same time, they are relatively less consumptive, and so less important to potential dispersal.

Low Omni-Consumption.

Frugivores in this category are not as abundant as other frugivores. However, they consume low quantities of fruits from several woody plant species, including fruits from species which are not consumed by other frugivores. The Brown Thrasher (Thrs) exemplifies this category. The Brown Thrasher moves locally and individually throughout its range. Its movements occur late in the season, when few other frugivorous species are present. Thus, the Brown Thrasher becomes an important potential disperser of late fruiting plants.

High Specific Consumption.

Frugivores in this category consume large quantities of one fruit, and few other fruits. At the study site, one frugivorous species, the Yellow-rumped Warbler, was very abundant and primarily consumed large quantities of fruits from *Myrica spp.*.

These majority of plant-bird interactions at the study site involved more than one bird-plant pair. This fits models of "diffuse" coevolution in which species assemblages interact with a net selective effect. The interactions between the Yellow-rumped Warbler and *Myrica spp.* are an exception to diffuse mutualisms. The Yellow-rumped Warbler and *Myrica spp.* exhibit what may be called a "semi-specific" mutualism. Semi-specific interactions are unusual for temperate bird mediated dispersal (Herrera 1984, Thompson and Willson 1979).

Diffuse mutualisms

The evolution of bird-mediated dispersal systems involves some degree of coevolution. Seed dispersal by frugivores is intrinsically a mutualistic process, in which both birds and plants benefit. The term "diffuse" coevolution was coined by Janzen (1980) to describe the process in which two species assemblages interact and generate reciprocal selective pressures on a group to group , rather than species to species, basis (Herrera 1982). Thus, diffuse coevolution involves interactions between several species which contribute to the benefit of all (Herrera 1982). There is no unique reciprocal selection pressure between one frugivore and one fruit species. The species involved in the interactions are basically interchangeable. They fit a "category" of interaction which may be performed by any number of different species with the same net effect. Southward bird migrations are a predictable phenomenon, independent of fruit production. Since the majority of frugivores will be present regardless of fruit quality, low nutritional value fruits may be produced to attract dispersers at a low cost to the plant. A 'loose' dependency is promoted between frugivores, which consume a variety of fruits, and plants which are dispersed by a variety of frugivores.

Presumably, the interactions which provide the best possible advantage to both birds and plants will be favored by natural selection. Overwintering birds have probably evolved their residency status on the basis of the availability of rich food sources (Herrera 1982). If high quality fruits are not available in the winter, then birds will be forced to migrate or they will die. The availability of reliable potential seed dispersers in the form of resident winter frugivores may create selection pressure for winter fruiting plants to produce richer fruit pulps. Therefore, we may expect winter fruiting plants to be more likely to evolve specific mutualisms with potential dispersers (Herrera 1982).

Semi-specific mutualism

Specialized dispersal systems are considered more efficient than generalized ones because interactions are more predictable (Herrera 1981). The semi-specific mutualism between the Yellow-rumped Warbler and *Myrica spp.* may be interpreted in this context. The predictability of the interactions provides the Yellow-rumped Warbler with an abundant, lipid-rich winter food source, which allows it to avoid the costly energy expenditures usually associated with migration to the neotropics (Dolnik and Blumenthal 1964, Blem 1976). Likewise, the predictability of the interactions provides *Myrica spp.* with reliable dispersers. Although *Myrica spp.* do grow inland, they are most competitive in coastal habitats since they are salt tolerant and able to fix atmospheric nitrogen (Dirr 1983). As sea level changes, currents, winds and storms cause disrupt coastal habitats, dispersal to new sites becomes important to the success of *Myrica spp.*.

The fruiting patterns of *Myrica spp.* and *J. virginiana* fit the expectations of Howe and Estabrooks' (1977) model for specialized dispersal systems. *Myrica spp.* and *J. virginiana* produce small crops of persistent, nutritious fruits throughout a long growing season. Their fruits have high relative yields for lipids compared with other temperate fall fruits (Tables 3 and 11) This increases their value as a winter food (Herrera 1984). *Myrica spp.* fruits are cryptically colored and located sessile to branches amidst evergreen leaves. The lack of color contrast in *Myrica spp.* is similar to that of many tropical fruits which have specialized relationships with avian dispersers (Howe and Estabrook 1977). Specialized frugivores are considered to be better at locating and remembering the locations of fruiting plants (Willson 1983). Most temperate avian dispersed plants are not specialized, and their fruit displays have evolved to attract potential dispersers attention with easily accessible, brightly colored fruits and contrasting colored foliage (Willson and Thompson 1982, Stiles 1982).

The winter range of the Yellow-rumped Warbler and the range of *M.cerifera* coincide fairly closely (Figure 16). Although both *M.pensylvanica and M. cerifera* were present at the study site, it is likely that a semi-specific mutualism occurs primarily with *M. cerifera* because the Yellow-rumped Warbler's winter range overlaps the range of *M. cerifera* to a much greater extent than that of *M. pensylvanica* (Figure 16). The area of Virginia's Eastern shore and barrier islands is at the northern range limit for *M. cerifera,* the Southern Bayberry, and at the southern range limit for *M. pensylvanica,* the Northern Bayberry. *M. cerifera*'s range is much more extensive than that of *M. pensylvanica* (Little 1977). The winter distribution of the Yellow-rumped Warbler extends throughout the eastern U.S. to Texas, excluding the Appalachian mountains, and covers parts of California (Christmas Count Surveys 1987, 1988, 1989). Although *Myrica spp.* and the Yellow-rumped Warbler appear to have a semi-specific mutualistic relationship at the study site, and possibly throughout the east coast, the Yellow-rumped Warbler must rely on other fruits where it's range does not overlap with that of the *Myrica spp.* (Figure 16). It may be expected that elsewhere in it's winter range, the Yellow-rumped Warbler also selects high lipid fruits. This would be an interesting point for future investigations

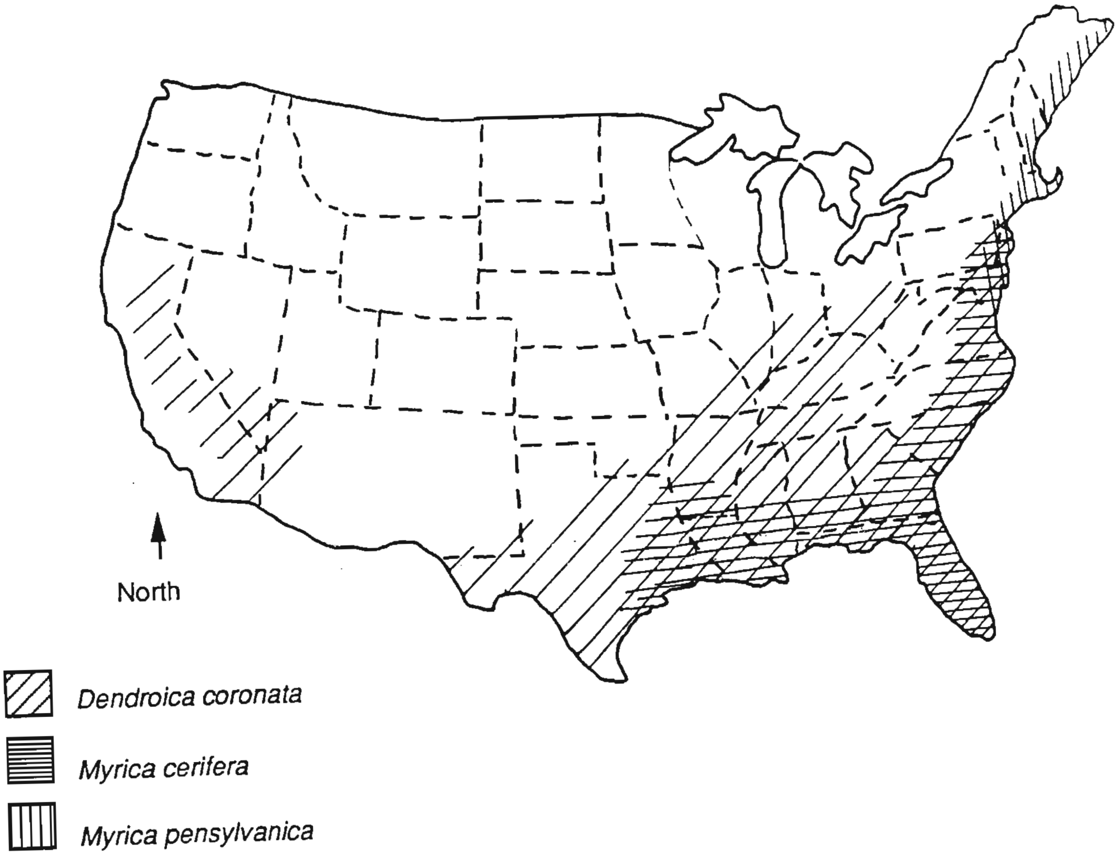

Figure 13. Distribution of *Myrica cerifera, M. pensylvanica* and the winter distribution of *Dendroica coronata* in the United States. Data from Little 1971 and Christmas Count Surveys of 1987, 1988 and 1989.

Summary

The majority of research on temperate bird-fruit interactions has been conducted in north temperate areas. These studies have indicated that the timing of ripe fruit production for most woody plants coincides with that of peak passerine migrations in autumn (Thompson and Willson 1979, Stiles 1980, Sorenson 1982). The present study supports this pattern of coincidence for south temperate regions, although the peak in both ripe fruit production and avian migrants occurs one month later than at north temperate locations.

Although peak ripe fruit abundance occurs during the middle of the migration season, the greatest number of species are in fruit at the end of the migration season. This is contrary to observations from northern temperate regions, and suggests that winter dispersal may be more common at this south temperate region (Thompson and Willson 1979). Fruit presentation at the end of the migration season may be more common at south temperate regions because there are more frugivorous winter residents act as dispersal agents. This would be an interesting point for future studies to investigate.

Few studies have examined patterns of plant-bird interactions from a community perspective. Principal components analysis provides an ideal method to examine the bird and plant assemblages to determine which interactions are most important for understanding the migrant refueling and potential seed dispersal. By essentially restructuring the data sets into smaller sets of components of the original variables, it was used in this study to elucidate major patterns in migrant frugivory and potential seed dispersal. Once determined, hypothesis about interrelated variables can be generated, and these interactions can then be investigated in more detail.

A principal components analysis of average fruit consumption was used to determine which woody plant species are most important to migrants for refueling. The consumption of three woody plant species explained the most variance in the analysis of migrant frugivory were *Myrica spp.*,(Bayberry) *Cornus florida* (Flowering Dogwood) and *Parthenocissus quinquefolia* (Virginia Creeper). A principal components analysis of total seed consumption was used to determine which frugivores are most important to woody plants as seed dispersal agents. The consumption patterns of four passerines explained the majority of the variance in the analysis of total seed consumption. These were Brown Thrasher, Northern Waterthrush, Common Yellowthroat, and Yellow-rumped Warbler.

The fruits of all woody plants at the study site were similar with respect to size and nutritional value, except for *Myrica spp.* (Bayberry) and *J. virginiana* (Eastern Red Cedar). The fruits of *Myrica spp.* and *J. virginiana* were smaller and higher in lipid content than other fruits. Three categories of fruiting are described based on timing, abundance and nutritional value of fruits. Primary fruiters produce abundant, nutritious fruits when migrants are present. *Myrica spp.* are described as a primary fruiters. Secondary fruiters produce low quality, but very abundant fruits when migrants are present. Three woody plant species are described as secondary fruiters; *Cornus florida* (Flowering Dogwood), *Rubus idaeus* (Red Raspberry and *Parthenocissus quinquefolia* (Virginia Creeper). Although *Prunus serotina* (Black Cherry) and *Celtis occidentalis* (Hackberry) produced very abundant fruits, they were not available to the majority of migrants due to early fruiting, and large fruit size, respectively. The remaining woody plant species are categorized as tertiary fruiters, which produce low quality, scarce fruits.

Grouping of factor loadings within the principal components space describing total seed consumption suggests that dispersal guilds may exist at the study site. In at least two of the groupings, there is one higher ranking and two or more lower ranking fruit producers. Consumption of fruits within these potential guilds is similar with respect to timing and dispersal agent. The consumption of higher-ranking fruiters may indirectly favor the consumption of lower-ranking, coexisting plants. The maintenance of these relationships is dependent on the varied diets of frugivores. These relationships are similar to the "guilds" described in Mediterranean scrublands in which plants are functionally interdependent for dispersal, so that individual species benefit from coexistence with other species (Herrera 1984).

Three categories of migrant frugivory are suggested. These categories are essentially refinements of the specialized/opportunistic models of Howe and Estabrook (1977). The refinements may be useful for modelling dispersal interactions. Frugivores which fit into one of these categories are considered important in potential seed dispersal. In general, frugivores in these categories share two characteristics. They are relatively abundant, and they consume relatively large quantities of fruits of some woody plant species. The three categories are "omni-consumption-1", "specific consumption-1" and "omni- consumption-2".

The majority of bird-plant interactions suggest diffuse coevolution. Both fruit ripening and migration timing are subject to a variety of external and internal ques, making it impossible for tightly dependent interactions to evolve. Instead many interchangeable species interact to promote diffuse coevolution. However, the interactions between *Myrica spp.*, and *D. coronata* suggest a semi-specific mutualism. Semi-specific mutualisms are unusual for temperate bird-mediated dispersal.

Both *Myrica spp.*, and *D. coronata* may benefit through mutualistic interactions by attaining ranges that would not otherwise be possible. The winter range of *D. coronata* and the range of *Myrica cerifera* correspond fairly closely in the eastern seaboard of U.S.. However, *D. coronata's* range extends beyond that of *Myrica spp.* in the mid-eastern U.S and in parts of California. Detailed studies of *D. coronata's* winter food habits throughout its range may aid in understanding the semi-specific mutualism that occurs between this species and *M. cerifera* in some areas.

Clearly, the interactions between migrating frugivores and woody plants are important to both birds and plants. Many migrating frugivores rely on the fruits of woody plants for food during migration, thereby becoming important in the potential seed dispersal of many woody plant seeds and the structuring of woody plant communities. Understanding the different types of migrant frugivory and fruit presentation will help guide the development of migration stop-over site conservation programs. It is evident that a variety of woody plant species are necessary to supply migrants with refueling resources. Trends indicating the declines in many migrant species (Askins et al. 1990), and the ever present threat of urbanization add urgency to our need to understand these interactions.

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APPENDIX

Table 8. Life history characteristics of the four frugivorous migrants most important to the potential dispersal of woody plant seeds at the study site.

Species	Foraging area	Habitat	Diet	Range relative to study site
Nwth	Ground	Understory, near water	Primarily insectivorous: on both breeding and winter grds.	Breeds throughout VA. Winters primarily in neotropics
Thrs	Ground	Woodlands	40% vegetable: wild fruits mast (acorns) insectivorous: ground beetles	Breeds, on east coast, from ME to S. FLA Winters in S. part of breeding range Local and individual migrations
Coye	Low growth	Wet environ.	Primarily insectivorous for ground dwelling insects	Breeds throughout VA. Winters to West Indies. Study site is N. limit of winter range S. representatives do not migrate.
Yrwa	Varied	Breeding: coniferous N.E.forests winter:in US: primarily	Breeding: insectivorous Winter: fruit generally all kinds but especially *Myrica* spp.	Breeds: on E. coast, from Labrador to PA. Winters N. to Wash. D.C., S to neotropics
Ybch	Low growth	Dense thickets and brush	Primarily insects; with some fleshy fruits	Breeds throughout U.S. Migrates to neotropics for winter season.
Gcat	Low growth	Dense thickets deciduous woods	Breeding: insectivorous Fall/winter primarily fleshy fruits	Breeds throughout U.S. east of Rockies, Winters in neotropics
Woth	Trees	Swamps and moist deciduous woods	Breeding: insectivorous Fall/winter: primarily fleshy fruits	Breeds in Eastern U.S Migrates to neotropics for winter season.
Gcth	Varied	Coniferous and mixed woodlands	Breeding: insectivorous Fall/winter primarily fleshy fruits	Breeds in northern Canada Migrates through U.S. to neotropics

Table 8 continued.

Species	Foraging area	Habitat	Diet	Range relative to study site
Veer	Low growth	Dense moist woodlands, streamside thickets	Breeding: insectivorous Fall: many fleshy fruits	Breeds in northern U.S Migrates through U.S to neotropics
Revi	Varied	Eastern woodlands	Breeding: insectivorous Fall: primarily insectivorous, some fleshy fruits	Breeds east of the Rocky Mtns. Migrates to neotropics for the winter.
Mock	Low growth	Thickets woodland edges	Breeding: primarily insectivorous Fall/winter: 50% insects, 50% fleshy fruits	Breeds and winters in southern U.S. Winters in southern part of breeding range. Individual and local migrations.
Bjay	Varied	Woodlands	Breeding: 50% mast crops. 50% animal food Fall/winter: primarily mast crops, some fleshy fruits	Breeds and winters in Eastern U.S, with local group migrations in fall.
Heth	Varied	Coniferous or mixed woods and thickets	Primarily insectivorous during breeding, 50% fleshy fruits during winter.	Breeds in northern U.S Winters in southern U.S. and neotropics.

Nwth=Northern Waterthrush
Thrs=Brown Tharsher
Ybch= Yellow-breasted Chat
Woth=Wood Thrush
Veer= Veery
Mock= Northern Mockingbird
Heth= Hermit Thrush
Coye=Common Yellowthroat
Yrwa=Yellow-rumped warbler
Gcat=Gray Catbird
Gcth= Gray-cheeked Thrush
Revi= Red-eyed Vireo
Bjay= Blue Jay

Diet information obtained from Martin et al. 1951.

Table 9: Summary of woody plant fruiting characteristics.

Total fruit consumption is the number of fruits consumed by all frugivorous migrants during the study season, from August 31 through November 15, 1991. See text for explanation of plant species. Relative fruit size, fruit time, display length and fruit abundance refer to comparisons with all woody plants which were in fruit during the study season. The total number of fruits consumed was determined by dividing the total number of seeds of each plant species found in samples from each bird species by the average number of seeds per fruit. The number of species consuming each plant species represents the total number of frugivorous migrant species caught during the study period.

Plant Species	Rel. Fruit Size	Rel. Fruit Time	Rel. Display Length	Rel. Fruit Abundance	Plant Form	Total Fruit Consumption	# Birds Consuming	Fruit Color
PRU	large	early	short	high	sm.tree	36	3	R/BK
RUB	large	early	med	high	bush	25	8	R/BK
VIT	large	mid	med	low	vine	19	5	BL/BK
CEL	large	mid	med	high	lg.tree	4	1	BL
TOX	med	mid	med	low	vine	9	3	BL/BK
LON	med	mid	long	low	sm. bush	13	4	BL/BK
PAR	med	mid	short	high	vine	593	14	BL
JUN	small	mid	long	med	sm.tree	57	1	GR/BL
MYR	small	mid	long	med	bush	3602	9	GR
SMI	med	late	short	low	vine	15	5	BL/BK
ROS	med	late	short	low	bush	3	1	R
ILE	large	late	short	low	sm./lg. tree	5	1	R/BK
COR	med	mid	long	high	sm.tree	47	5	R/BL

R=red BL=blue
BK=black GR=green

Table 10. Nutritional composition of fruits based on percentage of dry weight. Data complied from Stiles 1980, Herrera 1982c and Johnson et al. 1985.

Fruit Species	Sugars(%)	Proteins (%)	Lipids(%)
CEL	11.6	3.5	.36
COR	10	3.3	40.0
JUN	-	-	20.0
ROS	-	-	-
PRU	19.9	2.0	.42
RUB	35.9	5.5	3.5
LON	-	-	-
MYR	-	-	23.2
ILE	-	-	7.9
VIT	12.4	2.2	.81
PAR	-	3.9	25.7
SMI	14	4.0	.84
TOX	-	-	-

Table 11. Average fruit consumption of 13 woody plant species by 19 frugivorous migrant species during the migration season, from August 31, through November 15, 1991. Fruit consumption for each plant species was determined by dividing the total number of seeds consumed by each bird species by the average number of seeds per fruit. For each bird species, average fruit consumption of each plant species was determined by dividing total fruit consumption by the total number of birds captured during the study season. Plant and bird abbreviaions are discussed in the text. (Average number of seeds per fruit are listed in table 3.)

Example of average fruit consumption caluculations for plant species 1 by bird species 1:

Number of Fruits (for plant species 1)=

$$\frac{\text{\#seeds of plant species 1}}{\text{average \# seeds/fruit of plant species 1}}$$

Average Fruit Consumption (for plant species 1 by bird species 1)=

$$\frac{\text{number of fruits of plant species 1 consumed by bird species 1}}{\text{total number of individuals of bird species 1}}$$

Bird	Average Fruit Consumption for 75 Day Period												
Spp.	PRU	JUN	ROS	RUB	PAR	VIT	MYR	LON	COR	CEL	SMI	ILE	TOX
Amre	.70	0	0	.06	.045	0	0	0	0	0	0	0	0
Nwth	.04	0	0	.23	.11	.46	.03	.44	.02	0	0	.013	.04
Coye	.016	0	0	.10	2.86	.01	.05	0	0	0	0	0	0
Ybch	0	0	0	.22	.8	0	0	0	0	0	0	0	0
Veer	0	0	0	.15	0	.327	0	0	0	0	0	0	0
Oven	0	0	0	.06	0	0	0	.095	.31	0	0	0	.25
Bbwa	0	0	0	.42	0	.25	0	0	0	0	0	0	0
Bori	0	0	0	.17	0	0	0	0	0	2.0	0	0	0
Heth	0	0	0	0	0	0	.43	.21	.98	0	0	0	0
Swth	0	0	0	0	.32	.195	0	0	.33	0	0	0	.07
Gcat	0	0	0	0	6.32	0	.36	0	0	0	.01	0	0
Revi	0	0	0	0	.23	0	.4	0	0	0	0	0	0
Gcth	0	0	0	0	3.71	0	4.0	0	0	0	0	0	0
Thrs	0	0	.14	0	.23	0	1.14	.13	.2	0	.33	0	0
Mock	0	0	0	0	1.0	0	0	0	1.0	0	0	0	0
Woth	0	0	0	0	.095	0	0	0	0	0	0	0	0
Bjay	0	0	0	0	.762	0	0	0	1.48	0	.58	0	0
Mawa	0	0	0	0	.057	0	0	0	0	0	0	0	0
Yrwa	0	.05	0	0	.025	0	1.95	0	0	0	0	0	0

Table 12. Total seed consumption of 13 woody plant species by 19 frugivorous migrant species during the migration season, from August 31, through November 15, 1991. Abbreviations are discussed in the text. Total seed consumption was determined as the total number of seeds from each plant species that were found in samples from each bird species.

Bird	Total Seed Consumption for 75 Day Period												
Spp.	PRU	JUN	ROS	RUB	PAR	VIT	MYR	LON	COR	SMI	CEL	ILE	TOX
Amre	31	0	0	72	7	0	0	0	0	0	0	0	0
Nwth	3	0	0	81	65	36	37	5	53	6	0	5	11
Coye	2	0	0	334	1243	5	6	0	0	0	0	0	0
Ybch	0	0	0	30	14	0	0	0	0	0	0	0	0
Veer	0	0	0	22	0	17	0	0	0	0	0	0	0
Oven	0	0	0	52	0	0	0	6	6	0	0	0	13
Bbwa	0	0	0	37	0	2	0	0	0	0	0	0	0
Bori	0	0	0	34	0	0	0	0	0	0	4	0	0
Heth	0	0	0	0	0	14	12	18	41	0	0	0	0
Swth	0	0	0	0	20	0	0	0	9	0	0	0	3
Gcat	0	0	0	0	398	0	56	0	0	5	0	0	0
Revi	0	0	0	0	4	0	2	0	0	0	0	0	0
Gcth	0	0	0	0	130	0	40	0	0	0	0	0	0
Thrs	0	0	15	0	17	0	24	9	3	28	0	0	0
Mock	0	0	0	0	7	0	0	0	3	0	0	0	0
Woth	0	0	0	0	1	0	0	0	0	0	0	0	0
Bjay	0	0	0	0	8	0	0	0	71	7	0	0	0
Mawa	0	0	0	0	3	0	0	0	0	0	0	0	0
Yrwa	0	128	0	0	158	0	3425	0	0	0	0	0	0

Table 13. Occurence of woody plant species on the barrier islands of Virginia and relative fruit consumption by frugivorous migrants at study site on the Eastern Shore of Virginia. (N) =the number of islands out of 15 total islands on which a species occurred. Relative seed consumption reflects the potential seed dispersal for each plant species relative to other bird dispersed plants on the islands. Relative consumption was calculated bt determining the percent seed consumption of each plant species out of the total seed consumption of all woody plant species. Woody plant distributional data was collected and reproted by McCaffrey and Dueser 1990.

Plant Species	N	Relative Seed Consumption(%)	Fruit Display Time
Lonicera	1	.6	early-late fall
Smilax	6	.3	late fall/persistent
Myrica	11	82.4.	mid fall/persistent
Prunus	6	.8	late summer/early fall
Rubus	4	.6	late summer/early fall
Celtis	1	.09	early-mid fall
Parthenocissus	5	10.6	mid fall
Vitus	4	2.1	early-mid fall
Ilex	4	.1	late fall/persistent
Juniperus	10	2.1	mid fall/persistent
Toxicodendron	0	.6	early-mid fall
Rosa	0	.06	late fall/persistent
Cornus	0	.4	mid fall/persistent