

REPRODUCTIVE AND DISPERSAL ECOLOGY OF THE INVASIVE CORAL
ARDISIA (*Ardisia crenata*) IN NORTHERN FLORIDA

By

MICHAEL J. MEISENBURG

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This document is dedicated to my sister Marie Gedeon (1951-2006).

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To finish this—and to believe in myself enough to do so—I am grateful to my wife Vasiliki. Without her I would not have journeyed down this path. Most of us need someone in our lives to coach us on, to prod us along, and to pick us up when we stumble. She is that person in my life. I will never be all that I can be, or maximize my potential, but that is okay. My life is richer with her in it, and because of her I will accomplish more. It is because of her that I am about to finish this journey.

Despite much encouragement from my advisor and my committee, my friends and my family, and (most of all) my wife, this project took seven years to finish. In the end, I suppose that it was the impending early retirement of my advisor that finally forced me to complete what has become my personal 800-lb gorilla. My gorilla has accompanied me everywhere these last few years, and has been with me day and night. My gorilla taught me how to incorporate stress into my life, how to exist after nights with little sleep, how to maintain a 40-lb weight gain, how to abandon hobbies that I once enjoyed, how to despise writing, and how to avoid tasks and not reach my goals. Soon I will turn in my completed thesis, and I will lose my hairy companion. I will not miss him.

A special thank you is due to Alison Fox (my advisor) and Randall Stocker (Alison's husband and one of my committee members) for getting me through this. I hope they enjoy their travels.

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Abstract of Thesis Presented to the Graduate School
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REPRODUCTIVE AND DISPERSAL ECOLOGY OF THE INVASIVE CORAL
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By

Michael J. Meisenburg

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Coral ardisia was introduced into the New World from Asia more than 100 years ago and has become a part of Florida landscapes. It has since been recognized as being an invasive weed even though it is suspected that consumption of its fruits by possible seed dispersers is an uncommon event. The purpose of this study was to gain insight into the reproductive ecology of coral ardisia in its introduced range of northern Florida.

Tracking tagged plants showed flowered through the summer and fruits ripened in mid-winter. The fruits can persist on the plants for up to one year, with the greatest rate of fruit loss occurring in late April. Plants in a natural area lost fruits at a faster rate than those in an urban area, and isolated plants lost fruits quicker than those in denser populations. The period of greatest fruit loss coincides with the spring migration of birds through Florida and suggests that some consumption of fruits by birds is occurring. Fruits were found not to be nutritionally inferior to native fruits, nor were any other factors found that would suggest a reason why fruits of coral ardisia are rarely eaten.

Despite many hours in the field, observations of birds feeding on coral ardisia fruits were limited to a single day with a single bird species (gray catbird). Captive feeding trials found that six species of birds would eat coral ardisia fruits, but often favored the fruits of native species to those of coral ardisia. Gray Catbirds and European Starlings showed the greatest acceptance of coral ardisia fruits during captive feeding trials. Cedar Waxwings defecated seeds after eating fruits, while all other species regurgitated seeds. Seed germination rates were no different for 5 of 6 birds species tested between seeds defecated or regurgitated compared to those that were manually depulped. From damage incurred while manually trying to remove seeds from fruits, Fish Crows significantly decreased seed germination rates. However, Fish Crows ate the fewest coral ardisia fruits.

CHAPTER 1
UNDERSTANDING THE IMPORTANCE OF SEED DISPERSAL FOR NONNATIVE
PLANT SPECIES

Introduction

The human-assisted spread of species into new regions and the subsequent ecological effects that some of these species have on native ecosystems is recognized as one of the most serious contemporary threats to biodiversity. Indeed, Wilcove et al. (1998) regarded introduced species as being second only to habitat loss in terms of habitat impacts. Whether by accident or intention, humans have been moving organisms for thousands of years, but the recognition of the negative impacts to natural systems as well as the magnitude of these impacts are more recent (for a good description see Mack et al. 2000).

Although many taxa are represented, plants constitute some of the better-known examples, and within the state of Florida alone, millions of dollars are spent annually to control nonnative plants. For example, the Florida Department of Environmental Protection (FDEP) spent 6.3 million dollars in FY2003 to control nonnative weeds. As large as this expenditure is, it includes neither aquatic plants, with two of the worst introduced species, water hyacinth (*Eichhornia crassipes*) and hydrilla (*Hydrilla verticillata*), nor money allocated directly to the Melaleuca Program (FDEP 2004). One plant responsible for much of this expenditure in northern Florida is coral ardisia, *Ardisia crenata* Sims. (Myrsinaceae) (FDEP 2004).

Coral Ardisia in Florida

Native to southeastern Asia, coral ardisia grows from one to one and a half meters tall in shaded to partially-shaded areas. Initially single-stemmed, most plants eventually produce additional stems and maintain a multi-stemmed status for many years. After several years, stems begin growing short branches. With leaves growing at the ends, the initial function of the branches is energy production. After one to two years, a branch's purpose changes to reproduction as the leaves are replaced by flowers in a cyme. During the branch's final year, the flowers produce single-seeded drupes. Branches typically have about 5 to 20 fruits each and plants have from 1 to 10 branches. Branches fall from plants after the fruits are gone, and the lifespan of each branch is 3 to 4 years. The branches circle the stem, with the lowest branches being the oldest. Each year, the plant grows taller and produces a new set of branches, and each ring of branches advances to the next stage of its cycle. Plants may begin producing branches when about 20 cm tall. The pattern of continuously regenerating stems makes it impossible to estimate the age of the plant based on stem size and reproductive status.

Coral ardisia is a shrub that has been used for landscaping in Florida for more than 100 years (Royal Palm Nurseries 1900). At least three factors may have contributed to the popularity of this species. First, it grows well in sites with no direct sunlight, a condition many landscape plants cannot tolerate. Second, it produces large, bright red fruits just prior to Christmas that persist for months and contrast with its evergreen glossy, dark green leaves. Third, the plant seems to rarely suffer insect damage. By 1982 coral ardisia was recognized as escaping cultivation and invading moist woods (Wunderlin 1982).

In response to the plant's invasion, the Florida Exotic Pest Plant Council has placed the plant on its Category I list of invasive plants (www.fleppc.org); a designation indicating that the plant is not only invading natural lands, but altering native plant communities. In 2003, the FDEP's Upland Weeds Program ranked *Ardisia* spp. (which includes both coral ardisia and shoebutton ardisia (*Ardisia elliptica*)) as the seventh-most herbicide-treated taxon in the state (FDEP 2004).

While coral ardisia grows well in moist (mesic) sites, it also invades wet (hydric) woods. Mesic hardwood hammock seems to be the natural community most prone to invasion (Langeland and Burks 1998). The plant is not known to invade mesic or hydric pinelands (Dozier 1999).

Coral ardisia fruits seem to be removed from plants only occasionally (Dozier 1999), thus presenting a paradox in attempting to discover dispersal agents. If fruits are not often eaten, so that the seeds can be subsequently dispersed, then how has it spread throughout natural areas in the state? Because the plant is still used in landscaping, some dispersal is anthropogenic, but this does not account for the plant's widespread presence in natural areas (e.g. remote locations in San Felasco Hammock State Park, Gainesville, FL, Sam Cole, park biologist, personal communication). Birds are a likely candidate for non-human dispersers of this plant because coral ardisia does not possess mammalian-dispersed fruit traits, such as being sweet-tasting and falling to the ground soon after ripening (Stiles 1980). In addition, while coral ardisia's fruits are brightly-colored and highly visible in the forest due to this color, most mammals are color blind (Van der Pijl 1972). Fruits of a native congener (*A. escallonoides*) similarly seem not to be heavily

used by birds, except for during spring migration (John Pascarella, University of Miami, personal communication).

The Importance and Mechanisms of Seed Dispersal

There are several reasons why seed dispersal is important to plants. First, because sites suitable for growth vary in space and time, plants must be able to colonize new areas as conditions change (Howe and Smallwood 1982). Second, dispersal beyond the canopy is a means of avoiding competition between parents and siblings. Finally, the Escape, or Janzen-Connell Hypothesis (Janzen 1970, Connell 1971), indicates that dispersal from the parent is important because seed predators (rodents, insects, or microbes) often concentrate their efforts under parent plants where food density is highest.

Plants use various strategies for dispersing seeds beyond the range of their branches, and while the process is an important part of plant population dynamics, it is especially important if the plants are invasive, exotic species. Certain traits may influence a particular species' propensity to become invasive, but a species is much less likely to become a problem (beyond a local scale) without a reliable seed dispersal vector. Little is known about vertebrate-assisted seed dispersal of invasive plant species in Florida, and few dispersers have been adequately verified. Identification of dispersal agents relies heavily on assumptions (e.g. Morton 1982, Cronk and Fuller 1995), and there often seems to be a disregard of important subtleties (e.g. not distinguishing between those that eat fruit pulp and those that eat fruit seeds).

Many plants achieve seed dispersal through relatively simple processes such as via wind or water, but more complicated interactions can occur when plants use vertebrates to disperse their seeds. Ectozoochoric fruits or seeds attach to animals with hooks, barbs, or sticky secretions, while animals are usually enticed to eat endozoochoric seeds with a

fleshy fruit meal. Successful seed dispersal occurs only when still viable seed is dispersed. While seed dispersal may be an important initial step in a plant's life, it is only the initial step as germination and seedling establishment are also required.

Although fruit ingestion and subsequent seed dispersal of coral ardisia do not seem to be common events (Dozier 1999), even low frequency events could be important if plant mortality of seedlings was low. A trait shared by many nonnative plants is a lack of pathogens and predators, and indeed, insect damage on coral ardisia is rarely observed (personal observation). In other words, a limited frequency of seed dispersal may not negatively affect coral ardisia as much as it would a native species that has coevolved with a suite of pathogens, parasites, and predators, because coral ardisia may suffer lower rates of mortality predation at the seed and seedling stages.

A Diffuse Mutualism

Tight relationships between a specific fruit and frugivore are unusual, and not known to occur for invasive plants. Indeed, some non-native plant species have their seeds dispersed by bird species that did not coevolve with them. If they needed a specific disperser, introduced plants probably would not become a problem when introduced beyond their natural range. This type of seed dispersal represents a mutualism because both participants benefit; the frugivore with a meal and the plant with its seeds dispersed. However, the mutualism is only fulfilled if a viable seed is moved beyond the range of the plant's branches.

Following fruit consumption, seeds may be carried away from or dropped from the parent plant, with the latter resulting in no dispersal. For those seeds that are transported away from the parent, ingestion may increase (Renne et al. 2001, Bartuszevige and Gorchoy 2006, Figueroa and Castro 2002), decrease (Bartuszevige and Gorchoy 2006,

Meyer and Witmer 1998), or have no effect on seed germination rates (Meyer and Witmer 1998, Izhaki and Safriel 1990, Figueroa and Castro 2002). Seeds dropped under the parent plant and ingestion decreasing seed germination rates are non-mutualistic situations where the frugivore benefits but the plant does not.

The Flesh of the Fruit

Endozoochoric fruits typically consist of a digestible outer layer surrounding (at least) one seed, and in the majority of cases this is a fleshy pericarp consisting of pulp and skin. Alternatively, arillate fruits possess endozoochoric seeds in which the fruits open and reveal seeds that are covered in a digestible coating. Arillate seeds may have a fleshy aril, such as southern magnolia (*Magnolia grandiflora*), or a dry, waxy aril like Chinese tallow (*Sapium sebiferum*).

The nutrient content of fruits is usually assessed by measuring the levels of lipids, carbohydrates, and protein (Stiles 1980). Summer/early fall fruits tend to be higher in carbohydrates and water, while fall/winter fruits generally contain higher levels of lipids. Protein levels in fruits are usually low. Mammals feed more on summer and early fall fruits, which are often sweet-tasting, while the lipid-rich fruits of fall and winter are mostly utilized by birds (Stiles 1980).

Most species of temperate fruiting plants in the eastern U.S. set fruit in the fall, presumably benefiting from migrating birds (Stiles 1980). These birds need energy to fuel migration, and fruits provide a readily digested source in packages that are easy to procure. However, fruit set in Florida's natural communities may follow a different schedule because this geographic region is subject to the selective pressure of a large over-wintering bird population rather than the passage of fall migrants (Skeate 1987). While much of the state has a temperate flora and hence most plant species produce fruit

in the fall, it is thought that a greater fruit biomass is produced in the winter months when birds such as American Robins (*Turdus migratorius*), Cedar Waxwings (*Bombycilla cedrorum*), Gray Catbirds (*Dumetella carolinensis*), and yellow-rumped warblers (*Dendroica coronata*) over-winter in Florida (Skeate 1987).

The Dispersal Process by Birds

Seed Ingestion

For efficient flight it is essential that birds minimize unnecessary weight. One strategy to accomplish this is for birds to eliminate heavy, undigestible seeds as quickly as possible. Frugivorous birds can be divided into two groups: gulpers and mashers (Moermond and Denslow 1985). Gulpers are species that tend to swallow fruits whole, separate the seeds from the pulp internally, and then generally void the seeds at some distance from the parent plant (e.g., Northern Mockingbird (*Mimus polyglottos*)). Mashers tend to crush fruits in their bills separating the seeds from the pulp and swallowing just the pulp (e.g., northern cardinals (*Cardinalis cardinalis*)). Mashers typically drop seeds from the canopy of the parent plant. Generally, birds with heavier conical bills are mashers while those with thinner bills are gulpers.

Seed Deposition

How a gulper rids itself of seeds is also important relative to plant dispersal. The seed may be separated from the pulp in the crop with the seed regurgitated, or separation can occur further along the digestive tract with the seed defecated. The crop is an enlargement of the esophagus and while it is generally used to store food prior to entering the gizzard or stomach, it is also used for separating the pulp from the seeds. Birds can regurgitate seeds that are cleaned of even the most adhering pulp (such as those of coral ardisia). Murray et al. (1994) found that there is a positive correlation between the

distance over which a seed is dispersed and the length of time that a bird carries the seed. Since regurgitation is faster than defecation, method of voidance might affect seed dispersal distance. Meyer and Witmer (1998) found the mean seed defecation time of the native shrub *Viburnum dentatum* after fruit consumption by American Robins was 58 minutes versus a mean regurgitation time of 19 minutes. Although these authors studied both voidance methods for one type of seed using a single bird species, more often a bird species either regurgitates or defecates seeds based on seed size.

Recognizing that many factors can influence which bird species feed on which fruits (e.g., time of year ripening occurs, proximity to ground), it can be hypothesized that as a result of different voidance methods, plant population expansion rates could be influenced by which bird species tend to feed on the fruits.

The time of the year that ripe fruits are on the plant could influence the direction of seed dispersal. For example, a plant species whose fruits ripen in the spring may be most likely to experience a gradual northward population shift due to the spring migration of millions of birds. It should be remembered that each bird carries seeds a small distance at a time (depending upon flight speed and duration of seed retention), not for the thousands of miles of the whole migration route.

Seed Viability

A mutualism between bird and plant only exists if a viable seed is dispersed. Seed viability may be affected by the digestion process, and the severity of damage may increase with the length of time a seed is retained in the bird's digestive tract (Murray et al. 1994). Thus, there may be a trade-off for the plant between the distance seeds are carried prior to defecation (potentially improving seed dispersal), and the proportion of seed remaining viable (reducing viable seed dispersal).

In addition to frugivorous birds feeding on fruit pulp, granivorous birds may feed on the seeds of fruits. The granivorous house finch (*Carpodacus mexicanus*) is historically a western U.S. species that expanded its range into Florida following a 1940's introduction into the northeastern U.S. While they are commonly observed feeding on fruits, often they are actually cracking the seeds and feeding on the entire fruit (skin, pulp, and seeds). Similarly, with a gizzard that is capable of crushing pecans and acorns, wild turkeys (*Meleagris gallopavo*) and other members of the order Galliformes often digest the seeds passed through their digestive tracts. An observation of these species feeding on fruits can easily be misinterpreted as seed dispersal rather than the seed predation that it is.

Observations of Bird Behavior

A conclusive determination of endozoochoric seed dispersal by birds requires verification that the seeds are ingested, carried away from the parent plant, and voided in a viable condition. Observation of only fruit or seed consumption does not distinguish between seed dispersal and seed predation (Meisenburg and Fox 2002). However, documentation of seedlings distant from the rest of the plant population and in sites frequented by birds (e.g., under tree roosts, along fence lines) is an indication that bird dispersal is likely (McDonnell and Stiles 1983).

Project Goals

The goals of this study were to gain a greater understanding of coral ardisia reproductive phenology and to determine whether some bird species might have a role in dispersing viable seeds.

The objectives of chapter two were to determine when flowers, unripe, and ripe fruits first appear on plants, and then to determine their duration. Assessing fruit nutrient

content to compare to native species was the objective of chapter three. Finally, the objectives of chapter four were to determine if birds would eat the fruit of coral ardisia, conduct preference trials with other fruits, assess germination rates of voided seeds, and report on bird feeding activity in coral ardisia stands.

CHAPTER 2
REPRODUCTIVE PHENOLOGY OF *ARDISIA CRENATA*

Introduction

The fruits of coral ardisia have been observed to persist for most of the year on plants in northern-central Florida (Dozier 1999). For this reason it is often assumed that the fruits are rarely eaten by frugivores in Florida. Although it is possible that consumption rates are low, an alternative hypothesis is that fruit production continues for much of the year and thus gives the appearance that fruits are not removed.

If consumption of fruits is occurring, seasonal variation in fruit loss rate could implicate certain species as being major consumers of the fruit. For example, Florida is a corridor to millions of migrating birds every spring and fall, and if these events were correlated to increased rates of fruit loss from plants, this would suggest consumption by migrants. If viable seeds are voided, high rates of fruit consumption could lead to high rates of seed dispersal.

Fruit loss is the detachment of fruit from the plant, and this may be passive (e.g. senescence of peduncle) or active (i.e. removal by an animal). For the purposes of this study, mechanisms of fruit loss were not differentiated but the assumption is made that active removal may have accounted for some of the observed fruit loss.

With regard to fruit loss, several factors were taken into account because they could influence fruit loss rates. One such factor is habitat (Denslow 1987, Gosper et al 2006), probably because different bird species (with their specific food preferences and nutritional needs) occur in different habitats. Study sites were chosen in two habitats

with significant coral ardisia populations: intentionally-planted landscapes and near old homesites in natural areas with persisting coral ardisia populations.

It is possible that fruit height could influence loss rates. If this was the case, then certain types of dispersal agents may be implicated. For instance, some fruit-eating mammals are limited to foraging below a certain height relative to their size (though woody, coral ardisia stems could only support small mammals). The mammals that I considered to be potential consumers of ardisia fruit were all mid-sized (mesomammals): red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*), and the assumption was made that they were unlikely to feed on fruits above 0.6 meters from the ground.

Another factor in fruit loss rate is plant density. Denslow (1987) found that aggregated red elderberry (*Sambucus pubens*) plants had lower individual fruit removal rates than did isolated plants, and she hypothesized that competition among plants for frugivores led to decreased fruit removal rates for clumped plants. While recording data in the initial stages of this study, it appeared that the more isolated an ardisia plant was, the more quickly it lost its fruit. Consequently, I monitored plants for fruits loss across densities from relatively isolated to growing within dense stands.

The objectives of Chapter 2 were to determine the dates of flower and fruit production, and the duration of ripe fruit persistence on the plants as influenced by habitat, branch height, and plant density.

Methods

Site Descriptions

Three sites were selected in Alachua County, Florida. The first was near Rocky Point Road, Gainesville, on Paynes Prairie State Preserve property (hereafter called

PPSP), the second was east of Newnan's Lake (on private property owned by University of Florida Botany Department professor Francis J. Putz) (Putz), and the last site included several residences around southwestern Gainesville, Florida (City). Sites were selected on the basis of extensive ardisia infestations and permission to access the property.

The PPSP site was located in a hardwood forest that was principally upland with seasonal wetlands. Upland trees included live oak (*Quercus virginiana*), laurel oak (*Quercus hemisphaerica*), Southern magnolia (*Magnolia grandiflora*), American holly (*Ilex opaca*), and coral ardisia. Wetlands were primarily red maple (*Acer rubrum*) and black gum (*Nyssa sylvatica*).

The Putz site had experienced disturbance from logging and turpentine production, and consequently had a successional forest component. It contained live oak, laurel oak, sweet gum (*Liquidambar styraciflua*), loblolly pine (*Pinus taeda*), and American holly, and bordered a bayhead that contained sweetbay magnolia (*Magnolia virginiana*), loblolly bay (*Gordonia lasianthus*), and black gum. Coral ardisia was found throughout this site, but was most extensive in the successional forest.

The City site was comprised of ardisia plants in landscaped locations, as well as plants in undeveloped wooded lots adjacent to the residences. The plants at the residences were intentional plantings while the plants in the wooded lot appeared to be free-living and self sustaining populations, probably originating from the intentionally-planted populations.

Data Collection

Field data were collected to determine reproductive phenology and rate of fruit loss. Phenological data consisted of recording when flowers, green (unripe) fruits, and red (ripe) fruits appeared on plants. On each sampling date, each individual plant was

categorized according to the most advanced of the three stages of the flower/fruit cycle found. Following fruit maturation, periodic fruit counts were done to assess when plants lost their fruits. There was no distinction between those fruits that were removed by vertebrates and those that abscised naturally from the parent.

Phenologic data were gathered at the Putz and City sites during 2000 and 2001, and at PPSP during 2000. Fruit loss was followed at the Putz and City sites during 2001. Fruit loss was not followed at the PPSP site because a freeze in early January 2001 severely damaged previously tagged fruits and plants.

I monitored plants at the Putz site along on a 100-meter transect that encompassed several environmental variables (canopy cover, wetland proximity, and plant height and density). I stratified the transect into 10-meter sections because it was not practical to monitor all plants on the transect. Within each 10 x 1 meter section I used computer-generated random numbers to select plants for monitoring purposes. On each selected plant I chose up to three branches for periodic fruit counts.

Monitored plants in the City site were spread among four residences and an undeveloped wooded lot. The four residences were separated by a minimum of 100 meters. One residence had plants tagged in both the front and back yards, but no more than 15 plants were monitored in any one yard.

Sixty plants were initially monitored for fruit loss at the City site, and 100 in the Putz site. Plants that died were excluded from analysis, and the final number of plants consisted of 54 at the City site and 91 at the Putz site. Some plant deaths occurred as a result of trees falling, mowing, whereas others were due to unknown causes.

Two variables were recorded at Putz to determine if they influenced fruit loss rates: branch height and the density of ardisia surrounding the plant being monitored. Branches were grouped into two groups: those above and those below 60 cm. I believe that this value was a reasonable maximum height for mesomammals to reach if eating the fruits.

Plants were reported in three categories of density. “Minimal density” was 5 or fewer other ardisia plants within a 1-meter radius, “moderate density” was 6-10 plants within a 1-meter radius, and “maximum density” was >10 plants within a 1-meter radius. Generally, minimally-dense plants also had few other herbaceous or shrub species present, and bare soil was exposed on at least half of the 2-meter diameter circle. Moderately-dense plants usually contained laurel oak seedlings in the circles, and had little, if any, exposed soil. Ardisia plants in the densest circles usually had no other herbaceous or shrub species, and contained a considerable layer of forest duff.

Data Analysis

All fruit loss data were converted from actual numbers to percentages (as a change from initial counts) and then plotted as fruit loss over time. I used the PROC MIX statement in SAS statistical software (SAS Institute, version 8.2). I used logit transformation on the data transformation because the error variance was not constant, and logit was the appropriate transformation because the variance was dependent on the value of Y. Transformation produced linear equations where the slopes and Y-intercepts were compared for significance.

Another statistical program, MATLAB (MathWorks Inc., version 6), was used to produce probability density function graphs that displayed the average rate of fruit loss at any given time for the three densities tested. These graphs are the derivatives of the fruit loss graphs.

Results

Flowering and Fruiting Phenology

Ardisia flowered June through September, and peaked in late July-August (Figure 2-1). There were not sufficient replications for statistical testing, but monitoring multiple sites for multiple years indicated a trend for later flowering in 2000. In both years, a few City plants flowered earlier than any other plants.

Similar patterns existed for fruit production, as fruits appeared later in 2000 than in 2001, and emerged sooner on several city plants than other plants (Figure 2-2).

Flowering on individual plants lasted 4 - 6 weeks, with green fruits becoming clearly visible 3 - 4 weeks later. Fruits began ripening in December, approximately four months after formation. It was mid-late January before all plants had mature fruit (Figure 2-2).

Fruit Loss

Some fruits remained on the plants for the duration of the 10-month sampling period, by which time the next season's fruits were developing. Fruit loss at Putz appeared to be greatest between March and June, while the City site appeared to have a more constant fruit loss rate (Figure 2-3). The loss rates were significantly different between sites, with plants at Putz losing fruits more quickly than those in the City ($p < 0.0001$). The height of the branch above and below 60 cm did not influence fruit loss rate ($p = 0.478$, data not reported), but plant density did ($p = 0.0002$), with minimally dense plants experiencing the shortest fruit retention times (Figure 2-4.).

Probability density function graphs for the three densities (Figure 2-5) show average rate of fruit loss for the three densities tested. The peak of the curve represents the date of greatest fruit loss, and the end point is the expected date of fruit depletion. The end points were similar for minimal and moderate densities (161 and 165 days after

ripening, respectively), but was much later (332 days) for the maximum density plants.

The intervals between fruit loss rate peaks were similar between the minimal and moderate density plants (33 days) and between the moderate and maximum density plants (26 days).

Discussion

Fruiting Phenology

The results support rejecting the constant fruit production hypothesis, as fruits ripened in late December and January and were retained on the plants for much of the year (Figure 2-1). The plasticity shown in the timing of plant reproduction (flowering, fruit production and maturation) dates among years may be related to water stress. The spring of 2000 was considerably drier than 2001 in north-central Florida (Table 2-1), and flowering peaked 1-2 months later in 2000 (Figure 2-1). The notion that water influenced flowering and fruiting dates is also supported by those City plants that flowered in May (sooner than any other monitored plants), because those few plants received water from sprinklers. Furthermore, plants at Putz growing close to the bayhead (where soil may have been wetter) also flowered earlier. One problem with correlating flowering dates to rainfall is that it is difficult to know when rainfall is most important. Pascarella (1998) found that while rainfall strongly influenced flowering dates in the native *Ardisia escallonioides* in southern Florida, the implicated rainfall occurred during the previous rainy season.

Fruit Loss

Longevity of fruit persistence

Ardisia fruits persisted on the plant for up to ten months without decaying (Figure 2-3). Furthermore, on a few occasions (on unmonitored plants) I found fruits from the

previous year in good condition still on the plant in January with the new crop of ripe fruits.

The ability of fruits of many species to resist decay and microbial attack has been correlated to the presence of secondary compounds (Cipollini and Stiles 1992, Cipollini and Levey 1997a). These compounds are important because frugivores avoid eating infected fruits (Travaset et al. 1995, Garcia et al. 1999). However, the use of these compounds presents a paradox to plants: while vertebrates may select against infected fruits, they also prefer fruits from plant species that do not incorporate high levels of secondary compounds (Cipollini and Levey 1997b, Levey and Cipollini 1998).

The low rates of fruit consumption in the field for ardisia fruits by birds and mammals may be due to relatively high levels of secondary compounds, and the fruit's apparent resistance to microbial attack supports this hypothesis.

Influence of fruit/plant presentation on loss rate

The lack of a significant difference in fruit loss rates for branches above and below 60 cm may indicate that mesomammalian consumption of ardisia fruits in these sites is not common. This is supported by the lack of ardisia seeds found in mammal scat (see this study, Chapter 4).

While plant density was negatively correlated with fruit loss rate (Figure 2-4), a separate study would be needed to test for cause and effect. For example, ardisia may grow at lower densities where less tree cover leads to a drier microclimate, or in less fertile soils. If these conditions occur, they could result in plant stress that then causes a shorter duration of fruit retention. Without fruitfall traps to distinguish between removal and abscission, fruit fates could not be differentiated.

Several studies (Manasse and Howe 1983, Sargent 1990) have examined whether fruit abundance in the immediate vicinity influences removal rate, while Denslow (1987) studied the effects of plant density on removal rates. In conflicting results, Sargent (1990) found that greater fruit abundance enhanced removal rates while Manasse and Howe (1983) found lower fruit abundance led to higher removal rates. Both the Sargent and Manasse and Howe studies measured the fruit abundance in the immediate area, but my variable of interest was plant spacing and not fruit abundance. It is possible that both factors (numbers of fruits and plants in an area) can influence fruit removal rates from individual plants. Either through attracting more frugivores to the immediate vicinity or competing among each other for frugivores, the likelihood of an individual fruit being consumed may be influenced by neighborhood effects. Another possibility is that increased plant density could obstruct the birds' views while they are searching for fruits.

Denslow (1987) tested the effects of plant density on fruit removal rates, and found that the more isolated a plant was, the greater the fruit loss rate. Her findings agree with this study, and her interpretation was that competition for frugivores is greatest among bushes in close proximity to one another. Denslow studied plants growing in forest clearings along a river where the separate populations were not within sight of each other. My study differed in that the plants were all within a single population thus giving the frugivores the ability to choose the fruit from the plant that offered the preferred density of surrounding vegetation. At the Putz site different animal species may have been selecting for different plant densities.

There were many observations of fruits that were partially depulped while still on the plants, suggesting that small rodents (e.g. cotton mice, *Peromyscus gossypinus*) are

responsible for at least some fruit loss. In a pattern suggesting mouse consumption, depulping was usually in a circular pattern from the middle of the fruit cluster, where only the tops of the fruits were depulped. I also found rodent feeding platforms where ardisia fruits had been depulped, leaving piles of skins and seeds. These observations seemed more prevalent in the minimal-density plants, and appeared more often in April and May. This period coincides with a dry period in Florida (Table 2-1), and a hypothesis is that the mammals were using the fruits as a source of water. After losing their moisture-retaining pulp and skin, the seeds of many of these fruits shriveled and became hard, and probably lost viability. Probably due to their small size and ability to climb, feeding evidence from small mammals was found in all but the tallest ardisia plants. Investigation of mammalian consumption and the causes of different fruit loss rates among different plant densities would be interesting areas for further research. Not only would this mechanism of fruit loss appear to have no effect on long distance seed dispersal, but introduces a possible source of seed loss.

Another alternative hypothesis is that a bird species that I had not considered is responsible for the fruit loss in less dense plants. Wild turkey (*Meleagris gallopavo*) eat fruit when available (Martin et al. 1951), and could choose fruits from isolated plants over those in dense clusters to reduce the risk of predation.

Seasonality of Fruit Loss

The increase in fruit loss rate at Putz between March and June (Figure 2-5) may be due to migrating birds, because this period coincides with spring migration (Stevenson and Anderson 1994). That the quieter, less human-visited Putz site experienced this increased rate and not the City site could be due to habitat preferences of shy, frugivorous bird species (such as gray catbird, *Dumetella carolinensis*).

Fruit removal rates may also be influenced by the flocking tendencies of different bird species. At San Felasco Hammock State Preserve just north of Gainesville, FL, Skeate (1987) censused bird numbers through the year and assessed their usage of native fruits. Although he considered American Robins (*Turdus migratorius*) and Cedar Waxwings (*Bombycilla cedrorum*) to be common in the winter and spring, their numbers were erratic. These two highly frugivorous species often travel together in large flocks, and exhaust local fruit resources before moving on to another area (Skeate 1987, personal observation). Thus, fruit removal rates from these two species should show steep declines in relatively short periods of time, such as between my sampling dates. This was not observed in my study.

Skeate (1987) categorized the native fleshy-fruit producing plants according to when their fruits matured, and he found only four of 45 species fruited in winter. These were American holly (*Ilex opaca*), laurel cherry (*Prunus caroliniana*), American olive (*Osmanthus americanus*), and mistletoe (*Phoradendron leucarpum*). It is interesting to note that these four species shared the traits of being evergreen, and having fruits with high persistence and low rates of spoilage. Ardisia is also a winter-fruiting plant that has those same qualities. Skeate (1987) speculated that the fruit's ability to persist on the plant for long periods without spoiling was a coevolved relationship between the plants and the erratic behavior of the robins and waxwings that feed so heavily on those fruits. If they are not depleted by wintering birds, fruits of these species will persist into spring migration times (personal observation).

The ability of coral ardisia to retain its fruits for long periods is a trait that has been found with other introduced plants (White and Stiles 1992, Bartuszevige and Gorcho

2006). The majority of native species set fruit in the fall, a period that coincides with fall migration. Due to high consumption rates, these native fruits are considered to be very important to birds (Stiles 1980) with most usage occurring in late fall and winter. White and Stiles (1992), and Bartuszevige and Gorchov (2006) also concluded that if not removed from plants, the fruits of introduced species tended to persist for long periods without deteriorating. However, this quality may not reflect any taxonomic relationships, but rather selection by humans for particular landscaping features. For instance, if having persistent berries is not a common winter trait for plants, humans may select those species that have this feature. Indeed, this trait could have also increased the use of ardisia as a landscape plant (Kitajima et al. 2006).

In conclusion, ardisia flowered in the summer, peaking in July or August. There was some variation among years that was possibly due to water availability. Green fruits became visible 3 to 4 weeks following flowering, and took about four months to ripen. All fruits ripened in the winter, and ripening peaked in January. Fruits usually lasted on the plants through the summer, and some remained into October. Plant density affected loss rates, with the more densely growing plants retaining fruits for longer periods. Branch height did not affect loss rates. There were differences in fruit loss rates among sites, with the natural sites losing fruits more quickly than those in the city. The use of fruitfall traps to distinguish between active and passive loss would be a useful next study.

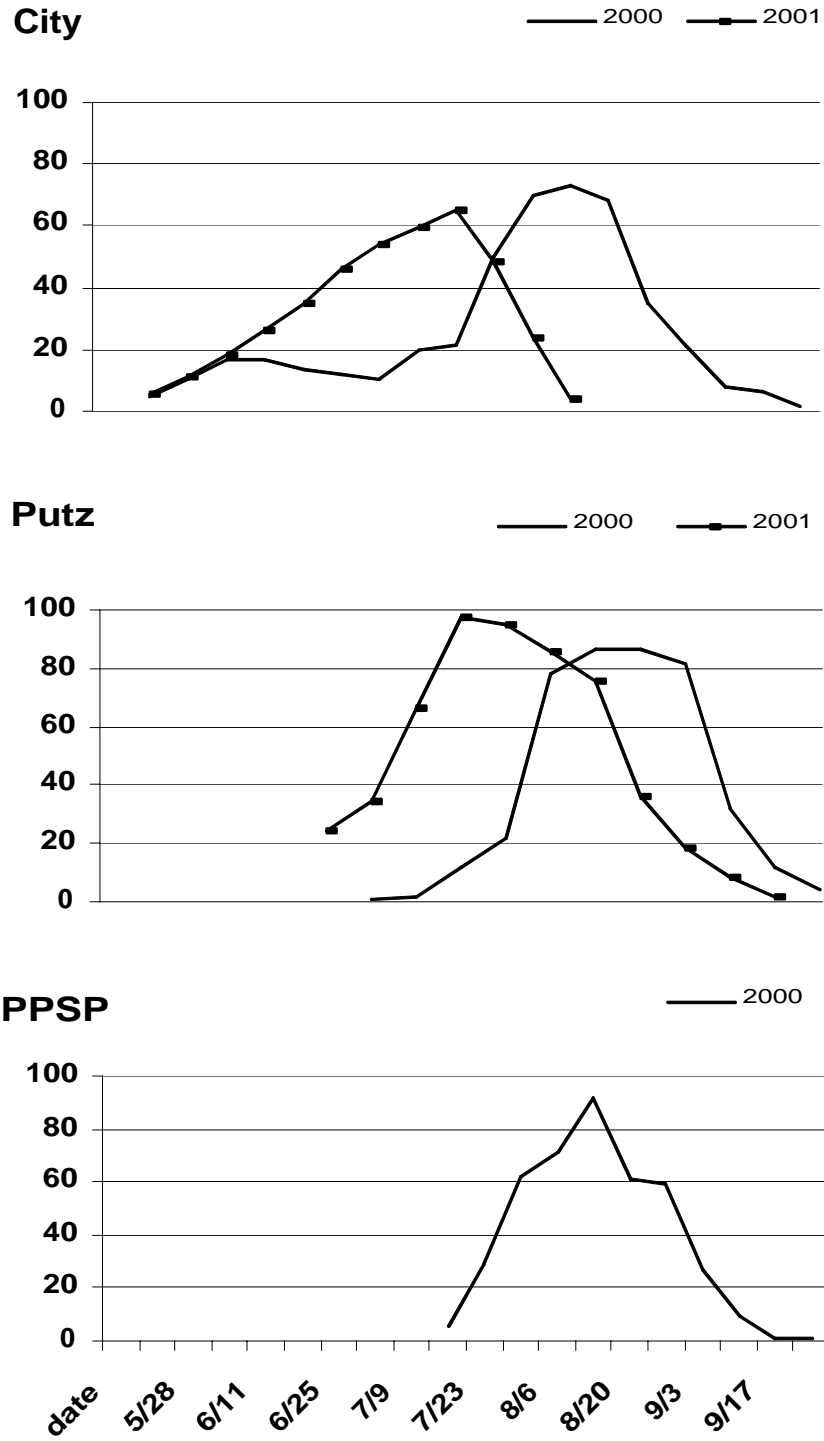
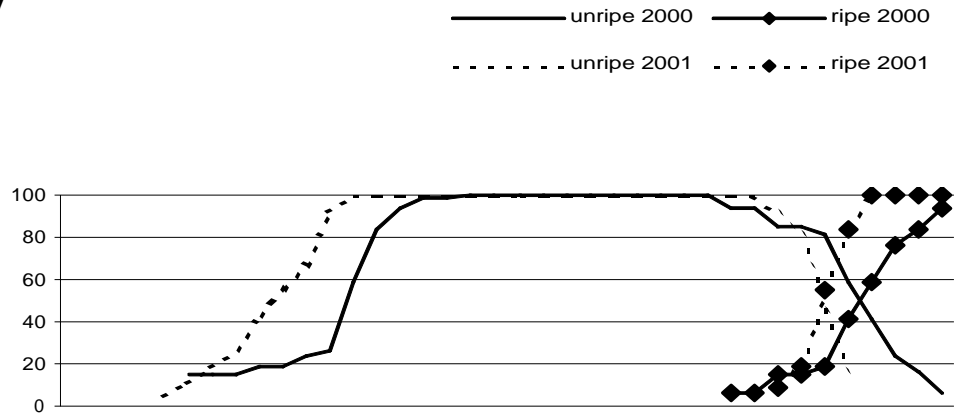
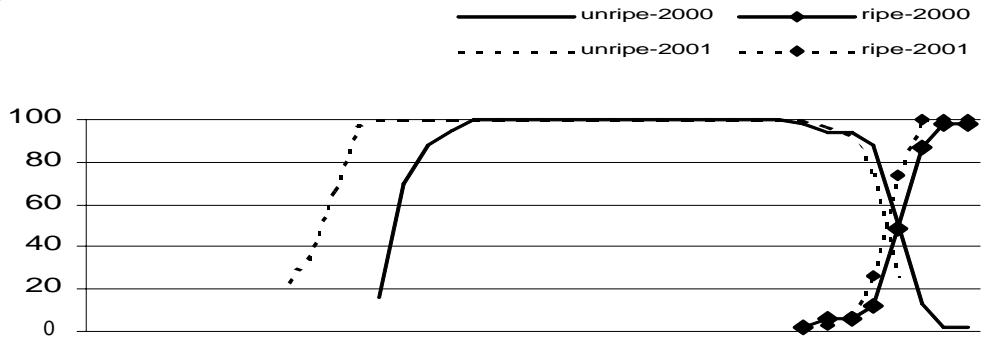


Figure 2-1. Flowering dates of *Ardisia crenata*.

City



Putz



PPSP

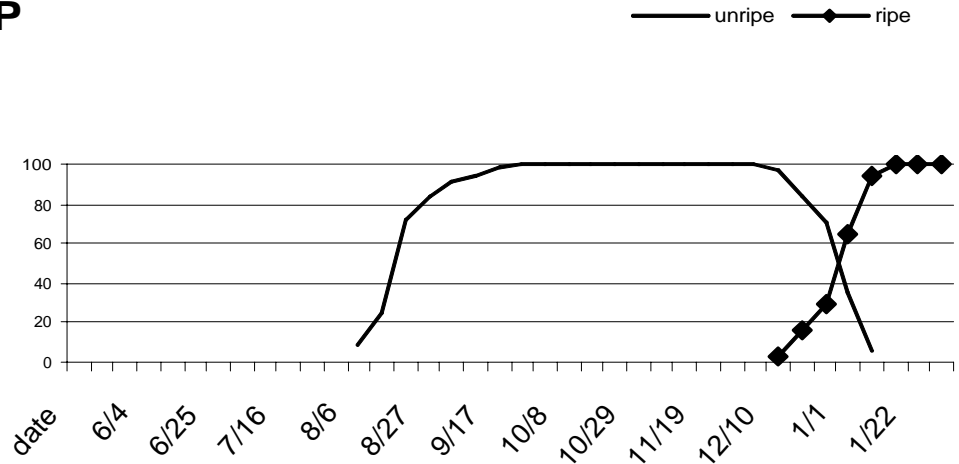


Figure 2-2. *Ardisia crenata* fruit production dates for three populations. Values on the Y-axes represent the % of monitored plants at that stage.

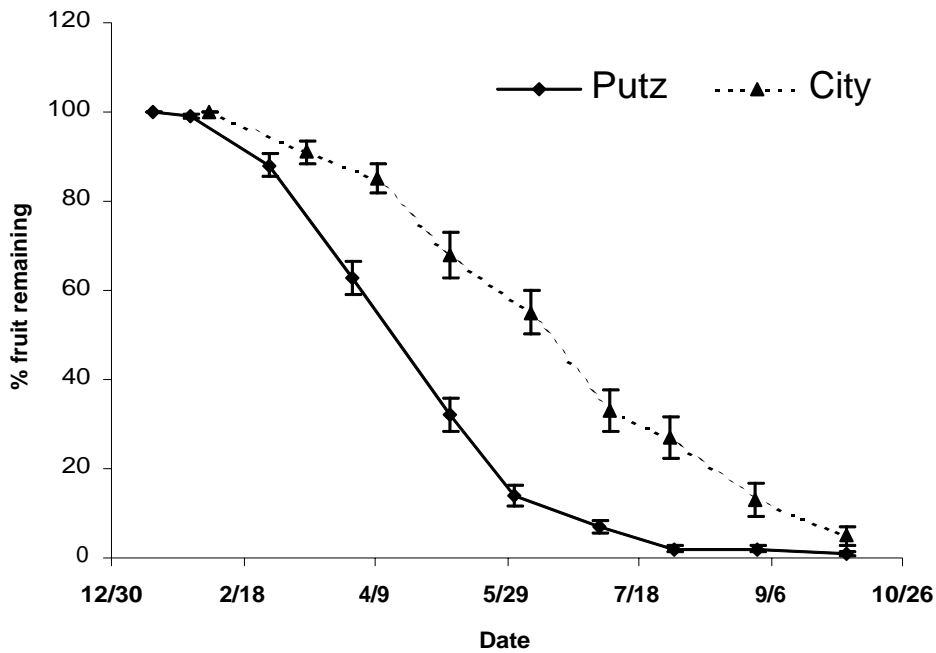


Figure 2-3. Fruit losses from *Ardisia crenata* plants at two sites during 2001. Error bars represent standard errors.

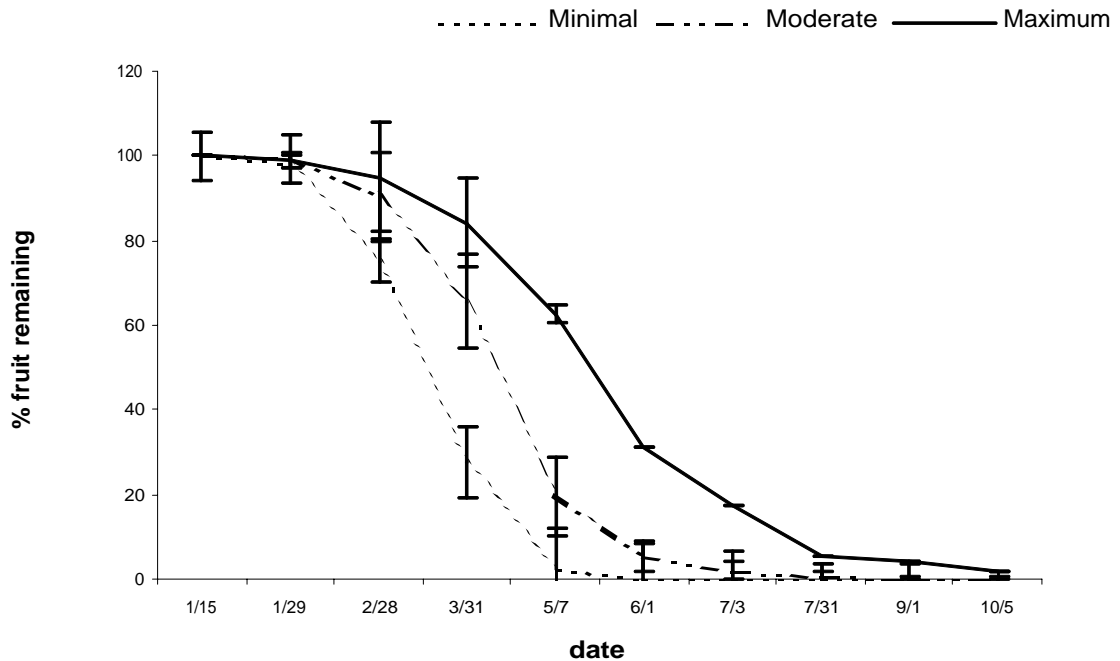


Figure 2-4. The loss rates of *Ardisia crenata* fruits at Putz during 2001. The three lines represent loss rates for three densities of *A. crenata* plants. Error bars show 95% confidence intervals.

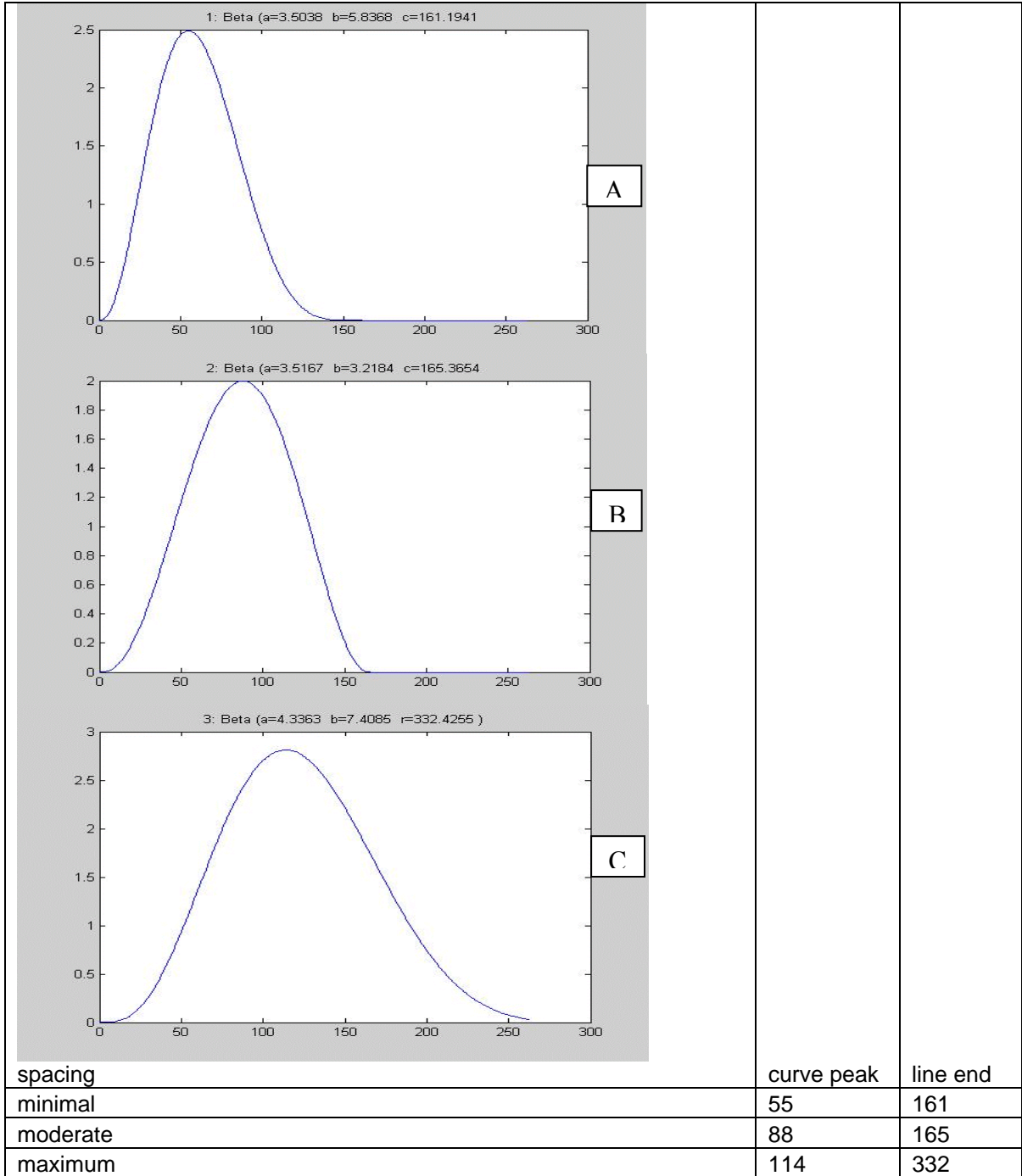


Figure 2-5. Probability density function graphs for *Ardisia crenata* fruit loss rates at three different densities of plants; A) minimal, B) moderate, and C) maximum. The values given at the top of each graph are the coefficients for the quadratic equation. Values on the X-axis are the number of days since fruit ripening. Peak curve values are when fruit losses are greatest, and the end of the line is the estimated last day of fruit persistence.

Table 2-1. Rainfall levels for Gainesville, FL (units are inches).

2000	Amount	2001	Amount	Average	Amount
January	3.17	January	0.80	January	2.60
February	0.69	February	0.91	February	3.27
March	2.13	March	5.36	March	4.11
April	0.92	April	1.01	April	3.48
May	0.51	May	1.36	May	3.72
June	5.78	June	10.83	June	6.64
Total	13.2		20.27		23.82

It is not known how many years data collection constitute averages (Gainesville Sun, June 30, 2002).

CHAPTER 3
NUTRITIONAL CONTENT OF *Ardisia crenata* FRUITS

Introduction

As a means to achieve seed dispersal, many plants have evolved fleshy fruits. Most fruits adapted for vertebrate consumption consist of seed(s), pulp, and skin, with the pulp (and to a lesser extent the skin) providing a nutritional reward to dispersers. Although invertebrates may occasionally be involved (Kaufmann et al. 1991), this type of seed dispersal is usually carried out by vertebrates.

The nutritional value of fleshy fruits is usually assessed by measuring protein, lipid, and carbohydrate levels (Stiles 1980), and studies have found that levels of these nutrients can help to explain the choices made by birds when selecting among the fruits of different plant species (Johnson et al. 1985, Lepczyk et al. 2000).

Another factor that can influence fruit choices by birds is the seed load. Seed load is the proportion of fruit mass that is undigestible seed, and not surprisingly, birds may prefer fruits with lower seed loads (Howe & Vande Kerckhove 1981, Stanley & Lill 2002, Russo 2003).

The research described in Chapter 3 assessed the nutritional content of coral ardisia fruits and compared the results to other fruit species that represent alternative choices for birds in northern Florida. If ardisia is obviously nutritionally deficient, it may help to explain the low rate of fruit consumption by birds.

Methods

Fruits were gathered from two populations on the University of Florida campus near Bivens Arm Lake and Lake Alice during May of 2002. Following collection, fruits were weighed and measured with calipers ($n = 58$). Pulp and skin were manually separated from seeds to calculate seed load and to determine lipid, soluble carbohydrate, and protein levels of the pulp and skin. Seeds were not included in the nutritional analyses because they were not digested during the bird feeding trials (Chapter 4). Fruit skin is commonly not digested, but after examining feces from feeding trials (Chapter 4), it appeared that much of the skin was at least partially digested. Consequently, fruit skins were included in the nutrient analyses.

Fruit material was freeze-dried to a constant mass. Freeze-drying was used rather than heat drying because high temperatures have been shown to influence the results of nutritional analyses (Mary Beth Hall, Department of Animal Sciences, personal communication).

Moisture content of fruits was calculated using the formula: $(\text{dry weight} / \text{wet weight}) \times 100$. Samples for lipid analyses were not ground. Samples for protein and carbohydrate estimates were ground in a Wiley mill with a 1 mm screen. Material was mixed together and subsampled for nutrition analyses. Three replicates were used for the lipid analysis and five replicates each for protein and carbohydrates.

Lipid content was assessed using the ether extraction method in which fruit material (pulp and skin) is dried, weighed, soaked in ether 6-8 hours, dried, and re-weighed. The difference in weight is due to the movement of lipids into the ether.

The amount of protein was calculated from nitrogen levels using the Kjeldahl extraction method (Association of Official Agricultural Chemists 1980) with a boric acid

modification during distillation, and a conversion factor of 6.25 to calculate protein (Pierce and Haenisch 1947).

Carbohydrate analysis was performed using an 80:20 ethanol/water solution to remove sugars, which are ethanol-soluble. Enzymatic analysis was performed on the residues to estimate starch content. Carbohydrates are reported as TESC (Total Ethanol Soluble Carbohydrates). The carbohydrates measured in this analysis include mono- and oligosaccharides (Hall et al. 1999).

Unless otherwise specified, data are presented as a percentage of dry matter.

Results

Fruit measurements and nutritional data are presented in Table 3-1. The fruits of coral ardisia averaged 8.9 mm in diameter (sd = 0.41 mm). The average fresh weight of whole fruits was 244.4 mg (sd = 60.74) with a mean seed mass of 91.4 mg (sd = 24.73), resulting in an average seed load of 37.6 %. Pulp and skin of fresh fruits averaged 88.5 percent water content (sd = 2.42). The lipid analysis found 8 percent (sd = 3.61) of dry matter was due to lipid weight. Crude protein levels were calculated to be 3.7 percent (sd = 0.09), and carbohydrate levels to be 47.8 percent (sd = 0.55).

Finding nutrient deficiencies may suggest why birds rarely eat the fruits of coral ardisia. To put the fruit nutritional data into context, I included data for other (native) species from White (1989) (Table 3-2). White (1989) did not provide intraspecific statistical data (i.e. means and error terms). The values in Table 3-3 are means for the native species listed, grouped together by seasonality. White (1989) also did not include seeds with his nutritional analyses. However, other authors have not made that claim (e.g. Stiles 1980), and failure to omit seeds may affect nutritional analyses with that part of the fruit that is not typically digested. Mono- and disaccharide concentrations from

White (1989) were reported in the present study as carbohydrate levels, and the differences in fruit dry mass are probably attributable to indigestible, structural carbohydrates.

Discussion

When foraging for fruits, birds often have multiple plant species available from which to choose. Patterns emerge as they consistently choose fruits of some plant species over others. While the choices can be observed and the preferences reported, explaining why the selections are made is not easy. To determine some of the factors involved in fruit choice, birds can be captured and fed artificial fruits where a single variable of interest is manipulated.

Stanley and Lill (2002) fed birds translucent artificial fruits containing either a single large or no plastic bead (which simulated a seed). The authors found that the birds showed a strong preference for fruits that contained no bead. The coral ardisia seed load value of 37.6% was within the range of 10.5% to 68.0% for winter fruits from native species (Table 3-2), and was very similar to the mean seed load for winter fruits (Table 3-3). All of the species listed for spring/summer are probably eaten with greater frequency than is ardisia (personal observation), and all of those species have lower seed loads than ardisia.

Conversely, poison ivy fruits are produced in winter and readily consumed by birds despite a seed load of 68.0%, a trait perhaps overridden by its 47.2% lipid value. Many fruits that ripen in the fall are high in lipids, and because this period coincides with fall migration it is assumed that this represents an advancement of the bird-fleshy fruit relationship by meeting the metabolic demands of migration with high-energy, lipid-rich fruits (Stiles 1980). Thus, high-lipid fruits are some of the most sought after fruits in the

fall. In addition to this temporal-related trend, certain fruit selections may also be on an avian taxonomic level, such as the high-lipid fruit preference exhibited by thrushes (Witmer and Van Soest 1998).

Lipid content of coral ardisia fruits (8.0%) falls within the extremes of winter (0.7% to 45.2%) and spring/summer (0.2% to 19.1%) native fruit species (Table 3-2). Lipid values for coral ardisia are less than the mean value for winter fruits, but greater than the mean lipid value for spring/summer fruits (Table 3-3). It is interesting to note that coral ardisia has a 10-fold greater lipid value than American holly, and the holly is probably the most preferred native winter species of those listed (personal observation). My observation of American Robins stripping American hollies of their fruits and ignoring the equally abundant coral ardisia fruits (Chapter 4) suggests that despite the higher lipid values of coral ardisia, other factors influence fruit selection.

The protein content in ardisia fruits (3.7%) falls within the extremes of winter (1.9% to 6.2%) and spring/summer (2.2% to 9.8%) native fruit species (Tables 3-2), suggesting that low protein levels is not why birds do not consume ardisia fruits. Similarly, the carbohydrate content in ardisia fruits (47.8%) falls within the range of winter (0.0% to 52.0%) and spring/summer (38.3% to 83.3%) fruits (Tables 3-2 and 3-3).

Carbohydrate content may not be very useful for predicting winter fruit usage, as the species with the highest content (gallberry) retains its fruits for months with seemingly little consumption by birds, and the species with no carbohydrates (poison ivy) often has its fruits removed quickly. Lepczyk et al. (2000) found that American Robins preferred high-sugar, low-lipid fruits in summer, but changed their preferences to low-sugar, high-lipid fruits in autumn.

It is difficult to draw any firm conclusions about the effects of coral ardisia's nutritional components on avian fruit preferences when compared to native species, because some of those species are more-or less-preferred over others (though probably all would be favored over ardisia fruits). For example, of the winter fruits listed in Table 3-2, greenbrier and gallberry are rarely eaten, whereas American holly and red cedar are consumed by birds much more frequently (personal observation). Without a ranking of the preference values for the native species listed in Table 3-2, those data should only be used to gauge the variability and "average" of fruit nutritional values.

There are no obvious qualities with regard to seed load or nutritional content that would explain why birds rarely eat coral ardisia fruits. However, the ability of the fruits to resist decay suggests high levels of secondary metabolites (Chapter 2), which have been shown to deter fruit consumption (Cipollini and Levey 1997b, Levey and Cipollini 1998).

To estimate protein using the Kjeldahl extraction method (Association of Official Agricultural Chemists 1980), nitrogen is measured and then multiplied with a conversion factor of 6.25. This conversion factor was derived from animal-based samples, where all nitrogen is associated with protein. However, while this factor is also used to estimate protein levels in plant-based samples, plants can contain nitrogen-based secondary compounds. Thus, it is possible to over-estimate the amount of protein in a sample of plant material if a 6.25 conversion factor is used. Levey et al. (2000) calculated conversion factors for fruits of 18 plant species in the southeastern United States, including coral ardisia. These authors determined that the correct conversion factor for estimating protein levels in coral ardisia fruits is 6.28 (corrected conversion factors

ranged from 3.11 to 6.77). This value is nearly identical to that for animal-based samples, and suggests that any secondary compounds present in coral ardisia do not contain high levels of nitrogen.

Based on the measured characteristics of the fruit size, seed load, and nutrient content, there is no reason to believe that birds would not eat coral ardisia fruits if provided no alternatives. Nor are there any obvious characteristics measured here that would lead us to expect that coral ardisia would not be preferred over many other fruits.

Table 3-1. Data for coral ardisia fruits (means and standard deviations). Percentages of nutrient data are on a dry matter basis.

	n	mean	sd
fruit diameter (mm)	50	8.9	0.41
fruit mass (mg)	100	244.2	60.74
seed mass (mg)	100	91.4	24.73
seed load (%)	100	37.6	5.17
moisture (%)		88.5	2.42
lipids (%)	3	8.0	3.61
ash (%)	2	5.3	
protein (%)	5	3.7	0.09
total ethanol-soluble carbohydrates (%)	5	47.8	0.55
starch (%)	5	16.3	0.14
free glucose (%)	5	18.1	0.15

Table 3-2. Nutritional data for fruits available in northern Florida natural areas, grouped together by season. Fruits from coral ardisia are generally available winter through summer; values of fall fruits were included as a reference. Data for all species other than coral ardisia are from White (1989).

Species		season	fruit mass (mg)	seed mass (mg)	seed load (%)	water (%)	lipid (%)	protein (%)	CHO (%)
<i>Ardisia crenata</i>	coral ardisia	w/s/s/f	244.2	91.4	37.6	88.5	8.0	3.7	47.8
<i>Ilex glabra</i>	gallberry	w	181.4	3.4	10.5	68.6	0.7	1.9	52.0
<i>Ilex opaca</i>	American holly	w	281.7	15.8	23.6	56.0	0.8	4.9	49.2
<i>Juniperus virginiana</i>	red cedar	w	46.3	9.4	25.1	48.4	7.2	3.8	41.7
<i>Rhus coppalina</i>	winged sumac	w	20.7	12.9	62.3	26.0	15.8	2.9	3.4
<i>Smilax rotundifolia</i>	greenbrier	w	241.6	35.4	38.1	74.9	0.1	6.2	17.7
<i>Toxicodendron radicans</i>	poison ivy	w	21.9	14.9	68.0	3.6	47.2	2.0	0.0
<i>Gaylussacia frondosa</i>	blue huckleberry	s/s	285.2	1.6	5.7	82.8	1.2	2.1	82.3
<i>Morus rubra</i>	red mulberry	s/s	780.1	1.6	3.9	85.6	1.1	5.9	66.4
<i>Phytolacca americana</i>	pokeweed	s/s	395.3	8.5	20.5	83.6	1.0	9.8	38.3
<i>Prunus serotina</i>	black cherry	s/s	613.4	108.9	17.8	77.5	0.4	3.9	62.0
<i>Rubus cuneifolius</i>	sand blackberry	s/s	915.3	2.3	7.7	88.9	0.2	5.8	67.0
<i>Sambucus canadensis</i>	elderberry	s/s	78.8	2.2	10.7	87.8	19.1	4.9	43.9
<i>Vaccinium corymbosum</i>	highbush blueberry	s/s	425.5	0.9	3.0	84.3	0.8	4.9	49.2

Table 3-2 continued

Species		season	fruit mass (mg)	seed mass (mg)	seed load (%)	water (%)	lipid (%)	protein (%)	CHO (%)
<i>Arisaema triphyllum</i>	jack-in-the-pulpit	f	257.8	72.2	39.2	83.3	0.4	5.8	27.5
<i>Aronia arbutifolia</i>	red chokeberry	f	293.5	11.5	10.2	73.8	0.4	4.4	12.5
<i>Cornus amomum</i>	swamp dogwood	f	203.2	42.9	21.1	78.8	2.0	4.8	54.8
<i>Crataegus crus-galli</i>	cockspur haw	f	786.2	80.9	20.6	68.9	0.9	2.4	30.7
<i>Euonymus americana</i>	hearts-a-bustin'-with-love	f	51.2	19.4	37.9	77.5	7.0	8.2	37.3
<i>Lindera benzoin</i>	spicebush	f	371.1	141.8	38.2	81.5	34.6	11.9	12.0
<i>Magnolia grandiflora</i>	Southern magnolia	f	135.9	56.1	41.3	41.7	36.7	5.2	23.6
<i>Nyssa sylvatica</i>	black gum	f	433.4	128.2	29.6	73.4	14.8	3.6	45.6

Table 3-3. The means and standard deviations per season of the fruit nutrient data from Table 3-2.

	seed load	lipids	protein	carbohydrates
coral ardisia	37.6 (5.17)	8.0 (3.61)	3.7 (0.09)	47.8 (0.55)
winter	37.9(22.89)	12.0(18.28)	3.6(1.70)	27.3(23.26)
spring / summer	9.9 (6.85)	3.4 (6.93)	5.3 (2.36)	58.4 (15.39)
fall	29.8 (11.76)	11.7 (16.52)	6.1 (3.09)	28.3 (14.87)

CHAPTER 4
CONSUMPTION OF ARDISIA CRENATA FRUIT BY BIRDS AND THEIR ROLE IN
SUBSEQUENT SEED DISPERSAL

Introduction

Two traits are evident in coral ardisia populations: fruits persist on the plant for a long time (up to a year, as per Chapter 2) and the ground beneath mature plants is often covered with seedlings (up to 300 stems per m², Kitajima et al 2006). These observations suggest that rates of both fruit consumption and seed dispersal are low. In spite of this, the plant has become invasive, signifying that at least some successful seed dispersal is occurring. In some locations, ardisia's dispersal is probably anthropogenic, but this does not account for the plant's presence in more remote natural areas.

The fruit's bright red color and subsequent high visibility suggests bird dispersal of the seeds is likely. Mammals, most of which are color blind, tend to feed on odorous fruits (Van der Pijl 1972). Furthermore, fruits that utilize mammals for seed dispersal are usually sweet-tasting (Van der Pijl 1972), and fall to the ground soon after ripening (Stiles 1980). Using both field observations and laboratory experiments, the intent of the present study was to evaluate birds as dispersal agents of ardisia.

Field observations consisted of monitoring bird activity when working in ardisia stands during the collection of plant data (Chapter 2). Laboratory experiments consisted of: 1) determining if certain frugivorous birds would indeed eat the fruits, 2) measuring their preference for ardisia fruits compared to another native fruit, and 3) assessing any effects of consumption on seed viability. If successful, the methods from these feeding

and germination trials would be used to develop a protocol to further assess birds as seed dispersal agents of other introduced plants.

Methods

Field Observations

While collecting the life-history data reported in Chapter 2, approximately 100 hours of field observations were conducted to document birds feeding on the fruits of both ardisia and native species. Although fruit traits do not suggest mammalian consumption, it does not mean that it can be ruled out. Consequently mammal scat found near ardisia stands was examined for ardisia seeds.

Selection of Birds for Experiments

Because coral ardisia fruits ripen in the winter and most persist through the spring (Chapter 2), the bird species chosen for feeding trials were those that were considered to be the greatest fruit consumers during this period in northern Florida (Table 4-1). They included Gray Catbird (*Dumetella carolinensis*), American Robin (*Turdus migratorius*), Cedar Waxwing (*Bombycilla cedrorum*), and Northern Mockingbird (*Mimus polyglottos*). Two other frugivorous species were tested (European Starling (*Sturnus vulgaris*) and Fish Crow (*Corvis ossifragus*)) because they were already available in captivity where the feeding trials were conducted. The remaining four native bird species were captured using mist-nets at several locations in Alachua County.

Captive Feeding Trials

Captive feeding trials were performed at the USDA's National Wildlife Research Center, in Gainesville, Florida. The European Starlings, Gray Catbirds, and Northern Mockingbirds were housed and tested in individual cages measuring 18 inches x 18 inches x 18 inches. The Fish Crows were housed and tested in cages measuring 10 feet

long x 10 feet wide x 6 feet high. American Robins and Cedar Waxwings were held in the larger cages until they acclimated to captivity, and then were placed in the smaller cages for individual testing.

While in captivity, birds were fed a maintenance diet of moistened Purina kitten chow, fly pupae, and fruit. Several species of fruits were offered including both wild and cultivated species. The fruit were never of the same species used as control fruits tested for that bird species. This was done because fruits contain secondary metabolites that may affect consumption rates (Levey and Cipollini 1998, Cipollini and Levey 1997a, 1997b, 1997c).

Northern Mockingbirds were the quickest to acclimate, and would often begin feeding within an hour. American Robins and Cedar Waxwings took the longest to acclimate, and one Cedar Waxwing died after not feeding for the first three days. To entice birds to eat during acclimation, birds were often given a branch of a native plant that held fruits. It was found that presenting food that the birds may have been feeding on—and in a manner that they were accustomed to—helped their acclimatization. Before undergoing feeding trials, birds had to show that they would feed from cups suspended from the sides of the cages. The European Starlings and Fish Crows had been in captivity for some time and were already feeding freely. Birds were housed individually and could not see each other while in the test cages.

Testing lasted for three days. On the first day, birds were offered the fruits of a native species that would later act as a control fruit during preference trials. The purpose was to ensure that the birds being tested would eat the fruit of that plant species. On day two, birds were offered coral ardisia fruits only. If birds failed to consume fruits on

either of these two days, they would not proceed to the choice test and would be released. In the choice test on the third day, birds were offered equal numbers of test fruits (ardisia) along with control fruits, and the remaining fruits were counted hourly to determine which fruit species the birds preferred. The number of birds tested for each species ranged from five to ten.

During testing, food from the previous night was removed at 0730 hours, and birds were without food for one hour. Test fruits were placed in cups from 0830 until 1230. Twenty fruits of each species were placed in the same dish, and counted hourly for a total of five times ($t = 0, 1, 2, 3, 4$). If the birds ate all fruits before 1230, no additional fruit was provided and maintenance diet was placed back into cage. Birds often dropped fruits during the trials, and many fell outside of the cage. During the hourly counts, these fruits were returned to the feeding cups and listed as fruits remaining. Failure to return these fruits would have led to an over-estimation of fruits consumed. For some birds, a video camera was used to observe fruit handling during feeding trials.

Voided ardisia seeds were gathered to assess germination rates. Seeds were placed in petri dishes between two sheets of filter paper, wetted with deionized water, and put into germination chambers. The conditions in these chambers were 12 hours of light per day with temperature during the light period set at 25° C and 15° C during darkness. No more than 100 seeds from each bird species were evaluated, and no more than twenty seeds went into a single petri dish.

Selection of Native Plants for Experiments

The initial protocol called for the fruits of American holly (*Ilex opaca*) to be used as the native (control) fruits for preference trials. American holly grew naturally at two

of the field sites and fruited at the same time of the year as ardisia, and thus served as an alternative fruit choice similar in size and color to ardisia.

Because it was not known if European Starlings would eat American holly fruits, and because they were mainly used for protocol evaluation, the fruits of camphor trees (*Cinnamomum camphora*), sometimes eaten by starlings, were selected for use as the control fruits for European Starling testing.

American Robins arrived in Alachua County early during the winter of 2000-2001, which may have been due to very low temperatures earlier than usual. After their arrival into the county, it became difficult to find fruits on American holly trees. While American holly fruits were used for the American Robin feeding trials, alternative fruit species for all other birds had to be found. In selecting alternative control fruits, species were chosen that shared fruiting periods with ardisia (i.e. winter, spring), and those that I knew were eaten by the relevant bird species.

The fruits chosen for Cedar Waxwing were those from East Palatka hollies (*Ilex x attenuata*). This tree is commonly used for landscaping around North Central Florida, and like American holly, has red fruits winter through summer if they are not removed by birds. East Palatka holly is a hybrid between dahoon (*Ilex cassine*) and American holly.

Fruit choice for Gray Catbirds was Godfrey's privet (*Forestiera godfreyi*), a native shrub whose springtime fruits are often eaten by Gray Catbirds (personal observation).

Fruit choice for Northern Mockingbirds and Fish Crows was highbush blueberry (*Vaccinium corymbosum*). This commercially-important species also occurs naturally, and both of these bird species are known to eat the fruits in commercial groves (Mike Avery, USDA, personal communication).

Data Analysis

Data from choice test feeding trials were analyzed using GENMOD in SAS statistical software (SAS Institute, version 8.2). Data were logit transformed and Generalized Estimating Equations (GEE) (Agresti 1996) were estimated. These GEE estimates were the slope estimates of control and test results, and the slopes were then tested for significance from each other. Significant differences meant that the bird species being tested chose one fruit species over another.

Results

Field Observations

In December of 2000, a flock of about 40 American Robins come into the Putz site. The birds gorged themselves on American holly fruits, and most of the birds departed when the fruits were depleted. A couple of birds remained for several days and fed on what appeared to be the less desirable fruits of a *Smilax* spp. and American olive (*Osmanthus americanus*) until these fruits, too, were exhausted. There were numerous ardisia plants with ripe fruits in the area, but no robins were ever seen feeding on ardisia fruits.

In the second half of April 2002 at the Putz site, several Gray Catbirds were observed consuming ardisia fruits. There were about sixteen birds on three acres of ardisia plants, and each bird appeared to swallow approximately three fruits every six to fifteen minutes. This was the only time out of two and a half years (three spring migrations) that Gray Catbirds were observed in the ardisia stands, and Gray Catbirds were the only species observed to feed on ardisia fruits in the field.

Outside the study sites, I found regurgitated ardisia seeds under a Northern Mockingbird song perch at Carr Hall on the University of Florida campus, and was told

of a Northern Mockingbird eating fruits during an especially cold winter evening (Carmine Lanciani, Zoology Department, University of Florida, personal communication). Finally, the founder of Birdsong Nature Center in Thomasville, Georgia, reported a single occurrence of a flock of Cedar Waxwings feeding on the fruits of coral ardisia at the center (Kathleen Brady, Birdsong Nature Center, personal communication).

Mammal scat in the vicinity of the field sites often contained the seeds of other plants, but none contained ardisia seeds. On a single occasion I did find ardisia seeds in mammal feces, but not at any study site.

Feeding Trials

All six bird species consumed native and ardisia fruits during the no choice trials. Fish Crows were the most reluctant species to consume fruit, where only five of ten birds consumed ardisia fruit during no choice trials. Therefore, only five Fish Crows were used for the preference (choice) trials. Similarly, while five Gray Catbirds passed the no choice test, one of them ate nothing during the preference trials.

European Starling (Figure 4-1) and gray catbird (Figure 4-2) displayed no taste preference between control and test fruits (Table 4-2). The remaining four species, Northern Mockingbird (Figure 4-3), American Robin (Figure 4-4), Cedar Waxwing (Figure 4-5), and Fish Crow (Figure 4-6), showed significant preference for control fruits (Table 4-2). These four species ate few ardisia fruits until all the control fruits had gone.

Germination rates for voided seeds from Gray Catbirds, Northern Mockingbirds, American Robins, and Cedar Waxwings did not differ from manually depulped seeds (Table 4-3). Consumption by Fish Crows did significantly decrease seed germination ($p \leq 0.05$, Fischer's chi-square test) (Table 4-3), probably due to seed coat damage that was

incurred while attempting to depulp seeds with their beaks. Germination rates for seeds voided by European Starling were not determined.

All bird species swallowed ardisia fruits whole, and it appeared all species regurgitated seeds, with the exception of Cedar Waxwings, which defecated seeds. In addition to swallowing whole fruits, some Fish Crows also attempted to manually separate fruit pulp from the seed in a technique known as mashing (Moermond and Deslow 1985). However, because the fruits of ardisia have pulp that tightly adheres to the seed, they were not very successful. Some fruits had no pulp removed while others were partially depulped, but none were completely depulped through mashing. The only seeds that were completely depulped by the Fish Crows were those that were done so in their crops. Of these, the five birds completely depulped only 29 seeds (Table 3-2), and of those, a single bird was responsible for 17 seeds.

Discussion

Field Observations

When the American Robins exhausted the American holly fruits at the Putz site, they had two choices: either remain and feed on less-preferred fruits, or leave the site to forage for alternate food sources. Two individuals chose the former alternative, but most of the birds made the latter choice. Even for the two robins that remained, ardisia fruits were ignored.

The observation of Gray Catbirds feeding on ardisia occurred during spring migration, a period when only three native plants were observed to produce fruits. These include Godfrey's privet, red mulberry (*Morus rubra*), and blackberry spp. (*Rubus* sp.). However, like ardisia, winter-fruiting species retained fruits if they had not been removed by birds. These included East Palatka holly trees in urban communities where frugivores

were less common and a single American holly whose fruits the birds did not eat. It appeared that red mulberry and Godfrey's privet in Alachua County did not produce fruit in 2002, possibly due to a late hard freeze (18.8° F) on February 28 (<http://fawn.ifas.ufl.edu/>) that may have damaged the plants. Red mulberry produces one of the most frequently bird-consumed fruits in Alachua County (personal observation), and I have seen Gray Catbirds eating unripe red mulberry fruits while ignoring abundant and ripe ardisia fruits on the University of Florida campus. The choice of Gray Catbirds to feed on ardisia fruits during the spring of 2002 at the Putz site may have been related to the apparent crop failure of Godfrey's privet and red mulberry in Alachua County. If crop failure in other plant species forced Gray Catbirds to eat more ardisia fruits than normal in spring 2002, then my observations may not be indicative of a typical year.

Coral ardisia grows in dense patches of hardwood forest understory, a habitat it shares with its analogous congener in southern Florida, shoebutt ardisia (*A. elliptica*). Similarly, shoebutt ardisia's primary disperser seems to be Gray Catbirds (Koop 2004), and during spring migration (Tony Koop, personal communication). Gray Catbirds often remaining in dense low-growing vegetation. They are common in winter in Florida, and waves of migrants come through northern Florida from mid-April through mid-May (<http://myfwc.com/bba/GRCA.htm>). Stragglers linger into June.

Research discussed in Chapter 2 showed that fruits of coral ardisia can be expected on plants January through October. Fruit loss rates increased in March and continued through June, with loss rates peaking April through early May. This loss rate is consistent with populations of Gray Catbirds in northern Florida. Most American Robins leave Florida in February, with far fewer numbers remaining into March. Cedar

Waxwings begin leaving in April, although stragglers linger into May. Skeate (1987) found that winter flocks of American Robins and Cedar Waxwings in northern Florida were nomadic, remaining in an area as long as fruit were present, and then dispersing to other areas. Based on fruit loss rates, it would not appear that American Robins or Cedar Waxwings are responsible for much of the coral ardisia fruit loss.

The observations of Cedar Waxwings eating ardisia at Birdsong Nature Center fruits may be considered atypical behavior. Kathleen Brady reported that their ardisia plants grow under scattered mature trees, a habitat different from that normally invaded by ardisia: a closed-canopy forest (personal communication). Lima (1993) argued that birds choose habitats based upon their escape tactics from predators. He described Cedar Waxwing's escape strategy as aerial, and my observations of Cedar Waxwings being attacked by a merlin (*Falco columbarius*) while mist-netting support this. Based on Lima's reasoning, Cedar Waxwings might avoid the forest understory where their escape routes would be compromised.

Kaoru Kitajima (Botany Department, University of Florida) observed that rates of fruit loss in coral ardisia's native range (Japan) appeared to be greater than those in northern Florida (personal communication, unpublished data). In Japan, Brown-eared bulbuls (*Hypsipetes amaurotis*) are known to consume the fruit of ardisia, but other Asian forest-interior bird species, such as the pale thrush (*Turdus pallidus*), may consume the fruits as well (K. Kitajima, personal communication). Brown-eared bulbuls are the family Pycnonotidae, a family with no native North American representatives. This lack of closely-related species in North America could help explain ardisia's low fruit

consumption rates in its introduced range, and may be a situation where plant population and expansion is limited by a lack of suitable seed dispersers.

For many plant species, high mortality—especially at the seedling stage—tends to swamp out the importance of seed dispersal (Howe 1993, Howe et al. 1985, Schupp 1988, Chapman and Chapman 1995). Thus, while it is generally accepted that seed dispersal is not as important a stage in the life history of a plant as once thought (Schupp 1995), seed dispersal could be limiting for introduced species. It may be possible that coral ardisia lacks suitable dispersers because it lacks suitable fruit consumers.

Field observations indicate that Gray Catbirds may be the most important avian consumers of ardisia fruits. Some fruit may also be eaten by Northern Mockingbirds and Cedar Waxwings.

The lack of ardisia seeds in mammal scat supports earlier findings in this study (Chapter 2) where low-growing branches did not lose fruits at a greater rate than those that grew higher. However, the one instance of finding mammal scat containing ardisia seeds indicates that at least one species will consume fruits from this plant. Dozier (1999) reported ardisia seeds in mammal feces, and what she called “vomit piles.” On several occasions I also found piles of seeds (not in feces), but in my opinion they appeared to be the result of masticating a mouthful of fruits from which the pulp was sucked and the seeds spit out en masse. Furthermore, these were found within ardisia stands, and not at a distance away from the plants where one might expect to have passed for a toxin to trigger vomiting. Dozier speculated that the raccoons made the vomit piles, and I have no reason to disagree with that hypothesis. It is not known what effect these actions have on seed dispersal of coral ardisia.

Feeding Trials

No bird species preferred the fruits of ardisia over control fruits. While four of six chose control fruits over ardisia, the remaining two species (European Starling and gray catbird) showed no choice preference for either test or control fruits. Thus, laboratory feeding trials support field observations that that most birds prefer native fruits over those of ardisia.

The predictive ability of the feeding trials may be limited because they were conducted with a single species of control fruit. Birds often have several choices available when foraging for fruits, and they make their choices based on what is available, including more than just the two choices that I presented. Furthermore, I chose control fruits with the knowledge that the bird species being tested would eat that fruit, conceivably biasing selection for control fruits over ardisia fruits. However, the feeding trials showed that all species could eat coral ardisia fruits.

Northern Mockingbirds, Cedar Waxwings, and Fish Crows did not begin to consume ardisia fruits until nearly all control fruits were exhausted (Figures 4-3, 4-5, and 4-6, respectively). Thus, while these three species exhibited significant differences in fruit preference (Table 4-2), the values for those preference slopes could have been different if more fruits were used in the feeding trials. For example, if enough fruits were used of each species to meet the caloric requirements for the four hours of the feeding trial, these three species may not have eaten any of the coral ardisia fruits. Alternatively, if only five fruits were used for each fruit species, the metabolic demands of the birds might have forced them to consume all ten fruits in the first hour of the experiment. A fruit count at the end of the hour would have given the impression that there was no preference for either fruit species.

In an attempt to get fruits with similar caloric values, fruits were chosen that were of similar size as those of ardisia. However, the choice of highbush blueberry did not meet these criteria. Probably as a result of selective breeding by humans, the fruits of this species were larger than those of ardisia. Although the smallest fruits were used in feeding trials, they were still larger than the test fruits. Their large size could have resulted in less ardisia fruits eaten by Northern Mockingbirds and Fish Crows, especially if the blueberries met the caloric requirements for the five-hour test.

Wheelwright (1985) found that the gape width of birds was correlated to the size of the fruits they were able to swallow, with the wider-gaped species being able to swallow larger-diameter fruits. If birds tried to swallow fruits of a diameter larger or similar to their gape width, they were often unsuccessful and dropped fruits to the ground.

While the average diameter of coral ardisia fruits was measured and found to be 8.9 mm (sd = 0.41), the diameters of control fruits were not determined. The numbers of fruit dropped during feeding trials were not counted, but if fruits were a bit too large for the smallest of the birds tested, then the dropping and replacement of ardisia fruits may have affected the results by prolonging the period that coral ardisia fruits remained. Cedar Waxwings were the smallest of the birds tested, and their control fruits were noticeably smaller than those of coral ardisia. Cedar Waxwings were the species that dropped the greatest number of fruits.

Using their bill, some birds mash fruits to remove seeds prior to swallowing, a feat not possible with coral ardisia fruits. Coral ardisia fruit pulp adheres very strongly to the seed, a quality that may limit consumption to gulpers (see Chapter 1). Fish Crows appeared to be both mashers and gulpers. Initially, they tried mashing the fruits, but

when unsuccessful with separating the seed from the pulp, some became gulpers and swallowed fruits whole. Only a single bird was able to completely clean seeds of pulp before regurgitating them, and seed survivability was compromised when damaged during mashing (Table 4-3).

The experiences with Fish Crows suggest two negative consequences to plants with tightly-adhering fruit pulp. First, potential seed dispersal agents may be limited if fruit-mashing birds, such as Fish Crows, choose mashable fruits for consumption. When monitoring fruit loss rates (Chapter 2), I found some fruits with angled puncture wounds on the top and bottom of the fruit. The wounds suggested a heavy-beaked bird sampled and rejected the fruit. Heavy beaked birds are those that mash fruits (Moermond and Denslow 1985). Second, the tight-adhering pulp can result in seed mortality, as the Fish Crows damaged the seed while attempting to separate seed from pulp. Birds may lack the ability to control the method of seed voidance, as it seems that with the difficulty in separating seed from pulp in the crop, they would have allowed fruits to pass through their digestive tract where the seed would have been cleaned of digestible material.

Seed handling and depulping strategies were determined by observing the voided seeds and assessed using video footage. Defecated seeds were in feces, and were stained by the skin. Regurgitated seeds were very clean, with no stains or pulp remaining, with the exception of those regurgitated by Fish Crows. The video camera was useful to watch birds trying to swallow (and perhaps taste) the fruits, but because voidance happens so quickly, it was not always clear whether seeds were regurgitated or defecated. A plastic or glass section of the cage may have allowed better video recording than the wire mesh.

In addition, if determining the duration of seed retention were an objective, fruits should have been fed to the birds singly to be certain that the voided seed was from a certain fruit. Video footage showed birds eating several fruits over a period of time before ridding any seeds.

While it was not one of the objectives, better data concerning seed voidance strategies and seed retention times may have been helpful to further assess bird species as agents of seed dispersal, and would help to project plant population expansions.

The methods evaluated in this chapter appear to be capable of evaluating different species of birds as seed dispersal agents. The field observations suggest birds in the family Mimidae (especially gray catbird, but also Northern Mockingbird) are likely the greatest consumers of coral ardisia fruits. Captive feeding trials suggest Gray Catbirds as coral ardisia fruit consumers. None of the bird species that swallowed whole fruit negatively affected seed germination rates.

Coral ardisia was introduced into the New World over 100 years ago and has remained a part of Florida landscaping. It has since been recognized as being an invasive weed, and has done so despite that fact that consumption of its fruits by possible seed dispersers is an uncommon event. The purpose of this study was to gain insight into the reproductive ecology of coral ardisia in its introduced range of northern Florida.

It was found that plants flower through the summer and fruits ripen in mid-winter. The fruits can persist on the plants for up to one year, with the greatest rate of fruit loss occurring in late April. Plants in a natural area lost fruits at a faster rate than those in an urban area, and isolated plants lost fruits quicker than those in denser populations. The period of greatest fruit loss coincides with the spring migration of birds through Florida,

and suggests that some consumption of fruits by birds is occurring. Fruits were found not to be nutritionally inferior to native fruits, nor were any other factors found that would suggest a cause as to why fruits of coral ardisia are rarely eaten. Despite many hours in the field, observations of birds feeding on coral ardisia fruits was limited to a single day with a single bird species (gray catbird). Captive feeding trials found that six species of birds would eat coral ardisia fruits, but often favored the fruits of native species to those of coral ardisia. Gray Catbirds and European Starlings showed the greatest acceptance of coral ardisia fruits during captive feeding trials. Cedar Waxwings defecated seeds after eating fruits, while all other species regurgitated seeds. Seed germination rates were no different for 5 of 6 birds species tested between seeds defecated or regurgitated compared to those that were manually depulped. From damage incurred while manually trying to remove seeds from fruits, Fish Crows significantly decreased seed germination rates. However, Fish Crows ate the fewest coral ardisia fruits.

Even if the dispersal of coral ardisia fruit by birds to beyond the edge of a stand is a rare event, in the long-term these infrequent events may have a significant cumulative effect. Coral ardisia seedlings have been shown to have a very high survival rate in field studies (22 – 44%; Lindstrom 2002), so the dispersal of relatively few viable seeds into suitable habitats could result in the establishment of new populations.

To test the likelihood of this further it would be necessary to use fruit traps under the monitored plants so that the mechanisms of fruit loss could be better discerned. Now that it is known which are the most likely species of bird to eat coral ardisia fruits and the conditions under which coral ardisia fruits are most likely to be eaten, it might be worthwhile to conduct further studies similar to those of Bartuszevige and Gorchov

(2006), in their study of the spread of *Lonicera mackii* by birds. That could include, for example, capturing sufficient numbers of Gray Catbirds in and around coral ardisia stands to evaluate if any of them voided coral ardisia seeds. Also the time between ingestion and voidance could be measured and compared to how far the birds are likely to move during that time. Alternatively, it might be interesting to establish why coral ardisia fruit are not more appealing to native birds, either by examining fruit characteristics such as the content of secondary compounds or by a more realistic presentation of fruit on whole coral ardisia plants to birds in larger aviaries.

In conclusion, we have advanced from not knowing whether bird dispersal of coral ardisia was possible to being able to say that it could occur. Given the number of invasive plants for which bird dispersal is claimed but which lack sufficient evidence (Meisenburg and Fox 2002), there are many of other applications of these types of study that could be useful in improving our understanding of, and predictions about, the spread of invasive plant species.

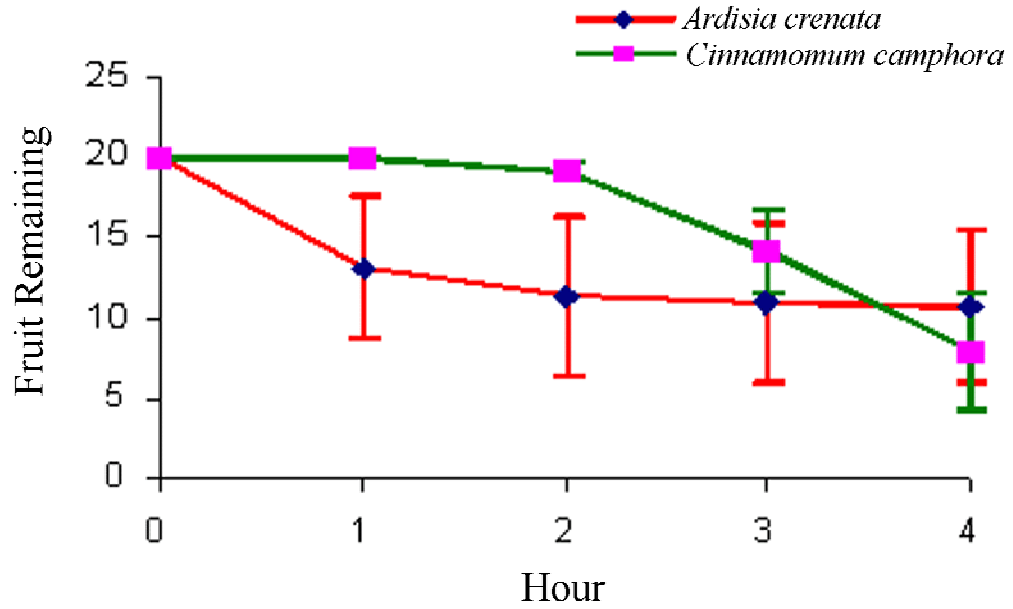


Figure 4-1. Results from European Starling feeding trials with fruits from *Ardisia crenata* and *Cinnamomum camphora* (n=4). The birds showed no preference for either fruit species. Bars represent standard error.

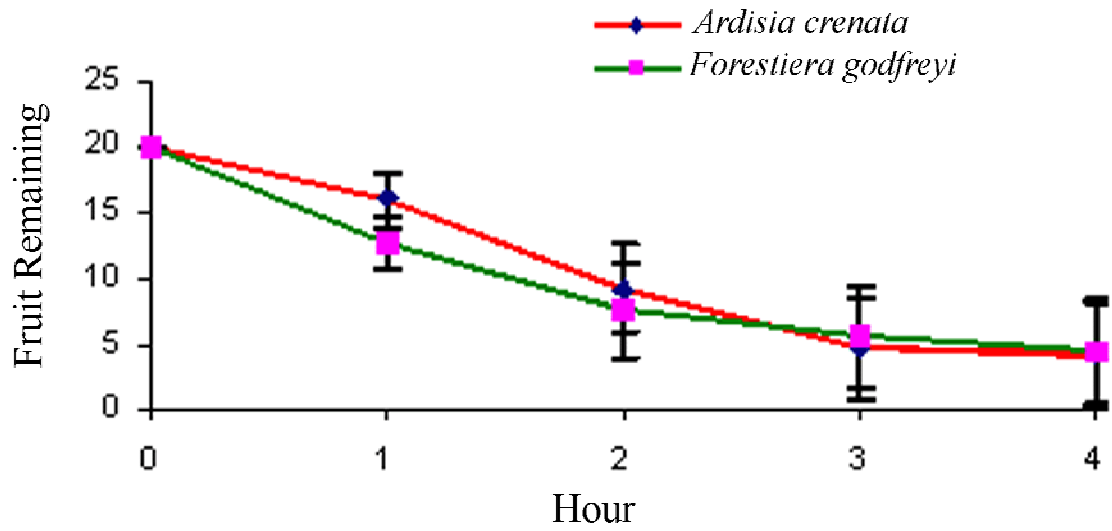


Figure 4-2. Results from gray catbird feeding trials with fruits from *Ardisia crenata* and *Forestiera godfreyi* (n=5). The birds showed no preference for either fruit species. Bars represent standard error.

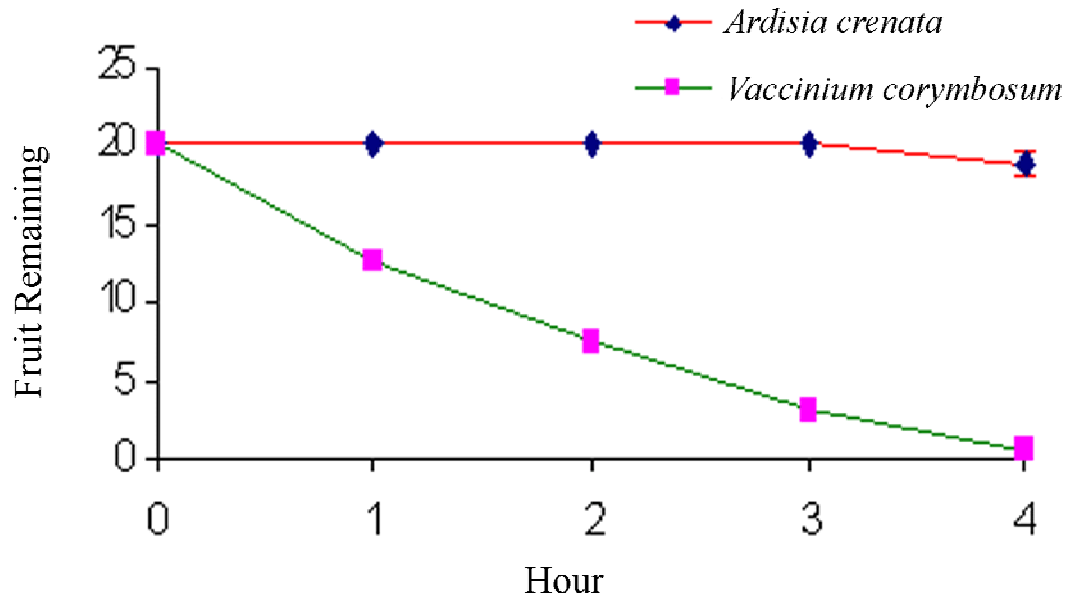


Figure 4-3. Results from Northern Mockingbird feeding trials with fruits from *Ardisia crenata* and *Vaccinium corymbosum* (n=5). The birds showed a preference for *V. corymbosum*. Bars represent standard error.

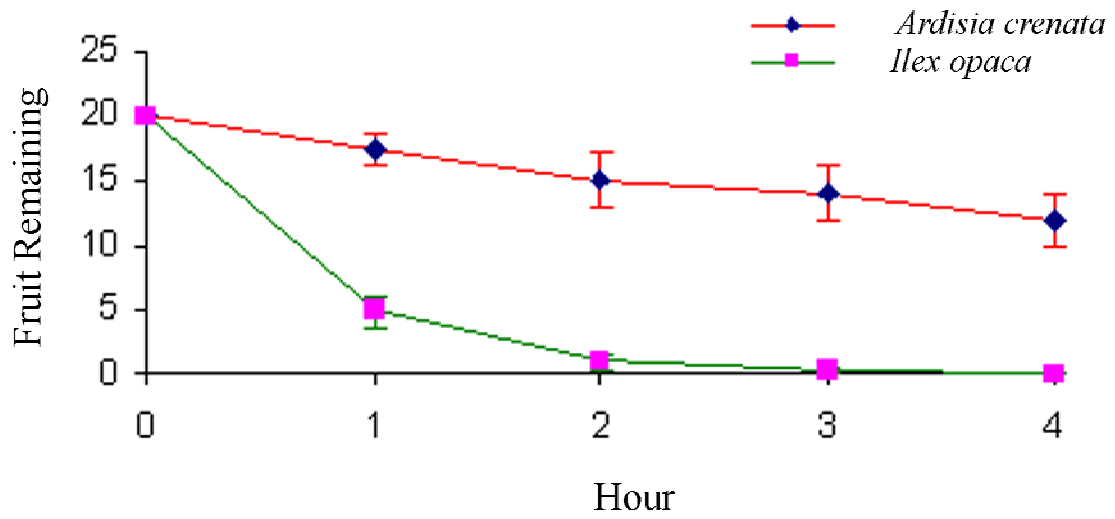


Figure 4-4. Results from American Robin feeding trials with fruits from *Ardisia crenata* and *Ilex opaca* (n=10). The birds showed a preference for *I. opaca*. Bars represent standard error.

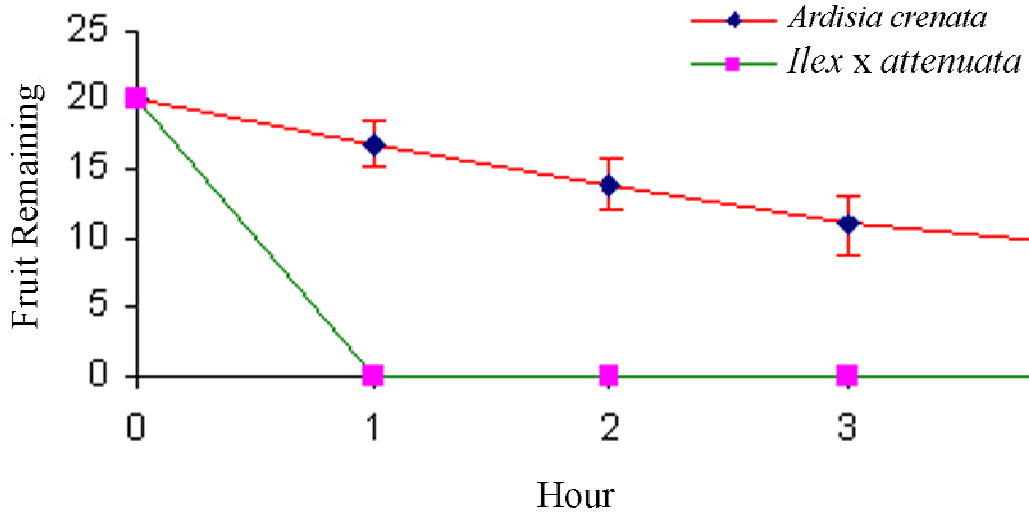


Figure 4-5. Results from Cedar Waxwing feeding trials with fruits from *Ardisia crenata* and *Ilex x attenuata* (n=10). The birds showed a preference for *I. x attenuata*. Bars represent standard errors.

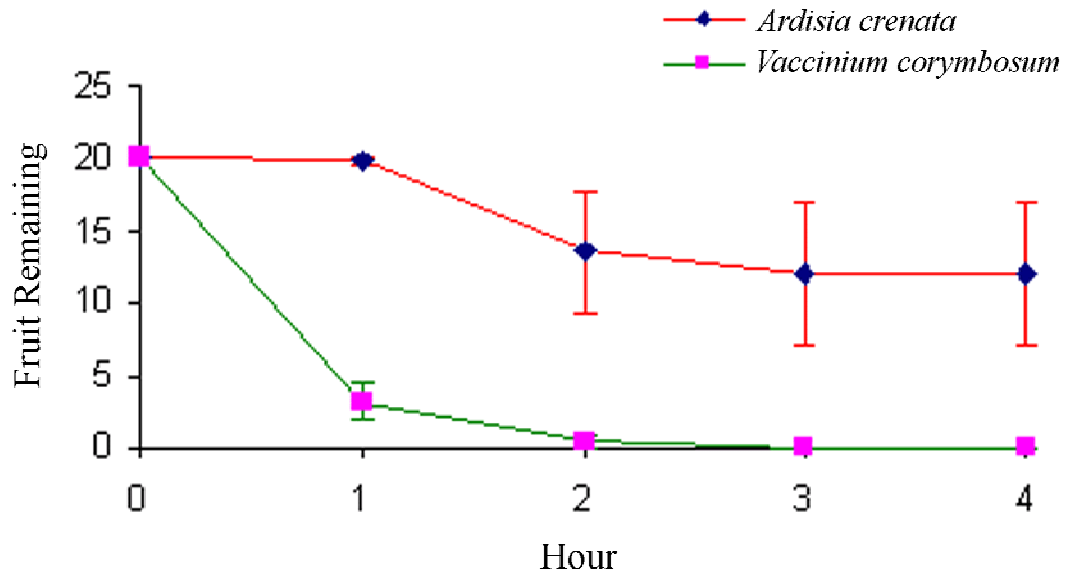


Figure 4-6. Results from Fish Crow feeding trials with fruits from *Ardisia crenata* and *Vaccinium corymbosum* (n=5). Bars represent standard error.

Table 4-1. Population statuses of the birds tested. Data are from Stevenson and Anderson (1994).

<i>Species</i>	<i>Alachua County status</i>
Fish Crow	Fairly common to common in summer, but uncommon to abundant in winter (irregular)
American Robin	Abundant in winter, majority leave before April
Gray catbird	Uncommon in winter, abundant mid-April to early May
Northern Mockingbird	Common to abundant year-round resident, numbers are reduced away from humans and in wooded communities
Cedar Waxwing	Common to abundant from late winter through spring
European Starling	Common to fairly common year-round, with population increasing from wintering individuals that depart February through March

Table 4-2. Transformed slope values from feeding trials. Significance levels indicate that two bird species did not significantly choose one fruit species over the other, while the remaining four bird species preferred control fruits over test (*A. crenata*) fruits.

	Slopes		level of significance
	ardisia fruits	native fruits	
European Starling	-0.86	-0.65	0.5961
Gray catbird	-1.06	-1.03	0.3566
Northern Mockingbird	0.0*	-1.83	<.0001
American Robin	-0.69	-3.46	<.0001
Cedar Waxwing	-0.85	-29.68	**
Fish Crow	-0.86	-4.77	<.0001

* = Did not differ significantly from zero.

** = SAS could not calculate due to its low value (there were no fruits after the first hour)

Table 4-3. *Ardisia* seed germination rates from seeds voided during feeding trials. Control fruits were those that were manually depulped.

	seeds	germinated	% germ	remarks
American Robin	100	100	100	regurgitated
control	100	100	100	
Gray catbird	100	100	100	regurgitated
control	100	100	100	
Northern Mockingbird	20	20	100	regurgitated
control	20	20	100	
Cedar Waxwing	100	100	100	defecated
control	100	100	100	
Fish Crow*	29	26	89.7	wholly depulped partially depulped-intact seed coat partially depulped- damaged seed coat
	16	14	87.5	
	9	5	55.6	
control	54	54	100	

* FICR frugivory significantly decreased seed germination rate at the 0.05 level.

LIST OF REFERENCES

- Agresti A. 1990. Categorical Data Analysis. Wiley & Sons, New York.
- Association of Official Agricultural Chemists. 1980. Official Methods of Analysis, 13th Ed., Association of Official Analytical Chemists, Arlington.
- Bartuszevige, A. M., and D. L. Gorchov. 2006. Avian seed dispersal of an invasive shrub. *Biological Invasions* 8:1013-1022.
- Chapman, C. A., and L. J. Chapman. 1995. Survival without dispersers: Seedling recruitment under parents. *Conservation Biology* 9:675-678.
- Cipollini, M. L., and D. J. Levey. 1997a. Antifungal activity of Solanum fruit glycoalkaloids: Implications for frugivory and seed dispersal. *Ecology* 78:799-809.
- Cipollini, M. L., and D. J. Levey. 1997b. Why are some fruits toxic? Glycoalkaloids in Solanum and fruit choice by vertebrates. *Ecology* 78:782-798.
- Cipollini, M. L., and D. J. Levey. 1997c. Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. *The American Naturalist* 150:346-372.
- Cipollini, M. L., and E. W. Stiles. 1992. Relative risks of microbial rot for fleshy fruits – significance with respect to dispersal and selection for secondary defense. *Advances in Ecological Research* 23:35-91 1992.
- Cipollini, M. L., and E. W. Stiles. 1993. Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. *Ecology* 74:751-762.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298-310 in P. J. den Boer and G. R. Gradwell, eds. *Dynamics of populations*. Proceedings of the Advanced Study Institute on Dynamics of numbers in populations, Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation, Wageningen.
- Cronk, Q. C. B., and J. L. Fuller. 1995. *Plant Invaders*. Chapman and Hall, London.
- Denslow, J. S. 1987. Fruit removal rates from aggregated and isolated bushes of the red elderberry (*Sambucus pubens*). *Canadian Journal of Botany* 65:1229-1235.

- Dozier, H. 1999. Plant introductions and invasion: history, public awareness, and the case of *Ardisia crenata*. Ph.D. Thesis. University of Florida.
- FDEP. 2004. Upland Invasive Exotic Plant Management Program Fiscal Year 2003-2004 Annual Report. Florida Department of Environmental Protection, Tallahassee.
- Figueroa, J. A., and S. A. Castro. 2002. Effects of bird ingestion on seed germination of four woody species of the temperate rainforest of Chiloe Island, Chile. *Plant Ecology* 160:17-23.
- Garcia, D., R. Zamora, J. M. Gomez, and J. A. Hodar. 1999. Bird rejection of unhealthy fruits reinforces the mutualism between juniper and its avian dispersers. *Oikos* 85:536-544.
- Gosper, C. R., G. Vivian-Smith, and K. Hoad. 2006. Reproductive ecology of invasive *Ochna serrulata* (Ochnaceae) in south-eastern Queensland. *Australian Journal of Botany* 54:43-52.
- Hall, M. B., W. H. Hoover, J. P. Jennings, and T. K. Miller Webster. 1999. A method for partitioning neutral detergent-soluble carbohydrates. *Journal of the Science of Food and Agriculture* 79:2079-2086.
- Howe, H. F. 1993. Specialized and generalized dispersal systems—where does the paradigm stand? *Vegetatio* 108:3-13.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola-surinamensis*). *Ecology* 66: 781-791.
- Howe, H. F., and Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201-228.
- Howe, H. F., and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62:1093-1106.
- Izhaki, I., and U. N. Safriel. 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology* 78:56-65.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501-528.
- Johnson, R. A., M. F. Willson, J. N. Thompson, and R. I. Bertini. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66:819-827.

- Kaufmann, S., D. B. McKey, M. Hossaert-McKey, and C. C. Horvitz. 1991. Adaptations for a 2-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). *American Journal of Botany* 78:971-977.
- Kitajima, K., A. M. Fox, T. Sato, and D. Nagamatsu. 2006. Cultivar selection prior to introduction may increase invasiveness: Evidence from *Ardisia crenata*. *Biological Invasions* 8:1471-1482.
- Koop, A. L. 2004. Differential seed mortality among habitats limits the distribution of the invasive non-native shrub *Ardisia elliptica*. *Plant Ecology* 172:237-249.
- Langeland, K. A., and K. C. Burks. 1998. Identification & Biology of Non-Native Plants in Florida's Natural Areas. University of Florida, Gainesville.
- Lepczyk, C. A., K. G. Murray, K. Winnett-Murray, P. Bartell, E. Geyer, and T. Work. 2000. Seasonal fruit preferences for lipids and sugars by American Robins. *Auk* 117:709-717.
- Levey, D. J., H. A. Bissell, S. F. O'Keefe. 2000. Conversion of nitrogen to protein and amino acids in wild fruits. *Journal of Chemical Ecology* 26:1749-1763.
- Levey, D. J., and M. L. Cipollini. 1998. A glycoalkaloid in ripe fruit deters consumption by Cedar Waxwings. *Auk* 115:359-367.
- Lima, S. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *The Wilson Bulletin* 105:1-47.
- Lindstrom, G. M. 2002. Life history characteristics of *Ardisia crenata* growing in natural areas in north Florida. M.S. Thesis. University of Florida.
- Mack R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.
- Manasse, R. S., and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59:185-190.
- Martin, A. C., H S. Zim, and A. L. Nelson. 1951. *American Wildlife & Plants, A Guide to Wildlife Food Habits; the Use of Trees, Shrubs, Weeds, and Herbs by Birds and Mammals of the United States*. Dover Publications, New York.
- McDonnell, M. J., and E. W. Stiles 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109-116.
- Meisenburg, M. J., and A. M. Fox. 2002. What role do birds play in dispersal of invasive plants? *Wildland Weeds* 5:8-14.

- Meyer G. A., and M. C. Witmer. 1998. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *American Midland Naturalist* 140:129-139.
- Moermond T. C., and J. S. Denslow 1985. Neotropical frugivores: patterns of behavior, morphology, and nutrition with consequences for fruit selection. Pages 865-897 in P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and N. G. Buckley, eds. *Neotropical Ornithology*. American Ornithologists' Union Monographs, 36. American Ornithologists' Union, Washington, DC.
- Morton, J. F. 1982. *Plants Poisonous to People in Florida and Other Warm Areas*. Southeastern Printing Company, Stuart.
- Murray K. G., S. Russel, C. M. Picone, K. Winnett-Murray, W. Sherwood, and M. L. Kuhlmann. 1994. Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology* 75:989-994
- Pascarella, J. B. 1998. Hurricane disturbance, plant-animal interactions, and the reproductive success of a tropical shrub. *Biotropica* 30:416-424. or Resiliency and response to hurricane disturbance in a tropical shrub, *Ardisia escallonioides* (Myrsinaceae), in south Florida. *American Journal of Botany* 85:1207-1215
- Pierce, W. C., and E. L. Haenisch. 1947. *Quantitative Analysis*, 2nd Ed. Wiley, New York.
- Renne, I. J., T. P. Spira, and W. C. Bridges, Jr. 2001. Effects of habitat, age and passage through birds on germination and establishment of Chinese tallow tree in coastal South Carolina. *Journal of the Torrey Botanical Society* 128: 109-119.
- Royal Palm Nurseries. 1900. Annual Mail-order Catalogue. Oneco.
- Russo S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136:80-87.
- Sargent, S. 1990. Neighborhood effects on fruit removal by birds: A field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* 71: 1289-1298.
- Schupp, E. W. 1988. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525-530.
- Skeate, S. T. 1987. Interactions between birds and fruits in a northern Florida hammock community. *Ecology* 68: 297-309.
- Stanley M. C., and A. Lill. 2002. Importance of seed ingestion to an avian frugivore: An experimental approach to fruit choice based on seed load. *Auk* 119:175-184.
- Stevenson, H. M., and B. H. Anderson. 1994. *The Birdlife of Florida*. University Press of Florida. Gainesville.

- Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *The American Naturalist* 116:670-688.
- Travaset, A., M. F. Willson, and J.C. Gaither, Jr. 1995. Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. *Oikos* 73:381-386.
- van der Pijl, L.. 1972. *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin, New York.
- Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808-818.
- White, D. W. 1989. North American bird-dispersed fruits: ecological and adaptive significance of nutritional and structural traits. Ph.D. Thesis. Rutgers University.
- White, D. W., and E. W. Stiles. 1992. Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of botany* 70: 1689-1696.
- Witmer, M. C., and P. J. Van Soest. 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12: 728-741.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48:607-615.
- Wunderlin, R. P. 1982. *Guide to the Vascular Plants of Florida*. University Press of Florida. Gainesville.

BIOGRAPHICAL SKETCH

Michael Meisenburg was born in North Tonawanda, New York, and graduated from Starpoint Central High School in 1982. After nearly 6 years in the Air Force, he moved to Port Orange, Florida, and soon landed a job spraying aquatic herbicides and algaecides. It was during this influential period in his life that he learned the joy that comes from killing invasive plants. He graduated from UF in 1999 with his B.S. in wildlife ecology and conservation, and currently works as a biologist for the Center for Aquatic and Invasive Plants at UF conducting research on killing invasive plants.

Michael is chair of the Control and Evaluations Committee of the Florida Exotic Pest Plant Council and president of Alachua Audubon Society. He has been married for 10 years to Vasiliki, and they have many animals together. Michael is an avid fisherman, gardener, birder, naturalist, and invasive plant killer.