

College of Humanities and Sciences
Virginia Commonwealth University

This is to certify that the thesis prepared by Sheri A. Shiflett entitled Avian seed dispersal on Virginia barrier islands: potential influence on vegetation community structure and patch dynamics has been approved by her committee as satisfactory completion of the thesis requirements for the degree of Master of Science.

Dr. Donald R. Young, Professor and Associate Chair, Department of Biology

Dr. Edward R. Crawford, Assistant Professor, Department of Biology

Dr. D'Arcy Mays, Associate Professor and Chair, Department of Statistical Sciences and Operations Research

Dr. Leonard A. Smock, Professor and Chair, Department of Biology

Dr. Fred M. Hawkrige, Interim Dean, College of Humanities and Sciences

Dr. F. Douglas Boudinot, Dean of the School of Graduate Studies

Date of Acceptance

© Sheri A. Shiflett 2008

All Rights Reserved

Avian seed dispersal on Virginia barrier islands: potential influence on vegetation
community structure and patch dynamics.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science at Virginia Commonwealth University.

by

SHERI A. SHIFLETT
B.S., Virginia Commonwealth University, 2006
B.A., Virginia Commonwealth University, 2006

Director: Dr. Donald R. Young
Professor
Department of Biology

Virginia Commonwealth University
Richmond, Virginia
August, 2008

Acknowledgements

I would like to thank my thesis advisor, Dr. Donald R. Young, for his continual confidence in my abilities, as well as teaching me the fundamental maxims of ecology. I also would like to thank The Virginia Coast Reserve, The Nature Conservancy, and the Coastal Virginia Wildlife Observatory. Thanks also to Dr. Robert Reilly, station master at Kiptopeke, for providing me with access to CVWO avian banding data for Kiptopeke from 2000-present. I would also like to thank my thesis committee, Dr. Leonard Smock, Dr. Edward Crawford, and Dr. D'Arcy Mays and my laboratory colleagues Dr. Julie Naumann, Steven Brantley, Jaclyn Vick, Spencer Bissett, and Jeremy Fennell for ensuring that there was never a dull moment in the laboratory. Financial support for this project was obtained from The Virginia Coast Reserve and a Virginia Commonwealth University Graduate Teaching Assistantship. Lastly, I am grateful to my husband, Travis, and my parents, Nancy and Danny, for their patience and support throughout my studies.

Table of Contents

	Page
Acknowledgements.....	ii
List of Tables	v
List of Figures	vi
Abstract.....	vii
Chapter	
1 Introduction.....	1
2 AVIAN SEED DISPERSAL ON VIRGINIA BARRIER ISLANDS: POTENTIAL INFLUENCE ON VEGETATION COMMUNITY STRUCTURE AND PATCH DYNAMICS.....	4
Abstract	5
Introduction	6
Methods	8
Results	11
Discussion	13
Acknowledgements	19
Literature Cited.....	21
Tables	28
Figure Legends	32
Figures	34
Literature Cited	41

Appendices.....	48
Vita.....	51

List of Tables

	Page
Table 1: Dominant physical and botanical attributes of Metompkin, Hog and Smith Islands (from McCaffrey and Dueser 1990)	28
Table 2: Species composition of vegetation along transects placed on each island and the seed species collected via fecal seed traps on each island. For each island, species are arranged in order of decreasing abundance.....	29
Table 3: Species composition of vegetation along each transect compared to seed species collected at each transect. For each transect, species are arranged in order of decreasing abundance	30
Table 4: Indices of similarity comparison of vegetation species composition and seed species composition for each transect using Jaccard's presence-community coefficient. * indicates the absence of species at one or more transects.....	31

List of Figures

	Page
Figure 1: Eastern Shore of Virginia including islands of study: Metompkin, Hog and Smith.....	34
Figure 2: Eastern Shore of Virginia denoting fecal collector transects. MG= Metompkin graminoid, MW= Metompkin woody, HG =Hog graminoid, HM = Hog marsh, HW = Hog woody, HS = Hog secondary dune, HP = Hog primary dune, SG = Smith graminoid, SW = Smith woody, and SW2= Smith second woody transect	35
Figure 3: Seeds per collector and abundance of seeds collected from artificial perches across all transects on Metompkin, Hog and Smith Islands from July 2007-June 2008. Collections were log ₁₀ transformed. J= <i>Juniperus virginiana</i> , M = <i>Morella</i> spp. including <i>M. cerifera</i> and <i>M. pensylvanica</i> , C= <i>Callicarpa americana</i> , I = <i>Iva frutescens</i> , P = <i>Parthenocissus quinquefolia</i> ., S= <i>Sassafras albidum</i> , and R= <i>Rubus</i> sp	36
Figure 4: Seasonal abundance of seeds collected from artificial perches across all transects on Metompkin, Hog and Smith Islands. Summer = July-September 2007, Fall = October- December 2007, Winter = January – March 2008, and Spring= April –June 2008.....	37
Figure 5: The total abundance of seeds collected at each transect on north Hog Island.	

The number below each transect represents the amount of species collected38

Figure 6: Number of birds banded and the number of birds banded per net hour at the Kiptopeke Banding Station in Cape Charles, Virginia from 2000-2007. Open circles represent number of birds banded and closed circles represent number of birds banded per net hour.....39

Figure 7: Precipitation for Oyster, Virginia from July 2007-May 2008 compared to the 30-year average for Painter, Virginia.....40

Abstract

AVIAN SEED DISPERSAL ON VIRGINIA BARRIER ISLANDS: POTENTIAL INFLUENCE ON VEGETATION COMMUNITY STRUCTURE AND PATCH DYNAMICS.

By Sheri A. Shiflett, Master of Science

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2008

Thesis Director, Dr. Donald R. Young, Department of Biology

Quantifying seed arrival as an ecological flux provides an understanding of patch dynamics and variations in community structure across the landscape. Because microsites favorable for germination are continually being created and destroyed in coastal ecosystems, successful species disperse seeds to multiple patches to increase probability of survival and growth. This study was conducted on three Virginia barrier islands: Metompkin, Hog, and Smith, which represent a range of size, topographic complexity and species richness. Artificial perches, with an attached fecal seed trap, were installed along transects positioned on each of the three islands. Deposited seeds were collected four times throughout the year. Seed dispersal varied seasonally with most dispersal occurring

during the spring versus the summer. Seed deposition was greatest on Hog Island and least on Metompkin Island. Spatial variation in island topography, vegetation structure, and island position were important for seed dispersal.

CHAPTER 1 Thesis Introduction

Barrier islands are highly dynamic interconnected coastal systems. Due to the interrelatedness of the system as a whole, spatial scale patterns play an important role in shaping community structure. Physical processes that affect vegetation composition and dynamics range from those operating on a local scale (e.g. soil development, seed rain) and an island scale (e.g. accretion and erosion) to those occurring at the scale of the barrier island complex as a whole (e.g. climate, storm frequency) (Hayden et al. 1991). Studying fluxes of organisms and materials across the landscape and the influence this has on ecosystem dynamics will provide insight into ecological processes operating at various spatial and temporal scales. For example, seed arrival is an ecological flux that can be quantified to gain a better understanding of patch dynamics and variations in community structure across the barrier island landscape.

Seed dispersal can be advantageous to plants for several reasons: 1) to allow for escape from density- or distance-dependant seed and seedling mortality, 2) colonization of suitable sites for germination and 3) directed dispersal to particular sites with a high probability of survival (Wenny 2001). Seed dispersal of offspring can increase the fitness of parent plants as well as prevent sibling competition and inbreeding (Willson and Traveset 2001). Selection may favor dispersal in order to increase the probability of finding a suitable location for germination. On barrier islands, microsites favorable for

germination are continually being created and destroyed by storm-related accretion and erosion (Hayden et al. 1991), by gap formation (Crawford and Young 1998a) and by nurse plant establishment (Joy and Young 2002); therefore, it is highly advantageous for seed dispersal to multiple patches in order to increase probability of survival and growth.

Ideally, seed maturation and dispersal would be timed to match the seasonal availability of favorable dispersal agents (Willson and Traveset 2001). Fleshy-fruited plants in the north-temperate zone commonly produce mature fruit crops in late summer and autumn when avian frugivores are abundant; however, at more southern latitudes, some fruit maturation occurs in winter when flocks of wintering and migrant birds are foraging (Thompson and Willson 1979). On the Virginia barrier islands, autumn bird migration occurs from August to October, coinciding with fruit maturation of woody species (Snow 1971, Stiles 1980).

Historically, the Delmarva Peninsula including both the Eastern Shore of Virginia and the barrier islands has been an important resource for migratory birds along the Atlantic migratory flyway (Mabey et al. 1993). Migrants are concentrated within the southernmost 10 km of the Delmarva Peninsula (Maybe and Watts 2000). Because both migratory patterns and seed dispersal patterns are fluxes that occur across a range of spatial and temporal scales, it is important to focus on fine, intermediate, and broad scales. Concerning the Virginia barrier system, fine-scale corresponds to seed dispersal to individual patches on a given island, intermediate-scale corresponds to seed fluxes among several patches on an island, and broad-scale corresponds to seed fluxes across several islands as well as several seasons throughout the year. Since the 1950s, plant ecologists

have recognized the importance of sampling scale in describing dispersion and distribution of species (Greig-Smith 1952). Landscape scale and structure should be relevant to animals as well, and influence their movement behavior (Farmer and Parent 1997). As a result, changes in spatial patterns of movement allow for an assessment of landscape scales and features to which animals respond (Crist et al. 1992). For instance, a migrant might consume fleshy-fruit(s) on the mainland and deposit the fruit(s) on one or more of the barrier islands. Migrants that are moving among the islands and the mainland are likely to disperse seeds back and forth in various combinations. If only one of the barrier islands were studied, then it would be difficult to ascertain the bigger picture that emerges at a broader scale investigation. Avian movement can influence both the scale and destination of seed dispersal and is therefore expected to significantly impact the communities through which volant frugivores move (Westcott and Graham 2000).

There has been little attention paid to seed fluxes between patches with birds as important vectors in temperate systems, particularly barrier islands (Wenny and Levey 1998, Crawford and Young 1998a, Crawford and Young 1998b). However, it has been previously established that *Juniperus virginiana* acts as a nurse plant for woody seedlings on a Virginia barrier island and influences directed dispersal by providing suitable perching sites (Joy and Young 2002). The objective of this study was to gain a better understanding of avian-mediated seed dispersal and the influence this has on vegetation dynamics across a range of spatial scales.

The following manuscript represents a summary of my thesis research and has been written in the form required for submission to the journal American Midland Naturalist.

CHAPTER 2

Avian seed dispersal on Virginia barrier islands: potential influence on vegetation community structure and patch dynamics

Sheri A. Shiflett and Donald R. Young¹

Department of Biology

Virginia Commonwealth University

Richmond, Virginia 23284

¹Address correspondence to D.R. Young

Email: dryoung@vcu.edu

ABSTRACT: Quantifying seed arrival as an ecological flux provides an understanding of patch dynamics and variations in community structure across the landscape. Because microsites favorable for germination are continually being created and destroyed in coastal ecosystems, successful species disperse seeds to multiple patches to increase probability of survival and growth. This study was conducted on three Virginia, USA barrier islands: Metompkin, Hog, and Smith, which represent a range of size, topographic complexity and species richness. Both Smith and Hog Islands are interspersed with tall shrub thickets (> 3 m) and several other woody species, while Metompkin Island is successionaly immature with sparse patches of young shrubs. Artificial perches, with an attached fecal seed trap, were installed along transects positioned on each of the three islands. Each island had at least one transect positioned at both a woody and a graminoid site. Deposited seeds were collected four times throughout the year. Seed dispersal varied seasonally with most dispersal occurring during the spring (n=248) versus the summer (n=4). Seed deposition was greatest on Hog Island (n=421) and least on Metompkin Island (n=5). *Morella* spp. (*M. cerifera* and *M. pensylvanica*), which accounted for 62% of the total seeds collected, represented the most abundant species deposited. Three species that appeared during spring seed counts, *Callicarpa americana*, *Rubus* sp. and *Sassafras albidum*, were not identified within a 10 m proximity of any of the transects. Spatial variation in island topography, vegetation structure, and island position were important for seed dispersal.

INTRODUCTION

Barrier islands are highly dynamic interconnected coastal systems. Due to the interrelatedness of the system as a whole, spatial scale patterns play an important role in shaping community structure. Physical processes that affect vegetation composition and dynamics range from those operating on a local scale (e.g. soil development, seed rain) and an island scale (e.g. accretion and erosion) to those occurring at the scale of the barrier island system (e.g. climate, storm frequency) (Hayden et al. 1991). Studying fluxes of organisms and materials across the landscape and the influence this has on ecosystem dynamics provides insight into ecological processes operating at various spatial and temporal scales. Seed arrival is an ecological flux that can be quantified to gain a better understanding of patch dynamics and variations in community structure across the barrier island landscape. The majority of woody plants on the barrier islands are bird dispersed (van der Pijl 1972, Ehrenfeld 1990). For this reason, it is essential to understand the underlying mechanisms of seed dispersal to make accurate predictions about the future community composition on the Virginia barrier islands.

Selection may favor seed dispersal in order to increase the probability of finding a suitable location for germination. On barrier islands, microsites favorable for germination are continually being created and destroyed by storm related accretion and erosion (Hayden et al. 1991), by gap formation (Crawford and Young 1998a) and by nurse plant establishment (Joy and Young 2002); therefore, it is highly advantageous for seed dispersal to multiple patches in order to increase probability of survival and growth. Additionally,

seed dispersal may be important for plants occurring in spatially isolated habitats like islands (Wongsriphuek et al. 2008) because most seeds lack the motility necessary to traverse waterways (Ridley 1930).

Ideally, seed maturation and dispersal would be timed to match the seasonal availability of favorable dispersal vectors (Willson and Traveset 2001). Fleshy-fruited plants in the north-temperate zone commonly produce mature fruit crops in late summer and autumn when avian frugivores are abundant; however, at more southern latitudes, some fruit maturation occurs in winter when flocks of wintering and migrant birds are foraging (Thompson and Willson 1979). On the Virginia barrier islands, autumn bird migration occurs from August to October, coinciding with fruit maturation of several woody species (Snow 1971, Stiles 1980).

Historically, the Delmarva Peninsula including both the Eastern Shore of Virginia and the barrier islands has been an important resource for migratory birds along the Atlantic migratory flyway (Mabey et al. 1993). Migrants are concentrated within the southernmost 10 km of the Delmarva Peninsula (Maybe and Watts 2000). Because both migratory patterns and seed dispersal patterns are fluxes that occur across a range of spatial and temporal scales, it is important to focus on fine, intermediate, and broad scales. Concerning the Virginia barrier system, fine-scale corresponds to seed dispersal to individual patches on a given island and bird/seed movements over hours and days. Intermediate-scale corresponds to seed fluxes among several patches on an island and bird/seed movements over several months or a season. Lastly, broad-scale corresponds to

migratory patterns and seed fluxes across several islands, as well as several seasons throughout the year or multiple years.

The purpose of this study was to examine the role of seed fluxes in influencing vegetation community structure and patch dynamics on the Virginia barrier islands. The main objectives of this study were: 1) to determine if patch type influenced seed deposition, 2) to discern if spatial variation in seed deposition existed among the islands, and 3) to compare the composition of seeds deposited relative to the vegetation of the surrounding landscape.

METHODS

Study site

Field studies were conducted on three islands of The Virginia Coast Reserve (VCR), an NSF funded long-term ecological research site managed by The Nature Conservancy. The three islands of interest were Metompkin, Hog and Smith, which represent a range of size, topographic complexity, and species richness and are positioned along a longitudinal gradient (Figure 1, Table 1). Metompkin Island ($37^{\circ}43' \text{ N}$, $75^{\circ} 34' \text{ W}$) is approximately 11 km long and ~250 ha (Young et al. 2007). Metompkin Island displays the least complex topography and species richness of the three islands. It is a successional immature island, with sparse patches of young shrubs (McCaffrey and Dueser 1990). Hog Island ($37^{\circ}40' \text{ N}$, $75^{\circ}40' \text{ W}$) is 753 ha, 10 km long, and lies 8 km off of the Eastern Shore peninsula of Virginia (Young et al. 2007). Vegetation on Hog Island

is predominantly grassland with extensive patches of tall shrub thicket (McCaffrey and Dueser 1990). Smith Island (37°07' N, 75° 54' W) is 11 km long, 399 ha and the southern end is wider than the northern end, with the northern end consisting of a narrow beach and low primary dune (McCaffrey and Dueser 1990, Young et al. 2007). Smith Island displays vegetation complexity ranging from pine and deciduous forest to tall (>3 m) shrub thickets (Dueser et al. 1979, McCaffrey and Dueser 1990). The southern end has a mixed pine-hardwood community and is covered by *Morella* spp. shrubs, which include both *Morella cerifera* and *Morella pensylvanica*, while the northern end has sparse grass cover (Bachmann et al. 2002). These islands were chosen to allow for comparisons among islands with varying degrees of topographic and vegetation complexity.

Seed Collection

For each of the three islands, at least one transect was positioned at a woody site and a graminoid site. Metompkin Island had a transect at both a graminoid site and a woody site (Figure 2) giving a total of 20 collectors. Hog Island had transects at both of these site classifications, in addition to a transect located at a marsh site, a transect located on the secondary dune, and one located on the primary dune (Figure 2). There were 37 collectors on Hog Island. Smith Island had a transect located at both a graminoid site and a woody site, as well as a transect located at a second woody site (Figure 2). Smith Island had 27 collectors. Collectors were placed 10 m apart along each transect. Once transects were established, artificial perches were installed in July 2007. The perches consisted of a

single vertical post approximately 2 m high with an attached fecal seed trap. The fecal seed trap was a plastic container with an opening approximately 5 cm across and flush with the top of each post (Joy 1996).

Once perches were established, seed collection containers were emptied and cleaned seasonally from October 2007– June 2008. Collected seeds were taken back to the laboratory for identification to genus and species level, when practical, and for quantification. A reference seed collection was also established to allow for identification of seeds collected via fecal traps. This reference collection was created using seeds collected during transect establishment and species surveying. Seeds were identified to genus level using identification guides and placed into labeled vials for future comparison to seeds collected via trapping (Martin and Barkley 1961, Young and Young 1992).

In order to compare seed deposition versus local-site species composition, a baseline vegetation survey was conducted for each transect. All woody species (i.e. vines, shrubs, and trees) were identified within 10 m of each fecal trap. Frequencies of occurrence were calculated for species based on the number traps at each transect.

Statistical Analysis

Jaccard's index of similarity was calculated to compare species found across each transect versus seeds deposited per transect to determine degree of species association (Mueller-Dombois and Ellenberg 1974, Gurevitch et al. 2002). The index is defined as the ratio of the number of species found in common in two communities to the total number of

species that are present in both. Jaccard's presence-community coefficient is represented

by the following equation: $IS_J = \frac{c}{A + B - c} \times 100$, where c is the number of common

species, A is total number of species in relevé A , and B is the total number of species in relevé B (Mueller-Dombois and Ellenberg 1974).

RESULTS

Four woody species were identified within 10 m of collectors located on Metompkin Island. These were *Pinus taeda*, *Baccharis halimifolia*, *Iva frutescens*, and *Morella* spp. (Table 2, Table 3). All of these species were found at the woody transect, while no woody species were located in the proximity of the graminoid transect. Five woody species were identified within 10 m of collectors on Hog Island: *Morella* spp., *P. taeda*, *Parthenocissus quinquefolia*, *B. halimifolia*, and *I. frutescens*. *Morella* spp. occurred within the proximity of all of the transects on the northern end of Hog Island, but not within the proximity of the graminoid transect. *P. taeda* and *P. quinquefolia* were only found at one site. Eight woody species occurred within 10 m of collectors on Smith Island: *Morella* spp., *B. halimifolia*, *I. frutescens*, *Juniperus virginiana*, *Prunus serotina*, *Persea palustris*, *Ilex vomitoria*, and *Smilax* sp. (Table 2, Table 3). *Morella* spp. and *B. halimifolia* were located at all of the sites on Smith Island. *Morella* spp. including both *M. cerifera* and *M. pennsylvanica* occurred on all three islands.

Collectors on Metompkin Island received seeds of one species throughout the sampling period (July 2007-June 2008), while collectors on Hog Island received seeds of seven species and collectors on Smith Island received seeds of one species (Table 2, Figure 3). Metompkin Island collectors received 5 *J. virginiana* seeds, but the graminoid site on Metompkin received no seeds (Table 3, Figure 3). Hog Island collectors received 266 *Morella* spp. seeds, 106 *J. virginiana* seeds, 47 *Callicarpa americana* seeds, six *I. frutescens* seeds, four *P. quinquefolia* seeds, two *Sassafras albidum* seeds, and one *Rubus* sp. seed (Figure 3). Collectors on Smith Island received 13 *Morella* spp. seeds (Figure 3). *Morella* spp. seeds accounted for 62 % of the total seeds collected (Figure 3).

Seasonal variation of seed deposition occurred as well, with only four seeds collected between July – September, 42 seeds collected between October- December, 156 seeds collected between January- March, and 248 seeds collected between April-June (Figure 4). Also, the number of species collected varied during the seasons. Three species were collected during the summer and fall sampling periods, two species were collected during the winter, and four species were collected during the spring sampling (Figure 3). Seed deposition was greatest on Hog Island for any given season with most of the seed deposition occurring at sites located on northern Hog Island (n= 426) as opposed to those located on southern Hog Island (n= 6), southern Smith Island (n= 13) or Metompkin Island (n= 5) (Figure 3).

When looking solely at sites on north Hog Island, seed collection generally increased from the bayside to the youngest thicket on the oceanside (Figure 5). The site located farthest inland (HM) collected a small number of seeds per collector (n= 5.7), the

next progressive site (HW) had fewer seeds per collector ($n= 0.5$), the secondary dune site (HS) collected more seeds per collector than the previous two ($n= 13.4$), and the site located closest to the colonizing thicket and the shoreline (HP) collected the most seeds per collector ($n= 37.4$) (Figure 5).

DISCUSSION

Quantifying seed arrival can provide insight into potential patch dynamics and community structure across the landscape. Given the low woody-species richness on Metompkin Island and the lack of structural diversity, finding only a few bird-dispersed seeds at the woody site and none at the graminoid site was not unexpected. Metompkin Island does not provide many fruit-sources or perches for birds and this may result in the infrequent use of the island by frugivorous species. Therefore, birds may not be the main contributing factor in the initial stages of the expansion of woody species on this island. Perhaps, it is only once structural diversity develops and therefore, more suitable perches arise that birds are attracted to an island as a stopover site. Equally arguable is that, although birds may be the primary means of seed dispersal and woody-species expansion on Metompkin Island, this process is one that is exceedingly slow because of the frequent set-back of autogenic successional processes due to storm-related disturbances (Thompson and Willson 1978, Hayden et al. 1991, 1995).

In comparison, Hog Island has tall shrub-thickets across the width of the northern third of the island, several tree species, and provides ample food sources and therefore, perches for avian species. Fecal collectors on Hog Island captured more seeds and more species than either of the other two islands, a result attributed to the diversity of woody species located on Hog Island, as well as its relative successional and geomorphic maturity compared to Metompkin Island.

Smith Island captured only a small number of *Morella* spp. seeds. *Morella* spp. (*M. cerifera* and *M. pensylvanica*) are the dominant woody species on both Hog Island and Smith Island (Ehrenfeld 1990, Crawford and Young 1998a, Young et al. 2007), so it follows that *Morella* spp. seeds were deposited on both islands and at six of the ten total transects for all of the islands. Because Smith Island has higher woody species diversity than Hog Island, we expected collected seed diversity to be higher than it was.

The results on Smith Island are an indication of the importance of location of the artificial perches. The sites chosen on north Hog Island were either within or very near the bands of dense shrub thickets, whereas the northernmost transect on Smith was not as close to the proximity of dense thickets. Instead, the transects located at woody sites were placed next to colonizing shrubs, north of which there was a broad expanse of open space before reaching the dense shrub thickets and maritime community on Smith Island. Perhaps, if the collectors had been placed in more suitable locations, they would have captured species diversity that was representative of the island diversity. The decision for transect placement on Smith Island was one of logistics and accessibility of sampling locations.

Location may not have been the only factor for low seed species diversity deposited in the Smith Island collectors. Last year yielded particularly low numbers for the autumn bird count at the Kiptopeke banding station (Figure 6). The count was lower than it had been for the past seven years, and almost half of what it was in 2006 (CVWO unpublished data). A one-sample t-test indicated that the average number of birds banded per net hour from 2000-2006 ($\mu = 0.76$) was significantly different from 0.46, the number of birds banded per net hour in 2007 ($p\text{-value} < 0.005$). Furthermore, comparing precipitation from September 2007-May 2008 to the 30-year average, 2007-2008 was considerably drier than the 30-year average ($p=0.017$) (Figure 7). This could indicate that less effort was put into fruit production by many plants on the barrier islands during the duration of this study, particularly during the summer and fall sampling.

Seasonality played a role in seed dispersal on the barrier islands, such that dispersal was least in the summer and greatest in the spring. During the summer, concentrations of arthropods on the islands are likely higher than during any other season, and because many frugivorous birds are also insectivorous, they may have preferred the relatively protein rich insects before resorting to fruit consumption (Morton 1973). Fall seed counts were lower than expected, but this may have been an extension of arthropod presence. Considerably more arthropods and arthropod parts were observed in collectors during the summer and fall than during the winter and spring collection periods.

Winter and spring yielded the highest seed counts. For the winter season 99 % of all seeds were *Morella* spp., whereas during the spring only 35 % of all seeds collected were *Morella* spp. This shows that winter dispersal is important for *Morella* spp., because

during the spring, when several other woody species present fruits, there are more options for frugivores. Also, other studies have suggested that where winter residents are plentiful, winter dispersal may be advantageous because there is reduced microbial decay and reduced competition for dispersers with insect food sources (Thompson and Willson 1978, Herrera 1982, Stapanian 1986). Furthermore, Kwit et al. (2004) found that winter removal rates of fruits of *M. cerifera* are higher in colder winters. They found that peak fruit ripeness occurred in November, but peak fruit removal occurred in the coldest months, December and January (Kwit et al. 2004). One previously mentioned factor is that arthropod species richness and abundance reach their lowest annual levels in winter in temperate regions (Hanula and Franzreb 1998), such as occurs on the Virginia barrier islands, which can induce diet switching by primarily insectivorous birds. Additionally, when ambient temperature drops, birds are forced to increase rates of food consumption to meet energetic demands (Calder and King 1974). *Morella* spp. fruits are low in water content, high in lipids, and can persist for months on the plant (Place and Stiles 1992), all factors which explain why such fruits are prominent in the diets of birds that are primarily insectivorous and are readily dispersed during the winter months (Fuentes 1994).

Not only did spring seed counts yield the highest number of seeds during the study duration, but spring seed counts represented the highest species diversity as well. This could be due to fruit persistence lasting until the spring season. Rapid removal of fruits from species that produce ripe fruits during summer and early fall is advantageous to plants because it reduces the probability of fruit destruction by invertebrates before dispersal (Thompson and Willson 1978). However, because several of the species found in

collectors throughout the year tend to ripen in late fall (Moss 1993), invertebrate destruction of fruits may not be much of a factor. Therefore, fruits of several species may be able to persist until spring and be available for consumption during the spring passerine migration.

Two of the species that appeared during the spring seed collection, *Callicarpa americana* and *Sassafras albidum*, and one species that occurred during the summer seed collection, *Rubus* sp., were not identified within the proximity of any of the transects. There is no record that *C. americana*, which was collected on the primary dune site, is present on Hog Island, although it has been sighted on Smith Island (Cook and Shugart 1990, McCaffery and Dueser 1990). Furthermore, *J. virginiana* was collected on Metompkin and Hog Islands, but was not within the 10 m proximity of transects on either of these islands. However, *J. virginiana* occurs on both of these islands. This indicates that although much of the dispersal occurring on the islands is likely local, some of the dispersal may come from longer-range sources. Wongsriphuek et al. (2008), who fed a known number of seeds to captive raised mallards, found that although almost all seeds were recovered within 24 hours, at least some seeds were recovered up to 48 hours, which suggests the potential for long-distance dispersal.

Spatial variation on north Hog Island played an important role in influencing seed dispersal. Considering that the greatest abundance and diversity of seeds was collected on the primary dune site, which was closest to the shoreline, this relates to natural trends in primary succession, where species attempt to colonize barren sites. Herrera (1984) noted that in most temperate forests, bird-dispersed plants typically have the greatest cover

values in edges, gaps, riparian zones and early successional sites, and occupy much less space in mature forests. Temperate forest openings can be classified in one of two groups and in one of these groups, birds perch in surrounding trees and woody species colonize from the edges of the openings (Smith 1975). Additionally, Thompson and Willson (1978) found that fruit removal rates for *P. serotina*, *Phytolacca americana*, and *Vitis vulpina* were faster in forest edge and light gap sites versus closed canopy sites. Thus, it follows that dispersal was greatest at the edge of the shrub thickets rather than in the more centrally located sites. Another factor for this particular site was that the artificial perches were the only suitable perches on the dune, whereas at several other sites, artificial perches were located near natural perches. When given the choice, birds likely gravitate towards natural perches and this could further explain why the Smith Island collectors located near woody shrubs did not fare as well as expected. Some of the sites were chosen because of the presence of natural perches, with the assumption that this would lead to more accurate sampling of natural dispersal, while other sites were chosen because of the lack of natural perches to discover what would be collected if a natural perch existed. Placing artificial perches on the primary dune on north Hog Island provided insight into seed deposition at the edge of the colonizing thicket. The nearest shrubs to this site were approximately 20 m away from the majority of the collectors and it was therefore assumed that what the collectors received was comparable to what birds perching on the nearest shrubs were depositing.

There were several limitations to this study, including attempting to capture a random and seasonally pulsed event such as seed dispersal over an expansive landscape

with a relatively few number of collectors. That limitation on its own makes it difficult to accurately predict whether the difference that existed between dispersal on Hog and Smith Islands was due to the differences in patch types or due to the limited number of collectors.

Concerning patch type, overall none of the graminoid sites collected more than six seeds, but there were woody sites that fared equally poorly. Also, there were sites that were only 29 % similar according to Jaccard's index of similarity for vegetation species composition, yet, the species composition for seeds collected were 100 % similar (Table 4). Conversely, there were sites that were 100 % similar for vegetation species composition, yet, the species composition for seeds collected were 25 % similar. This suggests that either patch type may be inconsequential, or is poorly defined. Patches in the context of barrier island communities become exceedingly complex when we take into account all of the factors that define a patch, not only the species composition and percent cover at a given site, but the elevation, latitude, distance to the ocean, and proximity to potential seed sources. Although this study indicates that spatial variation is an important factor in seed dispersal, it also points out that we need to have a better understanding of precisely what kind of spatial variation exists and how to better quantify such variation in order to make more accurate predictions about the future community composition of the Virginia barrier islands.

ACKNOWLEDGEMENTS

We would like to thank The Nature Conservancy, Virginia Coast Reserve and the Coastal Virginia Wildlife Observatory. Thanks also to Julie Naumann, Jaclyn Vick,

Steven Brantley, and Spencer Bissett for their laboratory help and guidance. Financial support was obtained from The Virginia Coast Reserve and a Virginia Commonwealth University Graduate Assistantship

Literature Cited

- BACHMANN, C.M., T.F. DONATO, G.M. LAMELA, W.J. RHEA, M.H.
BETTENHAUSEN, R.A. FUSINA, K.R. DU BOIS, J.H. PORTER, AND B.R.
TRUITT. 2002. Automatic classification of land-cover on Smith Island, VA using
HYMAP imagery. *IEEE Trans. Geosci. Remote Sensing* **40**:2313-2330.
- CALDER, W.A. AND J.R. KING. 1974. Thermal and caloric relations of birds. *In*:
Furner, D.S. and J.R. King (eds.). *Avian Biology*. Academic Press, London.
- COOK, T. AND H.H. SHUGART. 1990. Unpublished VCR/LTER dataset.
- CRAWFORD, E.R. AND D.R. YOUNG. 1998a. Spatial/temporal variations in shrub
thicket soil seed banks on an Atlantic Coast Barrier Island. *Am. J. Bot.*, **85**:1739-
1744.
- CRAWFORD, E.R. AND D.R. YOUNG. 1998b. Comparison of gaps and intact shrub
thickets on an Atlantic coast barrier island. *Am. Midl. Nat.*, **140**:68-77.

- DUESER, R.D., W.C. BROWN, G.S. HOGUE, C. MCCAFFERY, S.A. MCCUSKEY,
AND G.J. HENNESSEY. 1979. Mammals on the Virginia barrier islands. *J.
Mammalogy* **60**:425-429.
- EHRENFELD, J.G. 1990. Dynamics and processes of barrier island vegetation.
Aquatic Sciences **2**:437-480.
- FUENTES, M. 1994. Diets of fruit-eating birds: what are the causes of interspecific
differences? *Oecologia* **97**:134-142.
- GUREVITCH, J., S.M. SCHEINER, AND G.A. FOX. 2002. The ecology of plants.
Sinauer Associates, Inc., Massachusetts.
- HANULA, J.L. AND K. FRANZREB. 1998. Source, distribution and abundance of
macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded
woodpecker. *For. Ecol. Manag.*, **102**:89-102.
- HAYDEN, B.P., R.D. DUESER, J.T. CALLAHAN, AND H.H. SHUGART. 1991.
Long-term research at the Virginia Coast Reserve. *Bioscience* **41**:310-318.

- HAYDEN, B.P., M.C.F.V. SANTOS, G. SHAO, AND R.C. KOCHER. 1995.
Geomorphologic controls on coastal vegetation at the Virginia Coast Reserve.
Geomorphology **13**:282-300.
- HERRERA, C. 1982. Seasonal variation in the quality of fruits and diffuse coevolution
between plants and avian dispersers. *Ecology* **63**:773-785.
- HERRERA, C. 1984. A study of avian frugivores, bird-dispersed plants, and their
interactions in Mediterranean scrublands. *Ecol. Monogr.*, **54**: 1-23.
- JOY, D.A. 1996. *Juniperus virginiana*: nurse plant for woody seedlings on a Virginia
barrier island. MS thesis, Department of Biology, Virginia Commonwealth
University, Richmond.
- JOY, D.A. AND D.R. YOUNG. 2002. Promotion of mid-successional seedling
recruitment and establishment of *Juniperus virginiana* in a coastal environment.
Plant Ecology **160**:125-135.
- KWIT, C., D.J. LEVEY, C.H. GREENSBERG, S.F. PEARSON, J.P. MCCARTY, AND
S. SARGENT. 2004. Cold temperature increases winter fruit removal rate of a
bird-dispersed shrub. *Oecologia* **139**:30-34.

- MARTIN, A.C. AND W.D. BERKLEY. 1961. Seed Identification Manual. U. of California Press, California.
- MAYBE, S.E., J. MCCANN, L.J. NILES, C. BARTLETT AND P. KERLINGER. 1993. The Neotropical migratory songbird coastal corridor study: final report. A report of the Virginia Department of Environmental Quality to the National Oceanic and Atmospheric Administration's Office of Ocean and Coastal Resource Management, Richmond, VA.
- MAYBE, S.E. AND B.D. WATTS. 2000. Conservation of landbird migrants: addressing local policy. *Stu. Avi. Biol.*, **20**:99-108.
- MCCAFFREY, C.A, AND R.D. DUESER. 1990. Preliminary Vascular Flora for the Virginia Barrier Islands. *Vir. J. Sci.*, **41**:259-268.
- MORTON, E.S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *Am. Nat.*, **107**:8-22.
- MOSS, C. 1993. Interactions between passerines and woody plants at a migratory stop-over site: fruit consumption and potential for seed dispersal. Masters thesis, University of Virginia, Charlottesville.

- MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, Inc., New York.
- PLACE, A.R., AND E.W. STILES. 1992. Living off the wax of the land: bayberries and the yellow-rumped warblers. *Auk* **109**:334-354.
- RIDLEY, H.N. 1930. The dispersal of plants throughout the world. L. Reeve & Co. Ltd., Ashford, Kent, U.K.
- SMITH, A.J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* **56**:19-34.
- SNOW, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* **113**:194-202.
- STAPANIAN, M.A. 1986. Seed dispersal by birds and squirrels in the deciduous forests of the United States. *In*: Estrada, A. and T.H. Fleming (eds.). Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht.
- STILES, E.W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *Am. Nat.*, **116**:670-688.

- THOMPSON, J.N. AND M.F. WILLSON. 1978. Disturbance and the dispersal of fleshy fruits. *Science* **200**:1161-1163.
- THOMPSON J.N. AND M.F. WILLSON. 1979. Evolution of temperate fruit/bird interactions: phonological strategies. *Evolution* **33**:973-982.
- VAN DER PIJL, L. 1972. Principles of dispersal in higher plants. Springer-Verlag, New York.
- WILLSON, M. AND A. TRAVESET. 2001. The ecology of seed dispersal, p 85-110. *In*: M. Fenner (ed.). Seeds: The ecology of regeneration in plant communities. 2nd edition. CABI Publishing, Wallingford, UK.
- WONGSRIPHUEK, C., B.D. DUGGER, AND A.M. BARTUSZEVIGE. 2008. Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. *Wetlands* **28**:290-299.
- YOUNG D.R., J.H. PORTER, C.M. BACHMANN, G. SHAO, R.A. FUSINA, J.H. BOWLES, D. KORWAN, AND T.F. DONATO. 2007. Cross-scale patterns in shrub thicket dynamics in the Virginia barrier complex. *Ecosystems* **10**:854-863.

YOUNG, J.A AND C.G. YOUNG. 1992. Seeds of woody plants on North America.

Diocorides Press, Portland.

Table 1. Dominant physical and botanical attributes of Metompkin, Hog and Smith Islands (from McCaffrey and Dueser 1990).

Island	Features
Metompkin	Foredune-sparse grassland; dissected; overwash- and inlet-influenced
Hog	North: accreting beach, salt flats; tall shrub thickets, dune grassland, open dune-shrub thickets South: foredune grassland; erosion- and overwash- influenced
Smith	North: sparse grassland; overwash- and inlet- influenced South: dune ridges with shrub thickets and pine-hardwood forest, alternating with brackish marshes

Table 2. Species composition of vegetation along transects placed on each island and the seed species collected via fecal seed traps on each island. For each island, species are arranged in order of decreasing abundance.

Island	Local Species	Species Collected
Metompkin	<i>Baccharis halimifolia</i> <i>Iva frutescens</i> <i>Morella</i> spp. <i>Pinus taeda</i>	<i>Juniperus virginiana</i>
Hog	<i>Morella</i> spp. <i>Baccharis halimifolia</i> <i>Iva frutescens</i> <i>Parthenocissus quinquefolia</i> <i>Pinus taeda</i>	<i>Morella</i> spp. <i>Juniperus virginiana</i> <i>Callicarpa americana</i> <i>Iva frutescens</i> <i>Parthenocissus quinquefolia</i> <i>Sassafras albidum</i> <i>Rubus</i> sp.
Smith	<i>Morella</i> spp. <i>Baccharis halimifolia</i> <i>Iva frutescens</i> <i>Juniperus virginiana</i> <i>Ilex vomitoria</i> <i>Persea palustris</i> <i>Smilax</i> sp. <i>Prunus serotina</i>	<i>Morella</i> spp.

Table 3. Species composition of vegetation vs seed species collected at each transect. Species are arranged in order of decreasing abundance. MG= Metompkin graminoid, MW= Metompkin woody, HG= Hog graminoid, HM= Hog marsh, HS= Hog secondary dune, HP= Hog primary dune, SG= Smith graminoid, SW= Smith woody, and SW2= Smith second woody transect.

Site	Species Composition	Species Collected
MG	—	—
MW	<i>B. halimifolia</i> <i>I. frutescens</i> <i>Morella</i> spp. <i>P. taeda</i>	<i>J. virginiana</i>
HG	<i>B. halimifolia</i> <i>I. frutescens</i>	<i>I. frutescens</i>
HM	<i>Morella</i> spp. <i>B. halimifolia</i> <i>I. frutescens</i>	<i>Morella</i> spp.
HW	<i>Morella</i> spp. <i>P. quinquefolia</i> <i>P. taeda</i>	<i>P. quinquefolia</i> <i>Rubus</i> sp.
HS	<i>Morella</i> spp. <i>B. halimifolia</i>	<i>Morella</i> spp.
HP	<i>Morella</i> spp. <i>B. halimifolia</i>	<i>Morella</i> spp. <i>J. virginiana</i> <i>C. americana</i> <i>S. albidum</i>
SG	<i>B. halimifolia</i> <i>I. frutescens</i> <i>Morella</i> spp. <i>J. virginiana</i>	<i>Morella</i> spp.
SW	<i>Morella</i> spp. <i>B. halimifolia</i>	<i>Morella</i> spp.
SW2	<i>Morella</i> spp. <i>B. halimifolia</i> <i>I. vomitoria</i> <i>P. palustris</i> <i>I. frutescens</i> <i>Smilax</i> sp. <i>P. serotina</i>	<i>Morella</i> spp.

FIGURE LEGENDS

Figure 1. Eastern Shore of Virginia including islands of study: Metompkin, Hog and Smith.

Figure 2. Eastern Shore of Virginia denoting fecal collector transects. MG= Metompkin graminoid, MW= Metompkin woody, HG =Hog graminoid, HM = Hog marsh, HW = Hog woody, HS = Hog secondary dune, HP = Hog primary dune, SG = Smith graminoid, SW = Smith woody, and SW2= Smith second woody transect.

Figure 3. Seeds per collector and abundance of seeds collected from artificial perches across all transects on Metompkin, Hog and Smith Islands from July 2007-June 2008. J= *Juniperus virginiana*, M = *Morella* spp. including *M. cerifera* and *M. pensylvanica*, C= *Callicarpa americana*, I = *Iva frutescens*, P = *Parthenocissus quinquefolia*, S= *Sassafras albidum*, and R= *Rubus* sp.

Figure 4. Seasonal abundance of seeds collected from artificial perches across all transects on Metompkin, Hog and Smith Islands. Summer= July-September 2007, Fall= October-December 2007, Winter= January – March 2008, and Spring= April –June 2008.

Figure 5. The number of seeds per collector at each transect on north Hog Island. The number below each transect represents the amount of species collected. HM= Hog marsh, HW= Hog woody, HS= Hog primary dune and HS= Hog secondary dune.

Figure 6. Number of birds banded and the number of birds banded per net hour at the Kiptopeke Banding Station in Cape Charles, Virginia from 2000-2007. Closed circles represent the number of birds banded and open circles represent the number of birds banded per net hour.

Figure 7. Precipitation for Oyster, Virginia from July 2007-May 2008 compared to the 30-year average for Painter, Virginia.

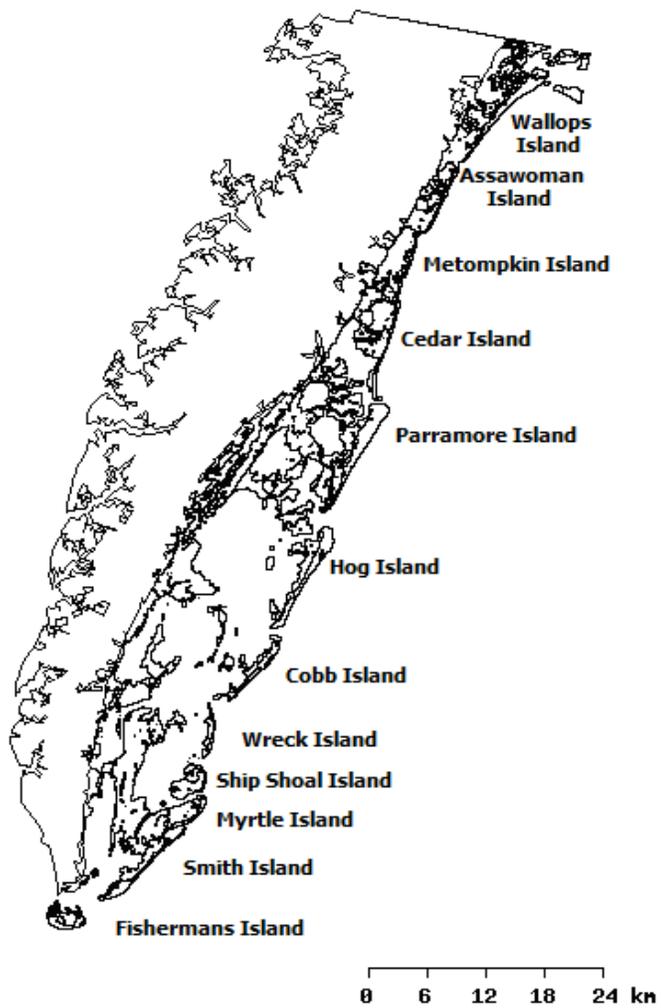


Figure 1

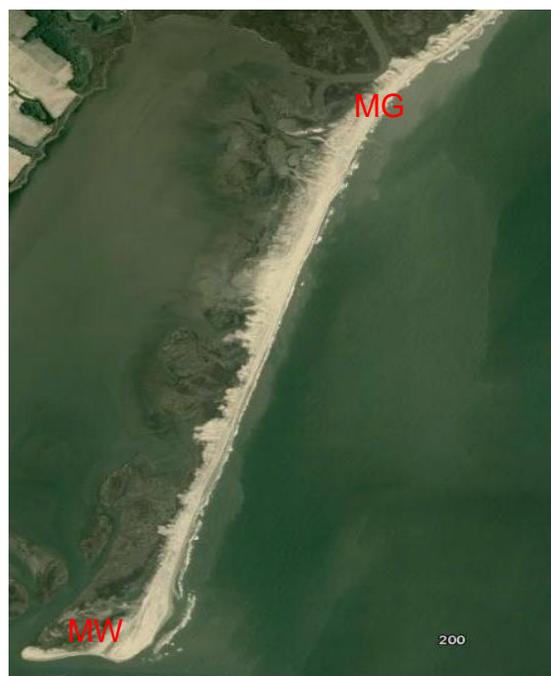
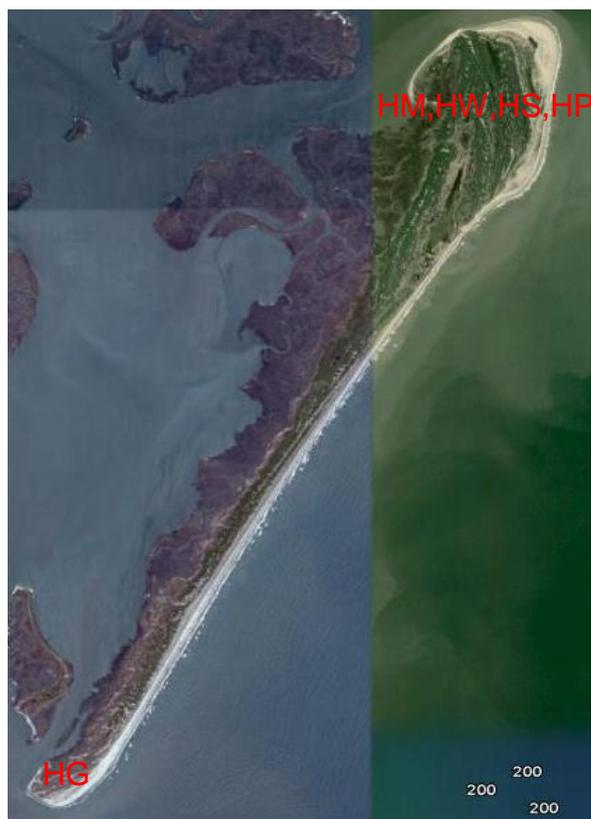


Figure 2

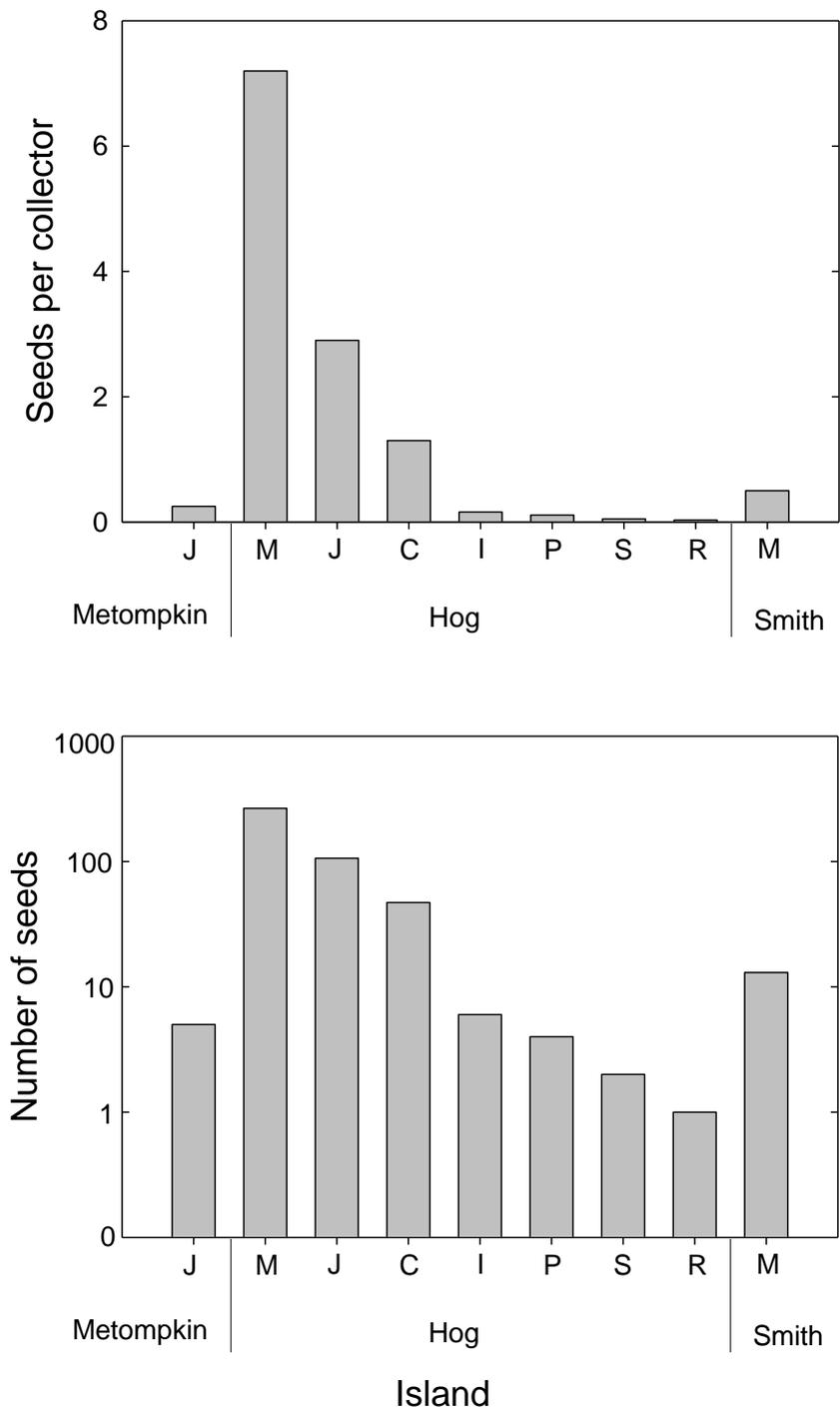


Figure 3

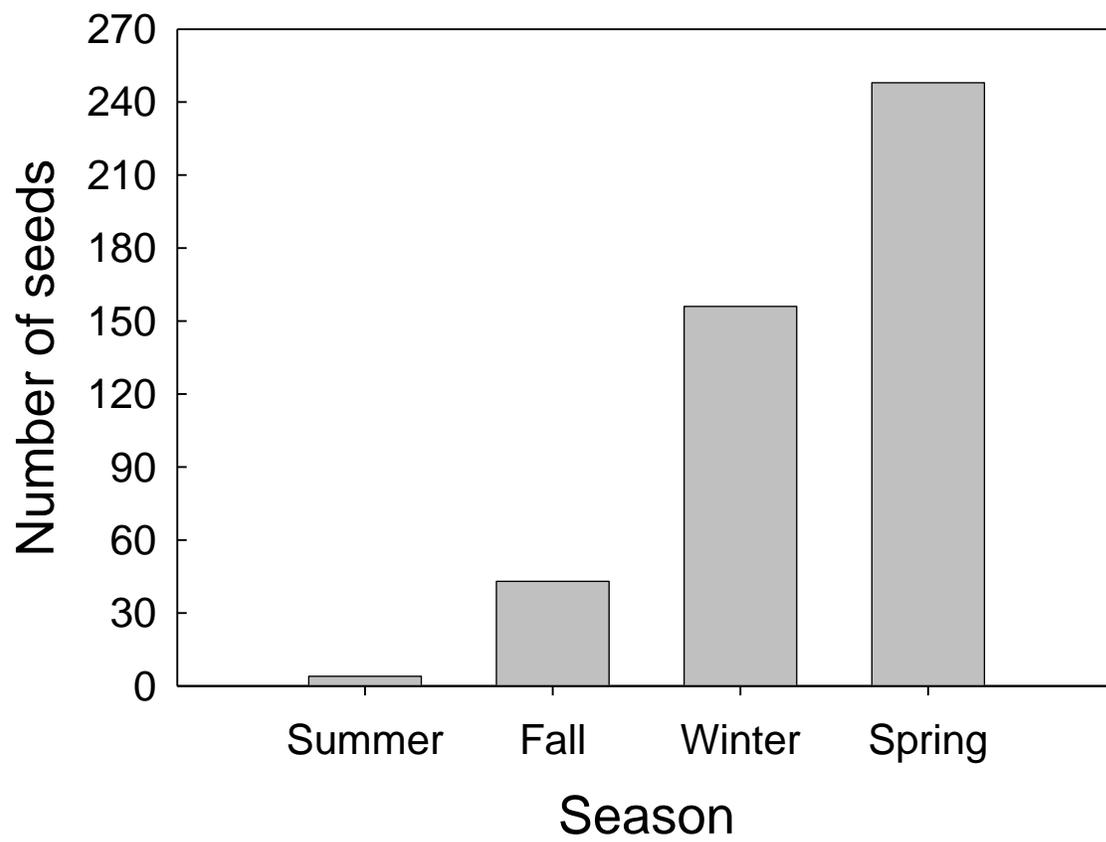


Figure 4

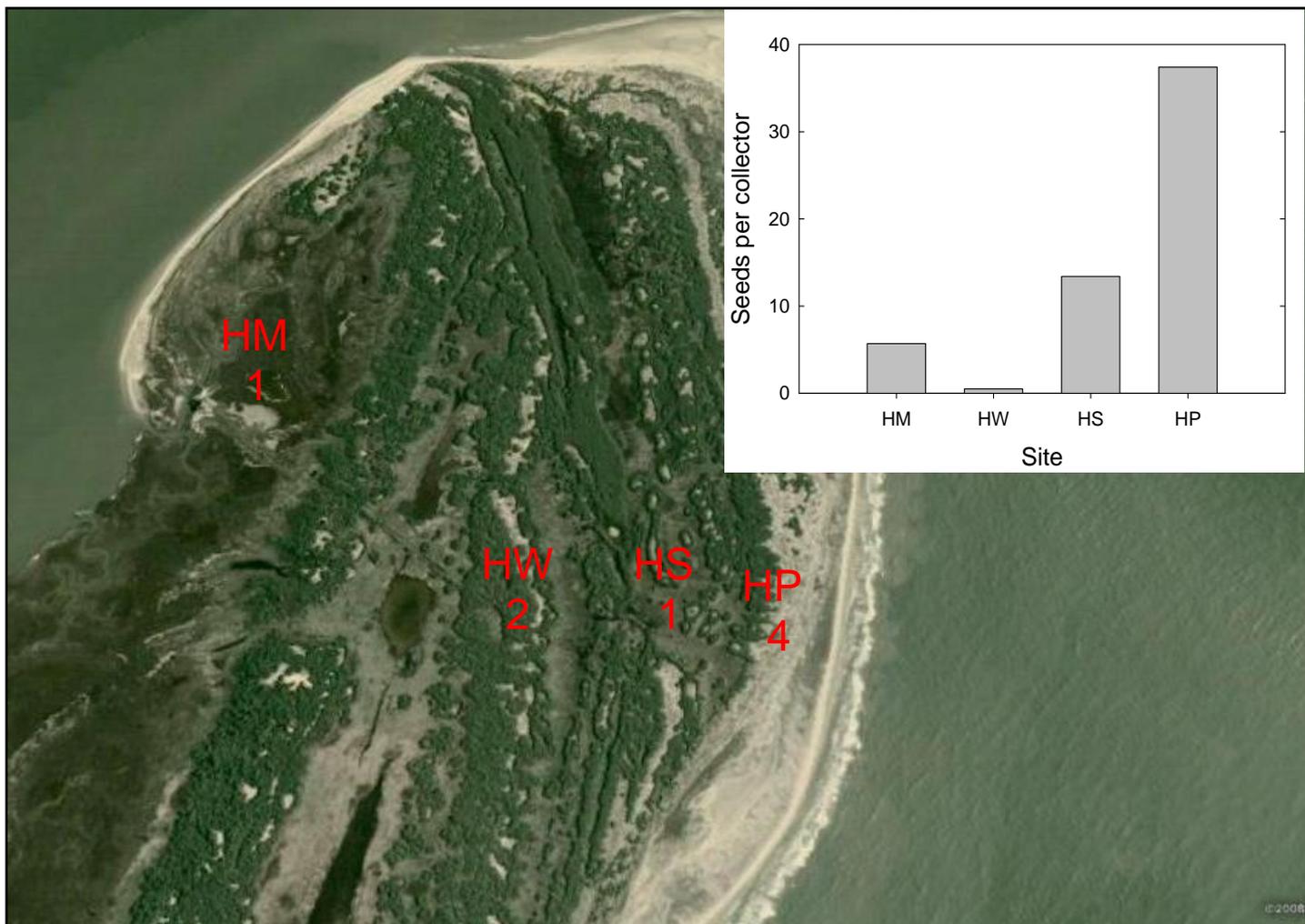


Figure 5

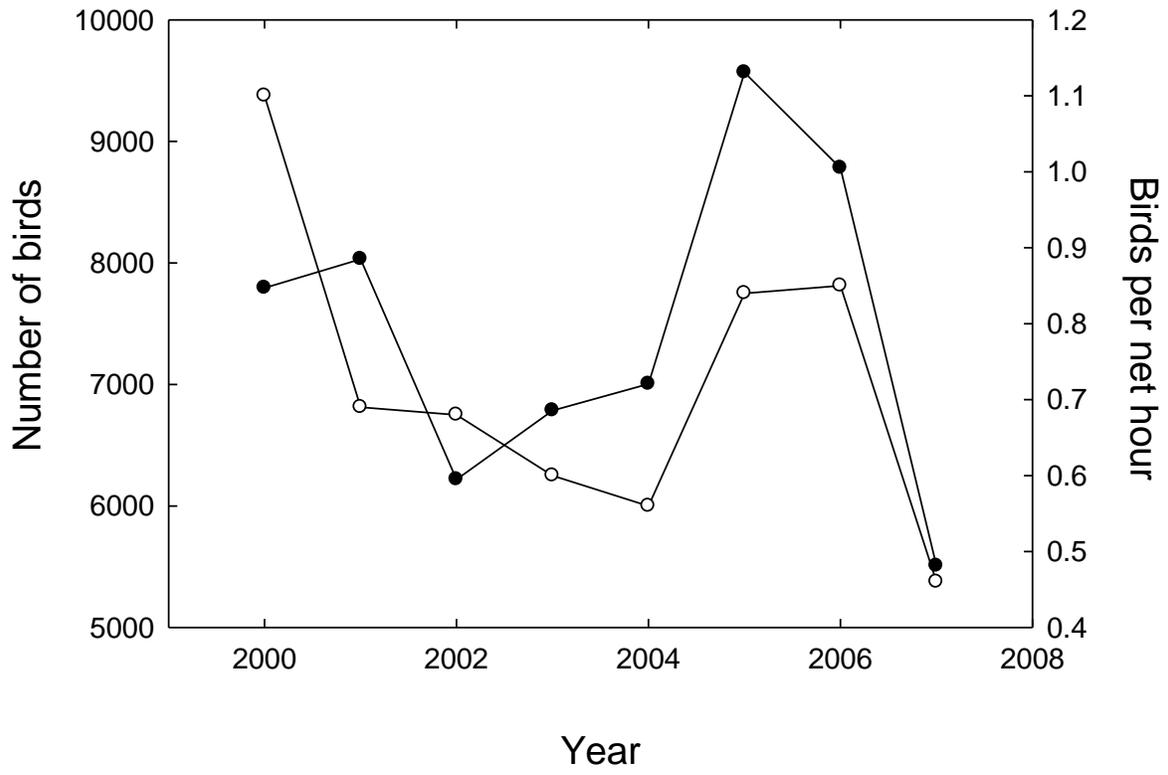


Figure 6

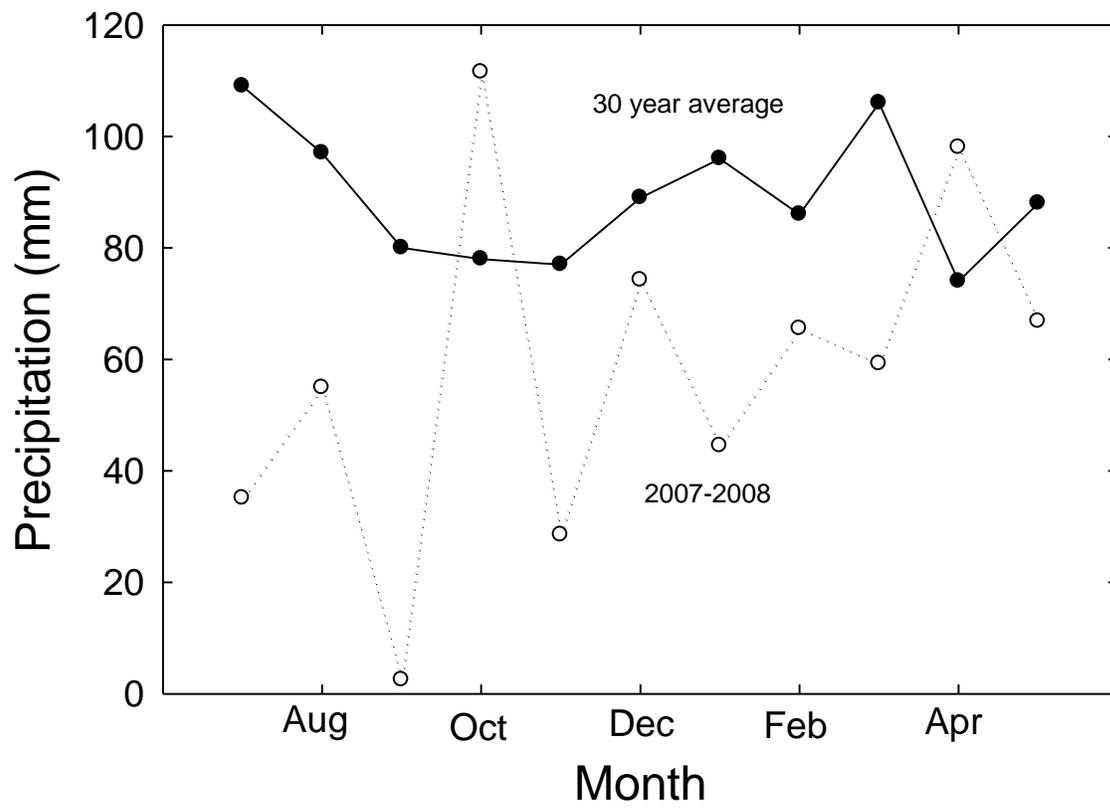


Figure 7

Literature Cited

- Bachmann, C.M., T.F. Donato, G.M. Lamela, W.J. Rhea, M.H. Bettenhausen, R.A. Fusina, K.R. Du Bois, J.H. Porter, and B.R. Truitt. 2002. Automatic classification of land-cover on Smith Island, VA using HYMAP imagery. *IEEE Trans. Geoscience Remote Sensing* 40:2313-2330.
- Calder, W.A. and J.R. King. 1974. Thermal and caloric relations of birds. In: *Avian Biology*. Furner, D.S. and J.R. King (eds.). Academic Press, London.
- Cook, T. and H.H. Shugart. 1990. Unpublished VCR/LTER dataset.
- Crawford, E.R. and D.R. Young. 1998a. Spatial/temporal variations in shrub thicket soil seed banks on an Atlantic Coast Barrier Island. *American Journal of Botany* 85:1739-1744.
- Crawford, E.R. and D.R. Young. 1998b. Comparison of gaps and intact shrub thickets on an Atlantic coast barrier island. *American Midland Naturalist* 140:68-77.
- Crist, T.O., D.S. Guertin, J.A. Wiens, and B.T. Milne. 1992. Animal movements in heterogeneous landscapes: and experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6:536-544.

- Dueser, R.D., W.C. Brown, G.S. Hogue, C. McCafferey, S.A. McCuskey, and G.J. Hennessey. 1979. Mammals on the Virginia barrier islands. *Journal of Mammalogy* 60:425-429.
- Ehrenfeld, J.G. 1990. Dynamics and processes of barrier island vegetation. *Aquatic Sciences* 2:437-480.
- Farmer, A.H. and A.H. Parent. 1997. Effects of the landscape on shorebird movements at spring migration stopovers. *Condor* 99:698-707.
- Fuentes, M. 1994. Diets of fruit-eating birds: what are the causes of interspecific differences? *Oecologia* 97:134-142.
- Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. *Annals of Botany, New Series*, 16:293-316.
- Gurevitch, J., S.M. Scheiner, and G.A. Fox. 2002. *The ecology of plants*. Sinauer Associates, Inc., Massachusetts.
- Hanula, J.L. and K. Franzreb. 1998. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. *Forest Ecology and Management* 102:89-102.

- Hayden, B.P., R.D. Dueser, J.T. Callahan, and H.H. Shugart. 1991. Long-term research at the Virginia Coast Reserve. *Bioscience* 41:310-318.
- Hayden, B.P., M.C.F.V. Santos, G. Shao, and R.C. Kochel. 1995. Geomorphologic controls on coastal vegetation at the Virginia Coast Reserve. *Geomorphology* 13: 282-300.
- Herrera, C. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63:773-785.
- Herrera, C. 1984. A study of avian frugivores, bird-dispersed plants, and their interactions in Mediterranean scrublands. *Ecological monographs* 54:1-23.
- Joy, D.A. 1996. *Juniperus virginiana*: nurse plant for woody seedlings on a Virginia barrier island. MS thesis, Department of Biology, Virginia Commonwealth University, Richmond.
- Joy, D.A. and D.R. Young. 2002. Promotion of mid-successional seedling recruitment and establishment of *Juniperus virginiana* in a coastal environment. *Plant Ecology* 160:125-135.
- Kwit, C., D.J. Levey, C.H. Greenberg, S.F. Pearson, J.P. McCarty, and S. Sargent. 2004. Cold temperature increases winter fruit removal rate of a bird-dispersed shrub. *Oecologia* 139:30-34.

- Martin, A.C. and W.D. Berkley. 1961. Seed Identification Manual. U. of California Press, California.
- Maybe, S.E., J. McCann, L.J. Niles, C. Bartlett and P. Kerlinger. 1993. The Neotropical migratory songbird coastal corridor study: final report. A report of the Virginia Department of Environmental Quality to the National Oceanic and Atmospheric Administration's Office of Ocean and Coastal Resource Management, Richmond, VA.
- Maybe, S.E. and B.D. Watts. 2000. Conservation of landbird migrants: addressing local policy. *Studies in Avian Biology* 20:99-108.
- McCaffrey, C.A, and R.D. Dueser. 1990. Preliminary Vascular Flora for the Virginia Barrier Islands. *Virginia Journal of Science* 41:259-268.
- Morton, E.S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *American Naturalist* 107:8-22.
- Moss, C. 1993. Interactions between passerines and woody plants at a migratory stop-over site: fruit consumption and potential for seed dispersal. Masters thesis, University of Virginia, Charlottesville.

- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, Inc., New York.
- Place, A.R., and E.W. Stiles. 1992. Living off the wax of the land: bayberries and the yellow-rumped warblers. *Auk* 109:334-354.
- Ridley, H.N. 1930. The dispersal of plants throughout the world. L. Reeve & Co. Ltd., Ashford, Kent, U.K.
- Smith, A.J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* 56:19-34.
- Snow, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.
- Stapanian, M.A. 1986. Seed dispersal by birds and squirrels in the deciduous forests of the United States. In: *Frugivores and seed dispersal*. Estrada, A. and Fleming, T.H. (eds.). Dr. W. Junk Publishers, Dordrecht.
- Stiles, E.W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* 116:670-688.
- Thompson, J.N. and M.F. Willson. 1978. Disturbance and the dispersal of fleshy fruits. *Science* 200:1161-1163.

- Thompson, J.N. and M.F. Willson. 1979. Evolution of temperate fruit/bird interactions: phonological strategies. *Evolution* 33:973-982.
- Van der Pijl, L. 1972. Principles of dispersal in higher plants. Springer-Verlag. New York.
- Wenny, D.G. 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecological Research* 3:51-74.
- Wenny, D.G., and D.J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences, USA* 95:6204-6207.
- Westcott, D.A. and D.L. Graham. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122:249-257.
- Willson, M. and A. Traveset. 2001. The ecology of seed dispersal, pages 85-110. In: M. Fenner (ed.). *Seeds: The ecology of regeneration in plant communities*. 2nd edition. CABI Publishing, Wallingford, UK.
- Wongsriphuek, C., B.D. Dugger, and A.M. Bartuszevige. 2008. Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. *Wetlands* 28:290-299.

- Young D.R., J.H. Porter, C.M. Bachmann, G. Shao, R.A. Fusina, J.H. Bowles, D. Korwan, and T.F. Donato. 2007. Cross-scale patterns in shrub thicket dynamics in the Virginia barrier complex. *Ecosystems* 10:854-863.
- Young, J.A and C.G. Young. 1992. *Seeds of woody plants on North America*. Diacorides Press, Portland.

Appendix A. Woody species present on Metompkin, Hog and Smith islands and the mode(s) of dispersal of each: bird (B), mammal (M), wind (W).

Island	Species	Mode of dispersal
Metompkin		
	<i>Atriplex arenaria</i>	W
	<i>Baccharis halimifolia</i>	W
	<i>Borrichia frutescens</i>	W
	<i>Calystegia sepium</i>	W
	<i>Juniperus virginiana</i>	B
	<i>Iva frutescens</i>	W/B
	<i>Morella cerifera</i>	B
	<i>Morella pensylvanica</i>	B
	<i>Parthenocissus quinquefolia</i>	B
	<i>Pinus taeda</i>	W
Hog		
	<i>Baccharis halimifolia</i>	W
	<i>Borrichia frutescens</i>	W
	<i>Diodia virginiana</i>	W
	<i>Euonymus japonica</i>	B
	<i>Ficus carica</i>	M/B
	<i>Hudsonia tomentosa</i>	W
	<i>Iva frutescens</i>	W/B
	<i>Juniperus virginiana</i>	B
	<i>Mikania scandens</i>	W
	<i>Morella cerifera</i>	B
	<i>Morella pensylvanica</i>	B
	<i>Opuntia compressa</i>	M/B
	<i>Parthenocissus quinquefolia</i>	B
	<i>Pinus taeda</i>	W
	<i>Pluchea purpurascens</i>	W
	<i>Prunus maritime</i>	M/B
	<i>Prunus serotina</i>	B
	<i>Rhus copallina</i>	B
	<i>Rhus radicans</i>	B
	<i>Rubus argatus</i>	B
	<i>Rubus</i> spp.	B
	<i>Salix nigra</i>	W
	<i>Sassafras albidum</i>	B

Appendix A. Continued.

<i>Smilax bona-nox</i>	B
<i>Solanum carolinense</i>	B
<i>Vitis aestivalis</i>	B
<i>Zanthoxylum clava-herculis</i>	B
Smith	
<i>Acer rubrum</i>	W
<i>Amelanchier obovalis</i>	B
<i>Aralia spinosa</i>	B
<i>Atriplex arenaria</i>	W
<i>Baccharis halimifolia</i>	W
<i>Borrichia frutescens</i>	W
<i>Berchemia scandens</i>	B
<i>Callicarpa americana</i>	B
<i>Calystegia sepium</i>	W
<i>Campsis radicans</i>	W
<i>Centrosema virginianum</i>	B/W
<i>Cheonopodium ambrosioides</i>	B
<i>Crataegus viridis</i>	B/M
<i>Diospyros virginiana</i>	M/B
<i>Helianthemum canadense</i>	W
<i>Hibiscus moscheutos</i>	W
<i>Ilex opaca</i>	B
<i>Ilex vomitoria</i>	B
<i>Iva frutescens</i>	W/B
<i>Juniperus virginiana</i>	B
<i>Liquidambar styraciflua</i>	W
<i>Lonicera sempervirens</i>	B
<i>Mitchella repens</i>	B
<i>Monarda punctata</i>	W/B
<i>Morella cerifera</i>	B
<i>Morella pensylvanica</i>	B
<i>Nyssa sylvatica</i>	B
<i>Opuntia compressa</i>	M/B
<i>Parthenocissus quiquefolia</i>	B
<i>Paulownia tomentosa</i>	W
<i>Persea palustris</i>	B

Appendix A. Continued.

<i>Pinus taeda</i>	W
<i>Prunus serotina</i>	B
<i>Quercus falcata</i>	M/B
<i>Quercus laurifolia</i>	M/B
<i>Quercus nigra</i>	M/B
<i>Quercus stellata</i>	M/B
<i>Quercus virginiana</i>	M/B
<i>Rhus copallina</i>	B
<i>Rhus radicans</i>	B
<i>Robinia pseudoacacia</i>	W/B
<i>Salix nigra</i>	W
<i>Sassafras albidum</i>	B
<i>Smilax bona-nox</i>	B
<i>Smilax glauca</i>	B
<i>Smilax rotundifolia</i>	B
<i>Solanum carolinense</i>	B
<i>Sorbus arbutifolia</i>	B
<i>Trachelospermum difforme</i>	W
<i>Ulmus americana</i>	W
<i>Vaccinium fuscatum</i>	B
<i>Vaccinium corymbosum</i>	B
<i>Vitis aestivalis</i>	B
<i>Vitis rotundifolia</i>	B
<i>Yucca filamentosa</i>	B
<i>Zanthoxylum clava-herculis</i>	B

VITA

Sheri A. Shiflett was born May 22, 1984 in Richmond, Virginia. She graduated from Meadowbrook High School in Richmond, Virginia in 2002 with an International Baccalaureate Diploma. She also received her Bachelor of Science in Biology and her Bachelor of the Arts in French from Virginia Commonwealth University in 2006. Sheri is fascinated by a variety of disciplines and will likely pursue several options before deciding on a permanent career.