ABSTRACT

Title of Dissertation:	WAX MYRTLE AND MYRTLE WARBLERS: RECIPROCAL SPECIALIZATION AND ITS CONSEQUENCES IN A TEMPERATE FRUIT-FRUGIVORE INTERACTION
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Interactions between fruiting plant and frugivorous species are considered to be highly generalized, resulting in diffuse mutualisms. Specialization has frequently been found to be either asymmetrical or the result of restricted options for frugivores. This dissertation documents a highly unusual case of reciprocal specialization between the myrtle group of yellow-rumped warblers (*Dendroica coronata coronata*) and wax myrtle (*Myrica cerifera*). Far from being one of a group of ecologically redundant dispersers, these warblers are the most valuable quantitative and qualitative contributors to this plant's recruitment on Assateague Island National Seashore, U.S.A.

Fecal samples collected over four years from migrant and wintering passerines and feeding trials in two years demonstrated that wax myrtle fruit was both the most preferred fruit and a consistently major food item for myrtle warblers throughout a 7-month residence. Abundance of wax myrtle fruit significantly affected this warbler's abundance in all years.   Similarly, compared to all other frugivorous species, myrtle warbler were the most frequent and consistent consumer of wax myrtle fruit in all years. Wax myrtle seed dispersal was significantly affected by yellow-rumped warbler abundance.

In order to evaluate disperser contributions to wax myrtle, I examined factors influencing seedling recruitment. Data derived from three sources 1) seed trap data from three replicated habitats, 2) experimental evaluation of the effect of time and place of seed deposition, and 3) seedling surveys confirmed that deposition was wide-spread, lasting until late April.   Recruitment was greatest in both scrub and meadow habitats, but seeds deposited in meadows, especially in spring, established at higher rates than in scrub because of post-dispersal predation rates associated with microhabitat seed deposition patterns of predation among habitats.

Fecal samples and observations indicated that wax myrtle has three primary dispersers: myrtle warblers, gray catbirds and tree swallows. Myrtle warblers, the only documented disperser after December, provided the greatest quantitative dispersal services. Although the germination rate and time of ingested seeds were unaffected by species identity of dispersers, post-foraging observations demonstrated that myrtle warblers were most likely to be the agent of wax myrtle seed emigration from established thickets to sites suitable for colonization.

WAX MYRTLE AND MYRTLE WARBLERS: RECIPROCAL
SPECIALIZATION AND ITS CONSEQUENCES IN A TEMPERATE FRUIT-
FRUGIVORE INTERACTION

By

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To Stephanie, my darling wife

vulnerasti cor meum soror mea sponsa

vulnerasti cor meum in uno oculorum tuorum et in uno crine colli tui

θαλαττα, θαλαττα

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Abstract

Current dogma is that specialization, especially reciprocal specialization, is rare among fruiting plants and frugivores. Supported by a sizeable body of literature, this view suggests that generalized or diffuse interactions are more beneficial to both fruiting plants and frugivores than specialized interactions. Exceptions to this trend are explained by unusual fruit morphology or pulp nutrient composition. Here, I document that the myrtle group of yellow-rumped warblers (*Dendroica coronata coronata*) and wax myrtle (*Myrica cerifera*), whose fruit is largely composed of wax, are reciprocally specialized on Assateague National Seashore, MD. During four seasons of field work, wax myrtle was found in over 98% of myrtle warbler feces throughout this migrant's seven-month residence. Feeding trials with four common fruit species indicated that the high frequency of use of wax myrtle fruit in the field was due to preference. Similarly, fecal samples from seven different bird species indicated that myrtle warblers were the most common frugivore to use wax myrtle fruit, although gray catbirds (*Dumatella caroliniensis*) were frequent consumers of wax myrtle fruit in autumn. These data, however, were not simply an epiphenomenon of relative species abundance. Comparison of the relative frequency of different fruit species in the fecal samples of myrtle warblers and gray catbirds indicated that catbirds had a significantly more diverse fruit diet. Feeding trials with

four fruit species confirmed that, in contrast to myrtle warblers, gray catbirds had no

preference for wax myrtle fruit and that their use of wax myrtle fruit was based on

relative abundance. Tree swallows (*Tachycineta bicolor*) commonly consumed wax

myrtle fruit, but their sporadic presence suggested an opportunistic relationship.

Survey data collected over three years indicated that in each year, wax myrtle fruit

abundance significantly influenced myrtle warbler abundance. Seed trap and warbler

abundance data collected in one season confirmed that the numbers of wax myrtle

seeds dispersed were significantly related to myrtle warbler abundance. These data,

together with previously published results, suggest that this relationship is among the

most specialized of fruit-frugivore interactions investigated to date.

Introduction

.Ecologists have focused on the importance of specialization in fruiting plant –

frugivore interactions since the publication of Snow's (1971) landmark paper. In

spite of initial predictions, an abundance of evidence has indicated that very few

interactions are specialized below the family level (e.g. Wheelwright and Orians

1982, Gautier-Hion *et al.* 1985, Fuentes 1995). When it does occur, specialization

appears to be largely asymmetrical (Jordano 1987, Herrera 1998) or the result of

restricted options (Hallwachs 1986, Hampe 2003). Most avian frugivores forage on

a wide variety of fruits in both the tropical (e.g. Wheelwright 1983, Wheelwright *et

al.* 1984, Loiselle and Blake 1990, Sun *et al.* 1997) and temperate zones (Skeate

1985, White and Stiles 1990, Whelan and Willson 1994, Parrish 1997) – a trend seen

also among primate frugivores (Lambert and Garber 1998). Similarly, most bird-

dispersed fruiting plants attract avian and primate frugivores that are taxonomically distant (e.g. McDiarmid *et al.* 1977, Carr 1992, Poulin *et al.* 1994, Kaplan and Moermond 1998, Lambert and Garber 1998). The current consensus, unchanged in nearly twenty years, is that fruiting plants and frugivores participate in diffuse, rather than specialized mutualisms (Janzen 1980, Howe 1984, Fleming 1991, Whelan and Willson 1994).

An array of ecological factors constrains the possibility of specialization in these interactions during periods of fruit presentation. First, ranges of individual mutualists rarely overlap completely (Wheelwright and Orians 1982, Jordano 1993). Even within areas of overlap, there may be significant habitat differences between mutualists (Willson 1986, Jordano 1993, 1995). Second, considerable spatio-temporal variability in fruiting phenology (Skeate 1985, Willson and Whelan 1993) and its seasonal nature (Stapanian 1982, Janzen 1985, Jordano 1987, see also Waser et al. 1996), as well as variability in the arrival time, abundance, and diet of frugivores can further deter specialized interactions (Martin *et al.* 1951, Thompson and Willson 1979, Carr 1992, Willson and Whelan 1993).

Additionally, generalized interactions are hypothesized to provide greater benefits to participants than specialized ones. A diverse fruit diet may be more balanced (White and Stiles 1990, Whelan *et al.* 1998) because the pulp of individual fruit species may not be nutritionally complete (Jordano 1987, Studier et al. 1988). A more catholic fruit diet also allows frugivores to respond to seasonal changes in nutritional needs (Wheelwright 1988, Bairlein 1990), energetic condition (Sorensen 1984), and digestive efficiency (Lepczyk *et al.* 2000). Furthermore, like vertebrate

herbivores (Freeland and Janzen 1974, Sorensen and Dearing 2003), those frugivores that adopt a generalist diet may avoid accumulating high levels of particular toxins (Herrera 1982, Izhaki and Safriel 1990, Cipollini and Levey 1997) and the consequent stress associated with their detoxification (Gugliemo *et al.* 1996, but see Streumpf *et al.* 1999).

Fruiting plants, too, may benefit from generalized interactions. Fruit abundance may exceed the ability of frugivores to remove them (Burger 1987, Snow and Snow 1988, Herrera 1995), resulting in competition among plants for avian and mammalian dispersers (Snow 1966, Herrera 1981, Denslow and Moermond 1982, Moermond and Denslow 1983, Thies and Kalko 2004). In such situations, fruiting plants attracting a larger number of species, and consequently a larger number of potential frugivores, may increase the likelihood of fruit removal and, consequently, seed removal. A larger disperser assemblage is also likely to remove seeds more rapidly (Snow 1971), decreasing the exposure time of crops to predispersal seed predators or abiotic elements that can substantially reduce fruit crop size (Courtney and Manzur 1985, Jordano 1987, Howe 1993, Willson and Whelan 1993, but see Herrera et al. 1994). Finally, a diverse group of dispersers may deposit seeds in a wider variety of habitats and microsites, thereby benefiting plants whose seeds do not have predictable or identifiable germination sites (Howe and Estabrook 1977, Wheelwright and Orians 1982, Courtney and Manzur 1985).

The only specialized fruit-frugivore relationships documented thus far in North America are between the phainopepla (*Phainopepla nitens*) and mistletoe (*Phoradendron californicum*) (Walsburg 1975, Larson 1996, Chu and Walsberg

1999) and possibly between Townsend's solitaire (*Myadestes townsendi*) and *Juniperus* species (Lederer 1977, Salomonson 1978, Poddar and Lederer 1982). Few other examples of specialization have been identified elsewhere (e.g. Greenberg et al. 1995, Hampe 2003). Although further investigations about the strength of these interactions at larger scales may be warranted (Burns 2004).

Identifying other specialized systems, especially those with reciprocal specialization, is relevant to ecology and conservation biology, alike. Specialized interactions provide an unusual opportunity to test both the validity of hypotheses about the ecological disadvantages associated with specialization (see Wheelwright and Orians 1982, Janzen 1983, Howe 1984, Herrera 1985), as well as its causes – questions recently considered in other types of mutualisms (e.g. Waser *et al.* 1996, Caillaud and Via 2000, Johnson and Steiner 2000, Bolnick *et al.* 2003, Vasquez and Aizen 2003). For conservation biologists, the identification of such restricted interactions would facilitate the preservation of the long term population viability of the species involved; specialization has been associated with extinction vulnerability (Bond 1994, Korkeamaki and Suhonen 2002, Davies *et al.* 2004). More particularly, such information could aid in identifying critical stopover and wintering habitat for migrant passerines, since abundance of preferred fruit can be a significant factor in determining habitat suitability for frugivores (Rey 1995, Parrish 1997, Carlo *et al.* 2003, Borgman *et al.* 2004, Kwit *et al.* 2004).

Observations by natural historians have long suggested that the interaction between the myrtle group of yellow-rumped warblers (*Dendroica coronata coronata*, Parulidae) and the dioecious shrub wax myrtle (*Myrica cerifera*, Myricaceae) may be

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reciprocally specialized (Chapman 1907, Whittle 1922, Bent 1963). There is no evidence of a similar relationship between the Audubon group (*D. coronata auduboni*) and western *Myrica* species. More recent studies confirm that at sites where myrtle warblers and wax myrtle are coincident, wax myrtle fruit is a major component of myrtle warbler diet (Skeate 1985, Davidar and Morton 1986) and an influence on the local abundance of myrtle warblers, but not of other more casual consumers (Borgman *et al.* 2004). On a geographic scale, myrtle warblers winter largely along the Atlantic coast from Massachusetts to the Gulf of Mexico (Hunt and Flaspohler 1998), but their greatest concentration lies within the range of wax myrtle (Root 1988). Similar results have been reported north of wax myrtle's range regarding the interaction of myrtle warblers and bayberry (*M. pensylvanica*) (Hausman 1927, Wiltz and Giampa 1978, Parrish 1997). Only recently, however, has this interaction attracted attention among ecologists (e.g. Borgman *et al.* 2004, Kwit *et al.* 2004), although the unusual chemical composition of the fruit (wax and not carbohydrates) that renders the fruit indigestible to most bird species, has been noted previously (Place and Stiles 1992). The objective of this paper is to examine the degree of specialization between migrating and wintering myrtle warblers and wax myrtle on Assateague Island National Seashore.

Specialization in plant-animal interactions has been defined in a variety of ways (Wheelwright and Orians 1982, Recher 1990, Sherry 1990). Some authors advocate identifying specialization by comparing relative resource use with abundance (e.g. Chesson 1983, Morse 1989). But this approach is ineffective if

relative resource abundance is so highly skewed that trends are not detectable (Johnson 1980).

Here I consider that reciprocal specialization has two parts. Firstly, specialization is indicated by the nearly exclusive interaction of one species with another (see Herrera 1984, Malmborg and Willson 1988). A necessary corollary is to determine whether an observed high frequency of association is due to choice rather than context (see Cushman and Beattie 1991, Bronstein 1994, Fuentes 1995, Herrera 1998). Feeding trials with different fruit species can establish a frugivore's fruit preference (e.g. Borowicz 1988).

Determining a plant's preference for particular frugivores is more problematic since in this context at least, fruiting plants are passive partners. Unlike pollination interactions where plant preference may be inferred from a match between floral and pollinator morphology (e.g. Nilsson 1988, but see Hurlbert *et al.* 1996, Waser *et al.* 1996, Johnson and Steiner 2000), most fruiting plants have few mechanisms for excluding different frugivores (Wheelwright and Orians 1982, Herrera 1985), aside from fruit size (see McKey 1975, Pratt and Stiles 1985, Wheelwright 1985, Snow and Snow 1988), which does not appear to be a common determinant of disperser identity in the temperate zone (Johnson *et al.* 1985). Fruit morphology (e.g. Greenberg et al. 1995) and pulp composition may also restrict a plant's potential visitors (Greenberg 1981, Tewksbury and Nabhan 2001). However, even if phenotypic traits of a fruit species do restrict the number of species that consume it (Fuentes 1995, Greenberg et al. 1995), assuming that present traits reflect current selective pressures exerted by current avian or mammalian frugivores is unwarranted without further evidence

(Janzen and Martin 1982, Herrera 1985, Hallwachs 1986). A convincing test for preference, therefore, is applicable only to an animal partner.

The second element of specialization is the dependence of one species on another for a reward, food for birds and seed removal for plants in fruit-frugivore interactions (Herrera 1984, Wheelwright *et al.* 1984, Larson 1996). Seed removal is, of course, only the first in a sequence of necessary steps for plant recruitment (Herrera 1985, Schupp 1993, 1994). However, its importance should not be ignored since the possibility of reaching subsequent steps [e.g.*,* escape from predators (Kollman and Pirl 1995, Howe and Miriti 2000), germination (Barton 1932, Traveset and Verdu 2002) and seedling survival (Augspurger 1984, Augspurger and Kitajima 1992)] largely depends on its successful completion.

To address the question of whether myrtle warblers and wax myrtle are reciprocally specialized, three types of data were collected. To test whether each was the other's primary partner, I documented fruit abundance, frugivore fruit use and the identity of each fruiting plant's frugivores throughout the fruiting season. Second, two main passerine frugivores, myrtle warblers and gray catbirds (*Dumatella carolinensis*, Mimidae), participated in feeding trials to determine the relative influence of preference and context on fruit use. Data on relative preferences of tree swallows, the third main consumer of wax myrtle fruit, were not included because these birds were never captured in mist nets. Third, I tested whether myrtle warblers and wax myrtle were dependent on each other by measuring the effect of declining wax myrtle fruit levels on myrtle warbler abundance over the course of three seasons

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and by comparing wax myrtle seed appearance in seed traps with myrtle warbler abundance during one season.

Individually, tests of these hypotheses offer only partial insight into the question of specialization. However, the combination provides an opportunity to measure reciprocal use, preference, and dependence. I hypothesized that if a reciprocally specialized interaction existed each would be the other's primary partner, and that myrtle warblers would show a preference for wax myrtle over fruits of other plant species. Additionally, myrtle warblers and wax myrtle would be dependent on each other for food and seed removal, respectively.

Methods

Study Area

Assateague Island is a dynamic barrier island located off the coast of Maryland and Virginia, approximately 45 kilometers in length, totaling approximately 16, 066 hectares. Over historical time, the island, which has a general north-south orientation, has moved westward, eroding on the ocean side and accreting on the westward coast, which is bordered by Sinepuxent Bay and Chincoteague Bay (Dolan *et al.* 1977). Herbaceous plants dominate vegetation communities on the sand dunes on eastern portion of the island, e.g. *Ammophila brevigulata, Panicum amarum*. Very few woody species are found in the vicinity of the primary dunes, with the exception of bayberry (*Myrica pensylvanica*), which is frequently found on the primary dunes and in other areas exposed to salt spray. Woody species become more prominent in scrub communities where wax myrtle tends to replace bayberry

toward the bayside. Other common woody species are groundsel (*Baccharis halimifolia*), blueberry (*Vaccinium* spp.) and poison ivy (*Toxicodendron radicans*). Winged sumac (*Rhus copallina*) and Virginia creeper (*Parthenocissus quinquefolia*) are also present. Forest communities, dominated by a loblolly pine (*Pinus taeda*) overstory, are found toward the west coast of the island, where they grade into high marsh. Small, nearly pure islands of wax myrtle dot the high marsh. Greenbrier (*Smilax* spp.) is a frequent component of the forest understory, also present in the understory, but less common, are poison ivy, blueberry (*Vaccinium* spp.) and wax myrtle. More detailed descriptions of the island's vegetation have been compiled previously (Higgins *et al.* 1971, Hill 1986, Stalter and Lamont 1990). Data were collected along an approximately 19 kilometer stretch of the island. Sites are identified with reference to the dune crossing to which they were closest (e.g. DC5). The only exceptions are Hungerford forest and marsh sites which are identified by these names.

Fecal Collection

Examining the seed and pulp composition of fecal samples provided an unambiguous evidence of diet (e.g. Parrish 1997). To sample the fruit selection by frugivores in the field, I captured birds using a total of 14 mist nets each year (2.6m in height and 6m in length, 36mm mesh size) in the Off Road Vehicle section of Assateague National Seashore during 1997 – 2000 and 2001-2002. Mist nets were generally operated during the period of greatest bird activity, from dawn to noon, approximately 5 days a week in autumn (October-December) and less frequently

afterwards (January-April). To obtain insight into among-site variation, up to seven

mist nets were set up at each of two different locations per year; the number of nets in

operation was influenced by weather and logistics. In 2001-2002, three sites were

sampled. Nets were arranged to maximize capture rates of passerines and were no

more than 150m from a central banding station at each site. In the first two seasons

(1997-1999), nets were located in both forest and scrub habitat. Because there was no

obvious distinction in fruit selection by birds between habitats, all nets in 1999 –

2000 and 2001 – 2002 were located in scrub habitats where bird abundance was

greater. Nets were checked approximately every 30 minutes and operated in

accordance with the principles outlined by Gaunt *et al.* (1997). All individuals

caught were identified to species, and sexed and aged when possible, following Pyle

et al. (1987).

Fecal samples of all birds were collected by using fecal bags (Parrish *et al.*

1994), and labeled with date, time of removal from net, net location, species of bird,

and unique U. S. Geological Survey band number that was applied to birds before

release. Fecal bags were made from athletic socks the toes of which had been

replaced with wire mesh. A re-sealable, plastic bag was then pinned to the sock so

that any fecal matter would be caught. Individuals that did not defecate within 20-30

minutes were released. Samples were frozen at the end of each day. Later these were

examined under a dissecting scope (0.7X – 3X). A sample was considered to contain

fruit if seeds, pulp or fruit skins were present (Jordano 1988); relying on seeds alone

could be biased if certain fruits tended to be regurgitated because these seeds would

be voided more rapidly than those defecated (e.g. Johnson et al. 1985, Levey 1987).

With the exception of *Myrica*, all seeds, pulp and fruit skins were identified to species by means of a reference collection of all fleshy-fruited species on Assateague Island. The presence of all species and the number of seeds present was recorded.

Although the fruits of wax myrtle and its congener, bayberry, are easily distinguished in the field based on fruit size, identification of their seeds was more difficult. To estimate relative consumption of these species by birds, I collected and measured the diameter of 45 seeds selected at random from 3 individual plants of each species. The mean diameter for wax myrtle was 2.2mm ± 0.05, for bayberry, 2.7 ± 0.05. Discriminate analysis (Proc Discrim, SAS version 8), indicated that seed size was an effective means for determining the species of collected seeds, correctly identifying wax myrtle and bayberry 95.6% and 91.3% of the time, respectively. To gauge the relative use of bayberry and wax myrtle during autumn, the only time bayberry was present in detectable amounts, the diameter of seeds in fecal samples from 4 different sites were compared to the confidence interval. Seeds with a diameter greater than the upper limit of wax myrtle and beneath the lower limit of bayberry were considered of unknown origin.

Fecal Collection: Fruit abundance

Relative fruit abundance was measured by surveys. On each day that fecal samples were collected, at a fixed point central to the mist nets, a haphazard direction was selected by spinning a pencil. Along this heading, two 300m transects radiating from the central point and two similar transects perpendicular to this initial line were established. Along each transect, a 10m radius circle was drawn every 50m,

providing a total of 24 circles for each day. The number of all fruits (up to 1,000) borne by all species located within each circle was recorded. Fruit abundance of individual species > 1,000 was recorded in increments of 1000, up to 10,000. When fruit abundance was >10,000, only the occurrence was reported, since more accurate estimation of such amounts was not deemed possible. Fruit abundance was subsequently recorded on a log scale.

To compare fruit use by gray catbirds and myrtle warblers in the field, I determined the number of fecal samples for each that contained (1) only evidence of *Myrica* consumption, (2) evidence of *Myrica* and another fruit species, (3) only other fruit species. Because gray catbirds were not always captured in sufficient abundance to analyze their relative fruit use, I was able to test four different data sets from three different sites in four years. Data were analyzed using Fisher's exact test (SAS Institute 1999).

Fruit preference trials

Fruit preference trials with captive birds were conducted in October 1999 and 2001. Gray catbirds and myrtle warblers were captured with mist-nets. All captive birds were housed singly at the study site in protected outdoor rabbit cages, measuring approximately 0.6 X 0.6 X 0.3 meters. A tray (fecal tray) was suspended beneath each cage to collect all fecal remains of captive birds. Each bird was provided with an acclimation diet of *ad libitum* water, semi-synthetic maintenance diet (Denslow *et al.* 1987) and wax worms (*Galleria mellonella*) purchased from Rainbow Mealworms and Crickets. Captive birds were acclimated for at least two

days before fruit preference experiments began. Food and water were inspected at least twice a day.

Preference trials in 1999 included gray catbirds (n=5) and myrtle warblers (n=8); data from trials in 2001 included only myrtle warblers (n=6). After acclimation, trials began at 0730 and lasted 48 hours. In addition to water, captive birds received wax worms (32 for gray catbirds, 20 for myrtle warblers) and an *ad lib.* amount of different local, bird dispersed fruits collected on Assateague Island: Virginia creeper (*Parthenocissus quinquefolia*), poison ivy (*Toxicodendron radicans*), winged sumac (*Rhus copallina*), and wax myrtle (*Myrica cerifera*) in separate, randomly placed bowls. In 2001, captive birds also received juniper fruit (*Juniperus virginiana*), which was rare at the study site but has been reported to be a major food item elsewhere (Martin *et al* 1951, Yarbough and Johnston 1965). All fruit species were considered to be suitable food items for both warblers and catbirds (Martin *et al.* 1951, Yarbrough and Johnston 1965, Hoppes 1987, Malmborg and Willson 1988, Parrish 1997). Because nutrient levels in fruits may differ between parent plants (Howe and Smallwood 1982), fruit was removed from five genets. To insure that the fruit contents of all bowls were inspected by each bird, the daily was divided equally between bowls. The heads of all worms were crushed prior to presentation to prevent their burrowing deep into the fruit. There was no indication that this affected their attractiveness to captive birds. Fruit and water were inspected each afternoon. Fouled water and fruit were replaced as were any wax worms that had been dropped into the fecal trays but not consumed. Seeds that had been deposited in either fruit or water bowls were removed and placed in the fecal trays so that they

would be counted. Water and fruit were replaced on the second morning shortly after

dawn, and an additional allotment of wax worms provided. On the third morning,

captive birds were released and the contents of each fecal tray were collected for

analysis.

The numbers of fruits ingested were calculated by the number of seeds

deposited in each tray. Although the number of Virginia creeper seeds varied

between fruits, the shape of seeds in each fruit was distinctive. Based on these

shapes, it was possible to reconstruct the number of seeds that each fruit contained

and thus the total number of fruits consumed.

Based on the numbers of fruit consumed, each species received a preference

rank. These data were analyzed using Friedman's X^2 (SAS Institute 1999) to

determine whether captive birds showed preference for any of the fruit species

provided. A Bonferroni adjustment was used to determine which species was

preferred when results from Friedman's test were significant.

Transect Surveys: Myrtle warbler abundance

During the non-breeding season in all years (1997-2000, 2001-2002), I

recorded the number of myrtle warblers detected by sight and sound along a total of

10 transects; five transects were located in each the two major habitat types on

Assateague Island in which warblers consistently were found: forest and scrub. Each

transect was 500m in length with a fixed width of 50m (2.5 hectares in total) and

divided into 50m segments. All transects were separated by at least 700m to increase

likelihood of independence and were located in areas with characteristic vegetation.

Transects were deliberately paired (one scrub and one forest). On days that surveys were conducted, a single pair of transects was visited. A sampling period was concluded when all 5 transect pairs had been visited once. The length of time (days) between sampling periods and the duration of each sampling period, which ranged from 5-14 days, were influenced by weather and logistical issues. The order of transect pairs within a sampling period was randomized to prevent a time bias.

To increase consistency of counts, I conducted surveys only on mornings with little or no precipitation and when wind did not interfere with auditory detection (see Rosenstock et al. 2002).   Surveys began approximately 90 – 180 minutes after dawn so that migrants had an opportunity to assess and choose from available habitats (Moore *et al.* 1990). Warblers were counted only when judged to be using the habitat. This did not include, for example, warbler flocks flying more than 5m over scrub habitat, which were apparently passing over habitat, but did include those flying beneath, but not over, tree canopies at forest sites.

Transect Surveys: Fruit abundance

Wax myrtle fruit abundance was measured at the conclusion of each day's survey in all years in scrub transects and for two years (1997-1998, 2001-2002) in forest transects. To estimate relative fruit abundance in each scrub transect and to assure balanced sampling throughout that transect, individual female wax myrtle plants were marked in each segment. Three females per segment were marked in the first two years of data collection (1997 – 1999), four females were marked in the following two seasons (1999 – 2000, 2001 – 2002). The number of female

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individuals marked varied among forest transects since these frequently contained fewer than four female plants per segment. In such cases, all females present were considered. The number of fruits on each plant was extrapolated from counts of the number of fruit on a single branch. Fruit abundance per plant was recorded on a logarithmic scale. Estimated abundance ranged from 0 to >10,000 fruits per individual.   Since the vast majority of fruit was ripe by the start of each year's earliest survey, fruit ripeness was not recorded.

To account for differences in the abundance of wax myrtle females between transects, the mean number of female wax myrtle plants in each transect was estimated from vegetation data collected in 1998 - 2000.   Three circles of 10m radius (0.0314 ha) were randomly located in each segment. In each circle, the number of female wax myrtle individuals was recorded. These data were collected only once because the number of individual plants on any transect did not change substantially over the course of the study. Multiplying the mean number of wax myrtle females present by the mean log number of fruit found on each transect provided an estimate of the number of wax myrtle fruit available at any one time.

Repeated measures analysis (Proc Mixed, SAS Institute 1999) was used to determine the relationship between myrtle warbler abundance and wax myrtle fruit abundance in scrub and forest habitats. To account for the temporal autocorrelation (see Verdu and Garcia-Fayos 1994), the spatial power law covariance structure [SP(POW)] was used, suitable for unequally spaced longitudinal data (Littell et al. 1996). Because mixed model analysis in SAS does not provide a coefficient of determination (r^2), this was calculated using regression (Proc Reg, SAS Institute

1999)). An insufficient amount of data was collected in 1997-1998 for analysis. Abundances of birds and fruit from both scrub and forest habitats were log transformed to meet the normality and homoscedasticity assumptions of regression.

Seed Dispersal

To examine the relationship between myrtle warbler abundance and numbers of wax myrtle seed dispersal, I measured the number of seeds and the number of seeds dispersed in two different habitats: forest and scrub.

To measure seed dispersal rates in different habitats over time, 100 seed traps were placed in a 100m by 100m grid (placing one every 10m) in three different habitats: salt grass meadows, scrub, and forest. Each trap was constructed using a 28 X 56 cm plant flat, lined with plastic screen to prevent seed loss and covered with hardware cloth to exclude rodents (see Chapter 2 for a more detailed description). Each habitat type was replicated three times. Seed traps were located along existing survey transects to allow for the comparison of bird and seed rain. Because bird surveys were not conducted in meadow habitat, only data from scrub and forest traps are presented here. A more complete treatment of seed dispersal in all habitats sampled, including salt grass meadows, will be presented in Chapter 2. I included bird survey data only from those three transects on which traps were located.

Data were collected between November 17, 2001 and April 30, 2002. The number and species of all seeds were recorded six times during the season in approximately 30 day intervals. After each inspection, all fruit and seeds contained in

each trap were placed in a plastic bag and removed from the site, in order not to influence concurrent seed predation experiments (See Chapter 2).

The total number of seeds present in forest and scrub traps during each period was regressed against myrtle warbler abundance on corresponding survey transects using Proc Reg (SAS Institute 1999). Because warbler surveys were not conducted between December 9, 2001 and January 8, 2002, seed rain data from that period were not included in this analysis. Data from forest sites required a log transformation to meet assumptions of normality and homoscedasticity. Scrub site data required no transformations.

Results

Fruit Use and Abundance

Fruit remains were detected in more than 95% of the fecal samples collected from myrtle warblers each month, although these warblers were highly insectivorous as well (Figure 1-1). Over 99% of the 1,866 fecal samples from these warblers that contained seeds or pulp displayed evidence of only *Myrica* fruit consumption (Table 1-1), indicating a consistent pattern of heavy, nearly exclusive use between late September and April. The diameter of *Myrica* seeds in fecal samples collected in two years (1998, 1999) were compared to mean diameter of seeds collected from both wax myrtle and bayberry. Seventy-two percent of 327 seeds measured in 1998, and 87% of 2,136 in 1999 fell within the 95% confidence limits of wax myrtle diameter. These results confirm that the majority of *Myrica* seeds in fecal samples were wax myrtle, even when bayberry fruit was also available. This reliance on fruit in general

and on wax myrtle fruit in particular contrasted with the diets of the other facultatively frugivorous passerine species which were almost exclusively insectivorous when they were present in autumn (Table 1-2).

The composition of *Myrica*'s consumer assemblage changed seasonally but showed less interannual variation. In autumn (late September-November), a variety of frugivores consumed *Myrica* fruit, but myrtle warblers and gray catbirds were the only consistent passerine consumers in this period (Table 1-2). However, myrtle warblers were significantly less likely to forage on other fruit species than were gray catbirds (Table 1-3). After November, myrtle warblers were the only passerine species that consumed *Myrica* fruit; gray catbirds were never mist netted between December and March and were very rarely observed. The two individuals caught in spring (2000) had been foraging only on *Smilax* fruit.

Wax myrtle was the most abundant fruit in most sites and in most months, with the exception of DC11 in autumn 1998 (Figure 1-2). At this site, bayberry fruit levels were responsible for the relatively high abundance of other fruit species. After November, however, wax myrtle fruit was substantially more plentiful than all other species combined. At all other fecal collection sites, bayberry fruit were present in very low numbers. At all sites, wax myrtle abundance declined substantially over the course of each season at each site, although fruit was still present at all sites visited in April. Wax myrtle fruit levels displayed some interannual variation in abundance at Hungerford Marsh. However, this appears to be either a localized phenomenon or an artifact of sampling methodology, because similar variability was not observed in fruit abundance patterns on survey transects (see Figure 1-3).

Fruit Preference

Captive myrtle warblers significantly preferred wax myrtle to other locally available fruit in two different preference trials (Table 1-4). In 1999, when presented with four fruit species, warblers did not randomly consume fruits (Friedman's $X^2_{0.05,3}$ =23.4156, $P < 0.0001$). Multiple comparisons confirmed that wax myrtle was significantly preferred to all others ($P < 0.01$). There was no inter-individual variation in the identity of the rank order of the two most preferred fruits: wax myrtle and poison ivy. No individual's diet, however, was confined only to wax myrtle.

A second preference trial (2001) that included juniper with the previously used fruit species provided similar results. Captive warblers (n = 5) again significantly preferred wax myrtle ($P < 0.05$), although the identity of the second most popular fruit was no longer unanimous. No warblers consumed either Virginia creeper or winged sumac in this trial and so these categories were not included in the analysis.

In contrast, gray catbirds (n = 5) showed no significant preference for any individual fruit species (Friedman's $X^2_{0.05,3}$ =2.28, $P > 0.2$) (Table 1-5). Contrary to the relatively uniform preference rankings demonstrated by myrtle warblers in both trials, there was substantial inter-individual variation among gray catbirds in the preference rankings of all fruits.

Myrtle warbler abundances

Myrtle warbler and wax myrtle fruit abundance in scrub habitats on Assateague Island followed similar seasonal abundance patterns in all years (Figure

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1-3). In the two years when survey data were collected in the early fall (1997 and

2001), annual warbler abundance peaked in October, and then declined. In all four

years, abundance reached a second peak in mid-winter, the timing of which differed

among years. Prior to this increase in abundance, myrtle warbler abundance showed

no clear relationship to the amount of wax myrtle fruit. After mid-winter, however,

myrtle warbler abundance consistently declined in concert with wax myrtle fruit

abundance. The timing of this decline began each year when the number of wax

myrtle fruit dipped below 1,500 on the abundance index.

Analyses indicated a significant relationship between abundance of myrtle

warblers and wax myrtle in scrub habitat in all three years (Figure 1-4), suggesting

that myrtle warblers consistently tracked wax myrtle fruit abundance in scrub

habitats. The relationship between warblers and wax myrtle fruit abundance in forest

habitats showed a similar trend, but was not significant ($F_{1,13} = 0.97$, $P > 0.1$).

Wax myrtle seed dispersal

Mixed model analysis indicated that the number of *Myrica* seeds dispersed in

scrub habitats per day was significantly influenced by the abundance of myrtle

warblers over time (Figure 1-5). This relationship was not significant at forest sites

($P > 0.2$). However, a post hoc power analysis indicated that a much larger sample

size (n = 155) at forest sites was needed to detect significance at $\alpha = 0.05$ than the one

available (n = 18).

Discussion

Myrtle warblers

These results indicate that migrating and wintering myrtle warblers on Assateague Island specialize on wax myrtle fruits. Warblers ate wax myrtle fruits from their fall arrival until their departure (October-April) and only rarely used other fruit species. This pattern of consistent, heavy use contrasts with specialized foraging behavior documented in other systems where specialization was most noticeable in times of low resource abundance (e.g. Morton 1971, Skutch 1980, Robinson and Wilson 1998). Myrtle warblers ate wax myrtle fruit whether it was fall, winter or spring, suggesting that the importance of wax myrtle fruit as a food item for myrtle warblers did not depend on falling insect abundance, a trend seen in food use of other temperate frugivorous species (Parrish 1997). Similarly, frequency of use did not decline in late autumn after the departure of more dominant congeners (Morse 1980), as seen elsewhere (Morse 1967, Pimm et al. 1985). The lack of interannual variation in diet is also noteworthy and in contrast with reports from other systems (Jordano 1988, Malmborg and Willson 1988, Herrera 1998). Although seed size measurements used to distinguish wax myrtle and bayberry seeds were collected in only two years, the large percentage of seeds whose diameter fell within the 95% confidence limits of wax myrtle and the documented relative abundance of the two species strongly suggest that the *Myrica* seeds collected from autumn fecal samples in all years were wax myrtle, and not bayberry.

Results from feeding trials confirmed that the nearly exclusive use of wax myrtle fruit by myrtle warblers was due to preference and not to the relative

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abundance of local fruit species, considered a major determinant of avian and mammalian fruit choice in other systems (Baird 1980, Jordano and Herrera 1981, Holthuijzen and Sharik 1985, Jordano 1989, Gautier-Hion *et al.* 1993, but see Guitian *et al.* 1994). Indeed, previously reported cases of apparent frugivore specialization frequently were more the result of diminished opportunity rather choice (Crome 1975, Sorensen 1981, Wheelwright et al. 1984, Jordano 1988, Banack 1998, Carlo et al. 2003). The unanimity in the top ranking of wax myrtle by captive warblers in both trials, unanimity not extending to any other fruit, further supports the hypothesis of specialization because specialists are expected to show little variability in choice (Seamon and Adler 1996, but see Robinson and Wilson 1998). The strong preferences of captive myrtle warblers also suggest that these frugivores would display similar fruit use patterns in the field at other locations as well and that these results not due to the restricted scale of this study (Burns 2004). The agreement between the controlled preference trials and field studies contrasts with results from trials with gray catbirds as well as with similar comparisons in other species (Sorensen 1984, McPherson 1988, Whelan and Willson 1994).

These findings are largely in agreement with other studies that examined systems containing both myrtle warblers and either of the *Myrica* species. Although myrtle warblers do consume other fruit species at sites lacking *Myrica* fruit (Yarbrough and Johnston 1965, Holthuijzen and Sharik 1985, Hoppes 1987, Malmborg and Willson 1988, Suthers et al. 2000), these warblers have displayed a remarkable appetite for the waxy drupes of this genus whenever present. For example, Wiltz and Giampa (1978) observed that myrtle warblers wintering in

Pennsylvania never foraged outside the distribution of bayberry at their site. On Block Island, a stopover site in Rhode Island containing over six fruiting species commonly used by other species, bayberry was found in over 97% of myrtle warbler fecal samples and other fruit species were rarely taken by myrtle warblers (Parrish 1997). Warblers wintering in Florida, the Carolinas and New Jersey were all heavy consumers of wax myrtle fruit (Yarbrough and Johnston 1965, Holthuijzen and Sharik 1985, Skeate 1985, Hoppes 1987, Malmborg and Willson 1988, Borgman *et al.* 2004, Kwit *et al.* 2004). Such agreement among results of fruit use at distant sites and among a variety of habitats by either avian or primate frugivores is highly unusual (Herrera and Jordano 1981, Gautier-Hion *et al.* 1993, Fuentes 1995, Levey and Martinez del Rio 2001). This geographical consistency strongly suggests that results reported here are not due to context and may be applicable to myrtle warblers throughout their wintering range wherever wax myrtle is present.

Results of the present study, on the other hand, represent a clear departure from those reported in previous investigations of avian fruit use patterns. Most frugivores display a generalized foraging strategy when selecting fruit (Greenberg 1981, Jordano and Herrera 1981, Wheelwright et al. 1984, Herrera 1985, Skeate 1985, White and Stiles 1990, Blake and Loiselle 1992). Even the resplendent quetzal (*Pharomachrus mocinno*) which feeds predominantly on Lauraceous fruit may eat over 40 species of fruit from 17 different families (Wheelwright 1983).

Survey data showing that myrtle warblers in scrub habitat tracked fruit in all years support the hypothesis that their abundance on Assateague Island was dependent on wax myrtle fruit abundance. This dependence was clearest in late

winter after wax myrtle fruit abundance dipped below 1500 on the fruit abundance index in all years. This does not imply that myrtle warblers are indifferent to fruit abundance earlier in the year or are responding to the fluctuations of an alternate resource (see Herrera 1981, Loiselle and Blake 1994). Instead, I suspect that apparent independence of myrtle warblers from wax myrtle fruit abundance was due to two factors. First, wax myrtle abundance was so vast in autumn and early winter that even substantial reductions in fruit levels were unlikely affect myrtle warblers' assessment of resource availability (see Johnson *et al.* 1985, Blake and Loiselle 1991). Second, the size of the local warbler population was also affected by arrival of waves of new migrants in mid-winter. The arrival of these transients, probably prompted by deterioration of conditions in the more northern parts of their range (see Herrera 1982), necessarily weaken the statistical association between birds and fruit on Assateague Island.

An alternative hypothesis that the decline in myrtle warblers is due to spring migration rather than declines in fruit abundance is rendered unlikely since myrtle warblers do not migrate until April from North Carolina (Yarbrough and Johnston 1965) and migrants can still be found in Maryland by late April (Lowe pers. obs.). Based on twelve years of data, Herrera (1998) speculated that in the northern portion of winter ranges, frugivore numbers may be affected by weather, whereas further south, food abundance may exert a greater influence. Whether this is true of the various populations of myrtle warblers wintering along the Atlantic coast, as seems reasonable, is currently unknown (Root 1988).

I suspect that the lack of a significant relationship between warbler and wax myrtle fruit abundance in forest habitat was caused by the relatively low levels of fruit present at all times in these sites. Survey data (Figure 1-3) suggested that, below a certain threshold, the ability of wax myrtle fruit to attract myrtle warblers diminished. Observations made during surveys in these transects suggest that myrtle warblers, which were frequently observed foraging in the canopy (Lowe unpublished data), visited pine forests to hunt for insects (Suhonen et al. 1992) and spent little time in the shrub understory. However, because the substantial differences in vegetation and structure of scrub and forest habitats are confounding variables, any comparisons must be made with caution. Nonetheless, at other sites, myrtle warblers have appeared plastic in habitat selection, responding opportunistically to food abundance, indifferent to different vegetative structure (Parnell 1969, Hutto 1985, Suthers *et al.* 2000, Kwit *et al.* 2004).

Based on the entire period of warbler residence on Assateague Island, these results are consistent with recent studies examining the relationship between myrtle warblers and wax myrtle over shorter periods of time in only winter. In South Carolina, Kwit *et al.* (2004) demonstrated that the abundance of myrtle warblers in different habitats was related to wax myrtle fruit abundance in January. However, the authors acknowledged that, although significant, the relationship was relatively weak and indicated that their results somewhat confounded by other habitat effects. More persuasively, when Borgmann *et al.* (2004) experimentally augmented wax myrtle abundance in February warbler numbers increased in treatment plots. Further, foraging observations indicated a significant increase in the number of birds foraging

in the shrub layer and, in particular, on wax myrtle plants after the fruit augmentation. It is not clear, however, whether such a relationship exists between myrtle warblers and bayberry fruit over time. The only data published thus far comes from Block Island, where myrtle warblers' abundance declined with experimental removal of bayberry fruit in autumn (Parrish 1997).

In general, results that show responsiveness of frugivores to fruit abundance are not unusual. Studies involving other fruiting plants and frugivores have frequently shown that changes in fruit abundance at a community level may influence frugivore abundance on a variety of scales (Levey 1988, Blake and Loiselle 1991, Jordano 1993, Loiselle and Blake 1994, Santos *et al.* 1999, Burns 2004). This phenomenon is not restricted to frugivores only. The abundance of Clark's nutcrackers may also be substantially determined by abundance of seeds of a variety of pine species (Tomback 1998). However, studies indicating that birds track the abundance of a single fruit species over time are rare. Blackcaps (*Sylvia atricapilla)* have been shown to track abundance of cultivated olives on a local and geographic scale in Spain (Rey 1995). However, this response of *S. atricapilla* may have reflected more the high density of olives in orchards relative to other fruit species than a dependence on olives per se, since blackcaps have been reported using a wide variety of other fruit species at other sites (Jordano and Herrera 1981, Jordano 1988). Perhaps the most convincing data to date come from phainopeplas, the abundance of which appears determined by fluctuations in mistletoe fruit abundance (Anderson and Ohmart 1978, Chu and Walsberg 1999). Similarly, my results indicate that myrtle warblers prefer wax myrtle to other fruits, use it consistently and begin to leave

Assateague Island when its levels decline below a certain threshold. Together these combined data suggest that myrtle warblers leave Assateague Island not only because the major fruit source is becoming scarcer, but because their preferred fruit source is disappearing.

Wax Myrtle

Results generally supported the hypothesis that wax myrtle is itself specialized on myrtle warblers. Fecal samples indicated that, among passerines, myrtle warblers are the most frequent consumers of wax myrtle fruit throughout the entire fruiting season. When present, two other seasonal frugivores, tree swallows (*Tachycineta bicolor*) and gray catbirds, also consistently used wax myrtle fruit. Tree swallows can occur in flocks numbering in the thousands and are noted for their consumption of *Myrica* species (Hausman 1927, Martin *et al.* 1951). Indeed, examination of tree swallow feces deposited by resting flocks on Assateague Island revealed that these birds ate only *Myrica* species when frugivorous (Lowe pers. obs.). However, tree swallows were not commonly frugivorous nor was their abundance affected by changes in wax myrtle fruit abundance over time. In fact, if tree swallow migratory patterns are influenced by resource abundance and not endogenously determined, data from DC 11 (Figure 1-2) suggests that they may be more influenced by bayberry fruit abundance, because tree swallows were rarely seen after mid-November when bayberry fruit levels dropped precipitously but when wax myrtle was still abundant. Further, tree swallows have been reported roving far north of their wintering grounds and subsisting on bayberry (Hausman 1927, Robertson *et al.* 1992) but only one

flock, of 8 individuals, was ever seen after December in all years on Assateague Island.

Gray catbirds, which are fruit generalists elsewhere (e.g. Parrish 1997, Suthers *et al.* 2000), were also frequent consumers of wax myrtle fruit. However, they were less constant than myrtle warblers and were significantly more likely to forage on other fruit species. Comparison of fruit use in the field with feeding trial results confirmed that gray catbirds had no innate preferences among local fruits and thus fruit use in the field was a function of wax myrtle's relative abundance and not indicative of preference. The very high degree of inter-individual variation in the preference rankings of the different fruits in feeding trials by gray catbirds is consistent with the hypothesis that gray catbirds are generalists.

These results correspond with those few that report the identity of *Myrica* seed dispersers at other sites. Borgmann *et al*. (2004) noted that other frugivores consume wax myrtle fruit which may be an important winter food for them, too. Yet only myrtle warblers responded to an experimental increase in wax myrtle fruit abundance (see also Kwit *et al*. 2004). Similarly, Parrish (1997) found that myrtle warblers consumed the vast majority of bayberry fruits during fall migration. In New Jersey, White (1989) documented that myrtle warblers and northern flickers (*Colaptes auratus*) were both major dispersers of *Myrica* seeds. But his data do not allow comparison of the patterns of relative use and were potentially biased by his data which were based on discovery of droppings at his site.

Assessing the interaction

The results presented here indicate that myrtle warblers and wax myrtle on Assateague Island are reciprocally specialized. Each is the other's primary partner and each is dependent on the other for food and dispersal, respectively, and there is no evidence of ecological asymmetry typical of many fruit – frugivore relationships (Jordano 1987, 1988, Murray 1988, Herrera 1998), and also plant-pollinator interactions (Bascompte 2003, Vazquez and Aizen 2004). Results presented here document the relationship between myrtle warblers and wax myrtle at only a single location, yet the congruence of these data with those from other geographically distinct sites strongly suggests that the tight relationship observed on Assateague Island may be typical at other locations is not merely a question spatial scale (Burns 2004).

These findings indicate that on Assateague Island, the interaction between myrtle warblers and wax myrtle is as mutually dependent as that between the more celebrated relationship between phainopeplas and mistletoe. Both are characterized by a large degree of range overlap (Root 1988, Chu and Walsberg 1999, USDA 2004), digestive adaptation by frugivores to unusual fruit chemistry (Walsberg 1975, Place and Stiles 1992), restricted disperser assemblage, and the influence of fruit crop on frugivore abundance (Anderson and Ohmart 1978).

Considered individually, both myrtle warblers and wax myrtle have characteristics that may predispose them to specialization. As a species, yellow-rumped warblers are facultative migrants capable of leaving sites with low food availability in the non-breeding season (Terrill and Ohmart 1984, Terrill and

Crawford 1988), allowing them to track fruit abundance on a geographic scale and to avoid the consequences of local resource depletion (Jordano 1993). Wax myrtle fruit, on the other hand, has unusual fruit chemistry rendering it indigestible to most vertebrates (Place and Stiles 1992), a trait associated with a restricted avian and mammalian disperser assemblages (Greenberg 1981, Fuentes 1995, Tewksbury and Nabhan 2001). What appears exceptional in this system is that these two specialize on each other.

The ecological consequences of such an interaction are important for both participants. These data provide evidence supporting the frequent claim that specialization on wax myrtle fruit allows myrtle warblers to remain further north than the majority of their congeners (e.g. Hunt and Flaspohler 1998), therefore experiencing lower mortality (Sillett and Holmes 2002), and also to migrate earlier in the spring than other Parulids (Hunt and Flaspohler 1998). This latter feature may, in turn, be of substantial consequence in territorial establishment and therefore nesting success (Marra *et al.* 1998) for these warblers which are considered to be socially subordinate to the majority of their congeners (Morse 1980).

The effects of specialization on wax myrtle are less clear. Waser *et al.* (1996) speculated that flowering plants would benefit from specialization if their pollinator were both abundant and effective. The relative effectiveness of wax myrtle's various dispersers will be more fully addressed in Chapter 3. However, my data indicate that myrtle warblers are indeed the most abundant and faithful disperser of wax myrtle seeds. Further, wax myrtle, growing well north of the wintering ranges of most neotropical migrants and producing an abundant crop of persistent fruits, does benefit

from a specialized relationship with a frugivore disposed to linger until fruit abundance drops to relatively low levels.

The degree to which this relationship has been shaped by selection is unexplored. The ability of myrtle warblers to digest wax appears to be the result of digestive adaptations (e.g. intestinal retrograde reflux, high levels of bile salts), which other warblers may lack (Place and Stiles 1992). Indeed, the most common consumers of wax myrtle and bayberry fruits are heterogeneric (Martin *et al.*1951, Parrish 1997). This suggests that the adaptation to digest wax has been driven by the benefits of exploiting the abundant and predictable crops of *Myrica* fruit available along the Atlantic coast of North America.

Alternatively, a visual review of the National Museum of Natural History's specimens of *Myrica* species found in North and South America reveal a striking similarity in the appearance of all species. This phenotypic congruence strongly suggests that wax myrtle's fruit composition and abundance is not the result of any recent selective pressure but is a plesiomorphic feature of the genus. In contrast to capsacin content of chillies which have been shown to reduce the likelihood of mammalian ingestion (Tewksbury and Nabhan 2001), the wax on wax myrtle fruit does not deter foraging mammals (Lowe, pers. obs.).

Regardless of the ecological benefits and the evolutionary origins, such a mutually specialized relationship inherently puts both participants at risk. These data suggest that declines, especially sudden declines, in the population of one partner will adversely impact the other. Concern about the long term viability of these species may appear to be alarmist since both myrtle warblers and wax myrtle are common.

However, projected climate change with the concomitant rise in sea level, increase in storm frequency and intensity and the resulting damage to coastal marshes (Gregory and Oerlemans 1998, Najjar et al. 2000, Rogers and McCarty 2000, Scavia et al. 2002, Knutson and Tuleya 2004) could reduce coastal populations of wax myrtle substantially (see Young et al. 1992, Aarssen 2000, Conner and Inabinette 2003, Graves and Gallagher 2003). Data presented here suggest that faced with local fruit scarcity, myrtle warblers would be forced either to winter further south in locations with sufficient insect levels to compensate for the lack of fruit availability or to move to more inland populations of wax myrtle, the fruits of which would be presumably depleted earlier in the season. In such a scenario, non-breeding mortality could to increase as migratory distances lengthen (see Terrill and Crawford 1988, Sillett and Holmes 2002). Additionally, if local wax myrtle fruit abundance dropped beneath the threshold needed to attract and then detain migrating warblers, remnant wax myrtle populations along the coast could be expected to disperse fewer seeds on a per capita basis.

These results highlight the need for more information about which species eats what fruit and which species is eaten by which frugivore. Over the past thirty years during which fruiting plant – frugivore interactions have been studied rigorously; great strides have been made in the field of fruiting plant-frugivore interactions. Yet there have been few studies that present comprehensive data on the degree of association between both fruiting plants and avian frugivores (Bronstein 1994). In spite of their potential importance, the role of mammalian dispersers has been largely neglected, especially in the temperate zone (Willson 1993, Motta-Junior

and Martins 2002). Such data are necessary both to understand better the ecology of fruiting plant – frugivore interactions as well as to understand how these interactions are likely to affect the viability of the species involved. Similar studies, quantifying use, preference and dependence, would also indicate whether the results presented here are reflective of the interaction between myrtle warblers and both *Myrica* species at other geographical locations as other studies suggest (e.g. Parrish 1997, Wiltz and Giampa 1978), or whether specialization at this one location is a quirk of context and not representative of the interaction elsewhere (Herrera 1998).

Table 1-1. Number (%) of fecal samples containing different fruit species collected from frugivorous myrtle warblers on Assateague Island National Seashore 1997-2000, 2001-2002. Data are pooled from all years and sites because there was no indication of interannual or between-site variation.

Month	Fecal Contents		
	Myrica fruit	Non-*Myrica* fruit	*Myrica* + Other species
September/October	1056 (99.6)	1 (0.1)	3 (0.3)
November	456 (99.6)	1 (0.2)	1 (0.2)
December	215 (98.6)	0	3 (1.4)
January[ψ]	28 (96.6)	0	1 (3.4)
February/March[±]	44 (95.7)	0	2 (4.3)
April[§]	55 (100)	0	0

ψ Data collected in 1997 only
± Data collected in 1998 and 2000
§ Data collected in 2000 and 2002

Table 1-2. Number (%) of all fecal samples from mist-netted birds containing evidence of frugivory and of *Myrica* fruit consumption in autumn (September-November), 1997-1999, 2001 on Assateague Island National Seashore, Maryland. All species listed are facultative frugivores during non-breeding season at other sites in North America (Martin *et al*. 1951, Parrish 1997).

	Fecal Contents	
Facultative Frugivores (n)	number (%) containing fruit remains	number (%) containing *Myrica* remains
Carolina Chickadee (7)	0	0
Eastern Phoebe (5)	0	0
Brown Creeper (12)	0	0
Golden-crowned Kinglet (33)	1 (3.0)	1 (3.0)
Ruby-crowned Kinglet (19)	4 (21.1)	3 (15.8)
Gray Catbird (119)	83 (69.7)	64 (53.8)
Swainson's Thrush (11)	3 (27.3)	1 (9.1)
Hermit Thrush (9)	1 (11.1)	1 (11.1)
Red-eyed Vireo (8)	0	0
White-eyed Vireo (5)	0	0
Black-throated Blue Warbler (55)	1 (1.82)	1 (1.82)
Myrtle Warbler (1537)	1519 (98.8)	1516 (98.6)

Table 1-3. Number (%) of fecal samples from gray catbirds and myrtle warblers containing remains of different fruit species collected in autumn from three different sites over three different years. Myrtle warblers and gray catbirds differed significantly in their use of non-*Myrica* fruit. Data were analyzed using Fisher's exact test and probabilities were calculated using Monte Carlo simulations for all comparisons, except Hungerford Forest.

| Year | Site | Species | Fecal contents | | | $P <$ |
			Only *Myrica* species	*Myrica* + another species	Only non-*Myrica* species	
1998	Hungerford forest	Gray Catbird	14 (93.3)	1 (6.7)	0	0.10
		Yellow-rumped Warbler	177 (100)	0	0	
1999	Hungerford Marsh	Gray Catbird	15 (83.3)	1 (5.6)	2 (11.1)	0.001
		Yellow-rumped Warbler	373 (100)	0	0	
2001	Hungerford Marsh	Gray Catbird	24 (77.4)	5 (16.3)	2 (6.45)	0.001
		Yellow-rumped Warbler	106 (99.07)	1 (0.93)	0	
2001	DC5	Gray Catbird	7 (53.8)	4 (30.8)	2 (15.4)	< 0.001
		Yellow-rumped Warbler	198 (100)	0	0	

Table 1-4. Preference ranks of local fruit species in two different feeding trials based on number eaten by captive myrtle warblers on Assateague Island in October. Fruit identity significantly affected preference rank in 1999 (Friedman's $X^2_{0.05, 3}$=23.4156, $P < 0.0001$) and in 2001 (Friedman's $X^2_{0.05, 2}$ = 10.1739, $P < 0.01$). *J. virginiana* was not presented to warblers in 1999.

Preference Ranks (number eaten)						
Year	Individual	*M. cerifera*	*J. virginiana*	*T. radicans*	*R. copallina*	*P. quinquefolia*
1999	1	1 (418)	.	2 (19)	3 (9)	4 (1)
	2	1 (268)	.	2 (9)	3 (1)	4 (0)
	3	1 (404)	.	2 (46)	3.5 (0)	3.5 (0)
	4	1 (245)	.	2 (8)	3.5 (1)	3.5 (1)
	5	1 (416)	.	2 (82)	3 (2)	4 (0)
	6	1 (124)	.	2 (17)	3 (1)	4 (0)
	7	1 (437)	.	2 (3)	3.5 (0)	3.5 (0)
	8	1 (471)	.	2 (4)	3 (1)	4 (0)
2001	1	1 (180)	2 (24)	3 (8)	0	0
	2	1 (126)	2 (6)	3 (4)	0	0
	3	1 (383)	3 (11)	2 (48)	0	0
	4	1 (92)	2 (70)	3 (11)	0	0
	5	1 (113)	1.5 (12)	1.5 (12)	0	0
	6	1 (323)	2 (98)	3 (4)	0	0

Table 1-5. Preference ranks of four local fruit species based on number eaten over two days by captive gray catbirds on Assateague Island, October 1999. Ranks were based on total number of fruits consumed over a two day period. There was no significant relationship between fruit species and preference rank when analyzed with Friedman's X^2 ($P > 0.5$).

	Preference Ranks (Number eaten)			
Individuals	*M. cerifera*	*T. radicans*	*R. copallina*	*P. quinquefolia*
1	1 (449)	3 (49)	2 (352)	4 (61)
2	3 (40)	4 (28)	2 (190)	1 (346)
3	3 (227)	1 (298)	4 (168)	2 (268)
4	2 (305)	4 (22)	1 (527)	3 (281)
5	3 (122)	4 (32)	1 (379)	2 (306)

Table 1-6. Repeated measures analysis of the effect of wax myrtle fruit

abundance on myrtle warbler abundance on Assateague Island in three different

years. Data were collected over the course of each fruiting season (autumn to

spring). Year 2 = 1998-1999, year 3 = 1999 – 2000, year 4 = 2001 – 2002. Year

1 was not analyzed because of insufficient data.

Year	Numerator DF	Denominator DF	F	$P <$
2	1	39	15.71	0.001
3	1	29	39.56	0 .001
4	1	34	35.44	0 .001
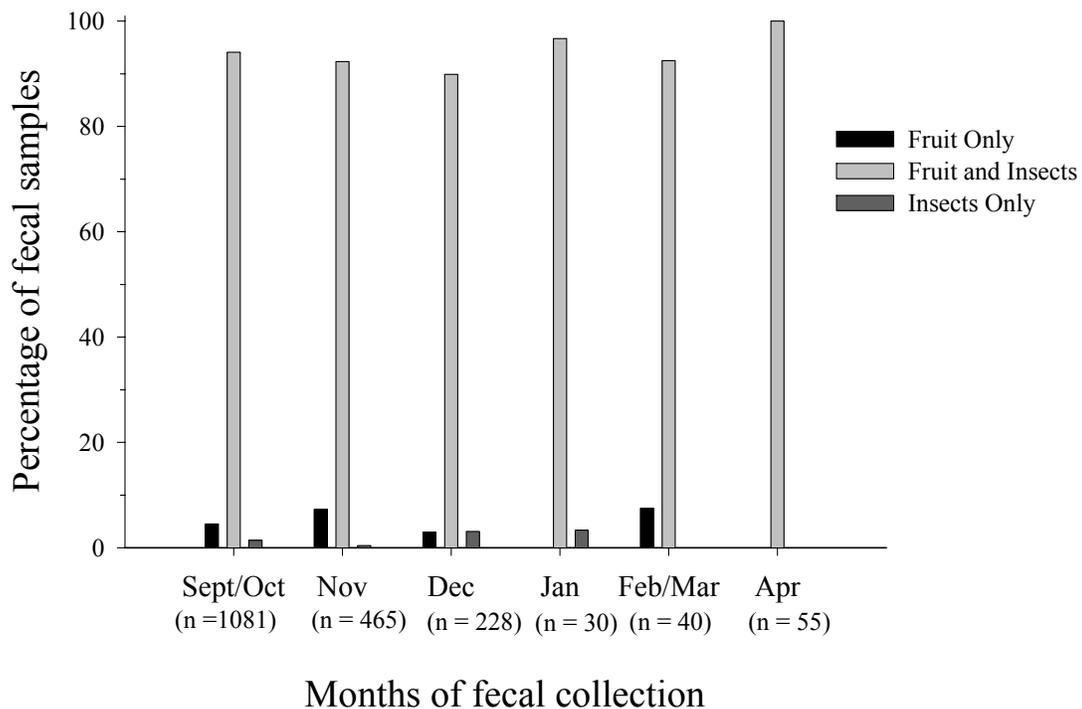
Figure 1-1. Percentage of fecal samples containing insect and fruit remains collected

from myrtle warblers on Assateague Island National Seashore 1997 – 2000, 2001 -

2002. Data are pooled from all years and sites of collection. Monthly data were

collected in all years except for January (collected in 1997 only), February and March

(collected in 1998 and 2000), and April (collected in 2000 and 2002).
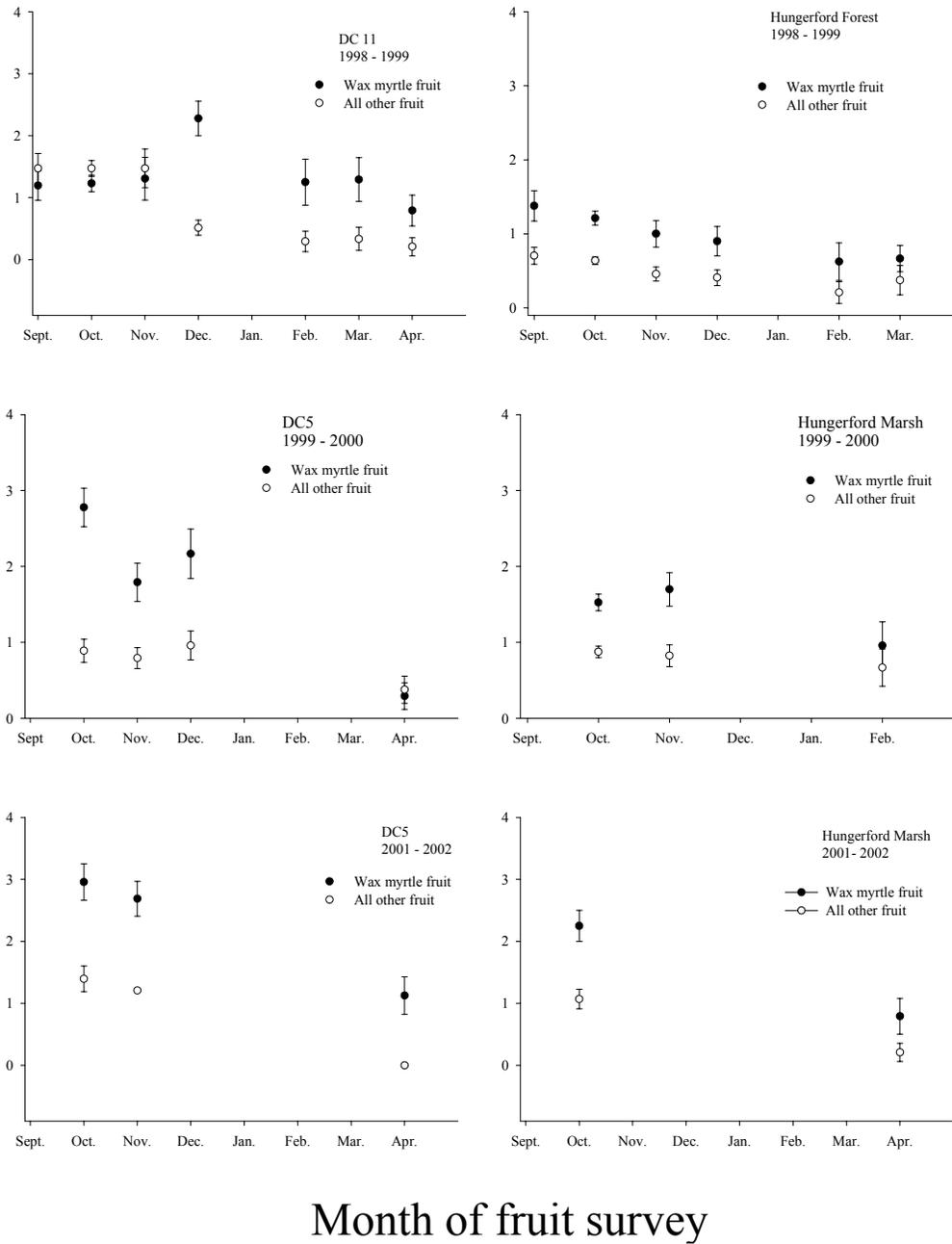
Figure 1-2. Comparative abundances of wax myrtle and all other fruit species combined at different fecal collection sites. Data points are the pooled results of fruit censuses conducted at individual sites in each month. Abundance is reported on a log scale. Minimum sample size is 24 survey circles/data point.
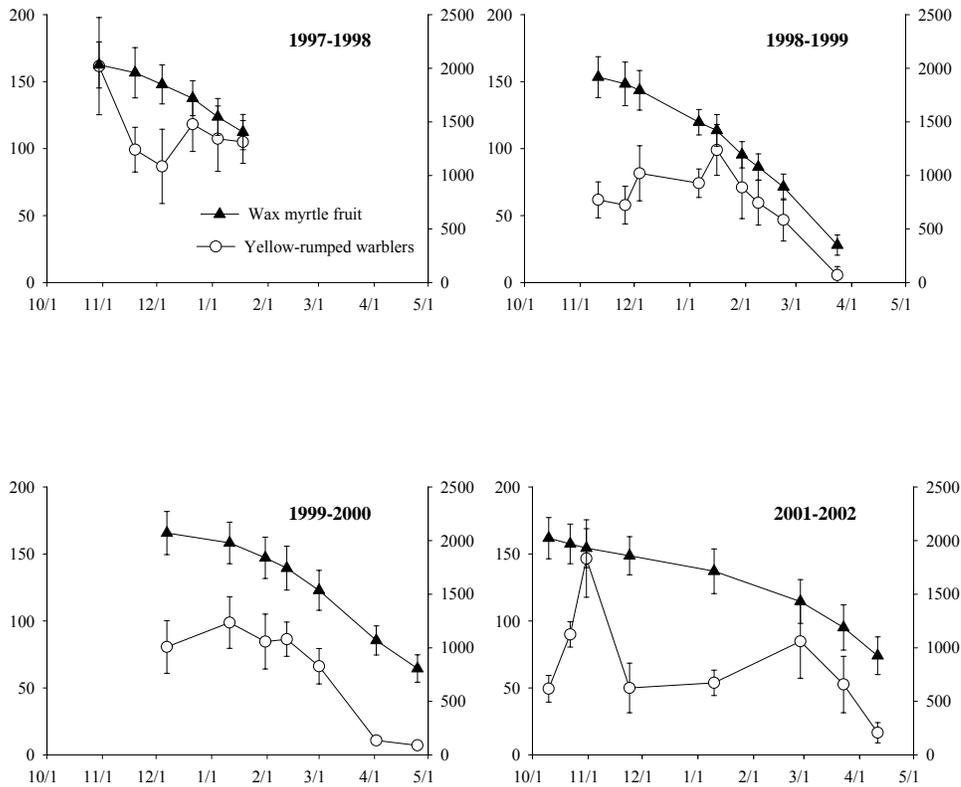
Figure 1-3. Relative abundances of myrtle warblers and wax myrtle fruit on transects (n=5) in scrub habitats on Assateague Island. Individual points are means (± SE) of warblers detected/transect/census period and of log number of wax myrtle fruits /plant [n = 30 (1997-1999), n = 40 (1999-2000, 2001-2002)] /transects/survey period X mean number of female wax myrtle individuals/transect. Mean survey date is the mean day on which surveys in each period were conducted.
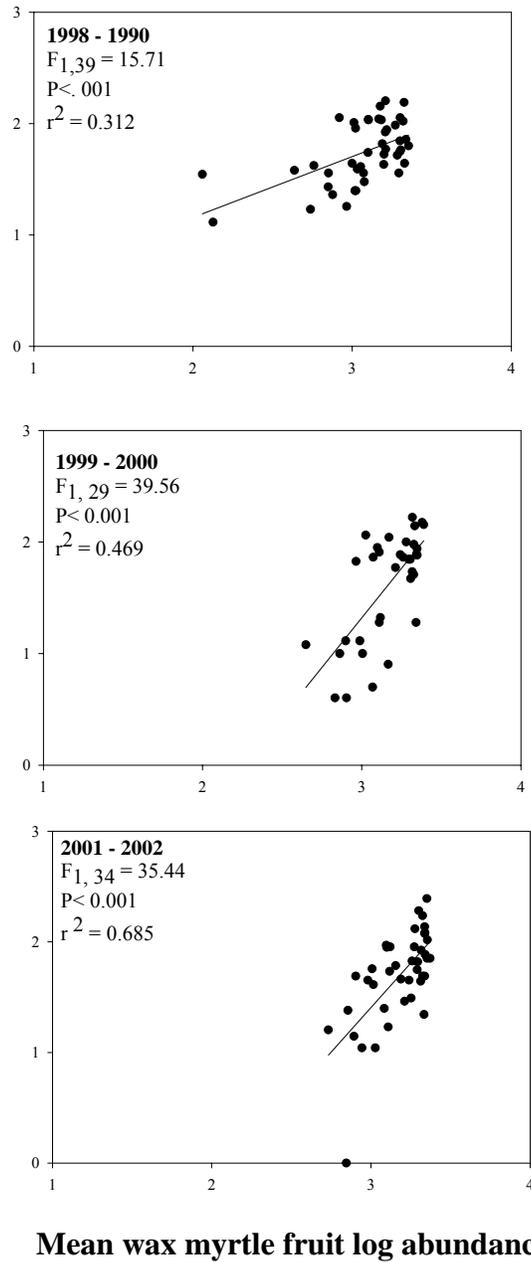
Figure 1-4. Relationship between wax myrtle fruit and myrtle warbler abundance in scrub habitat for three individual years. Data are presented on a log scale. Individual points are the sum of warbler numbers detected/transect/count and wax myrtle fruit abundance is the mean log number of wax myrtle fruit/transect/count multiplied by the mean number of individuals/transect (see text for further details).
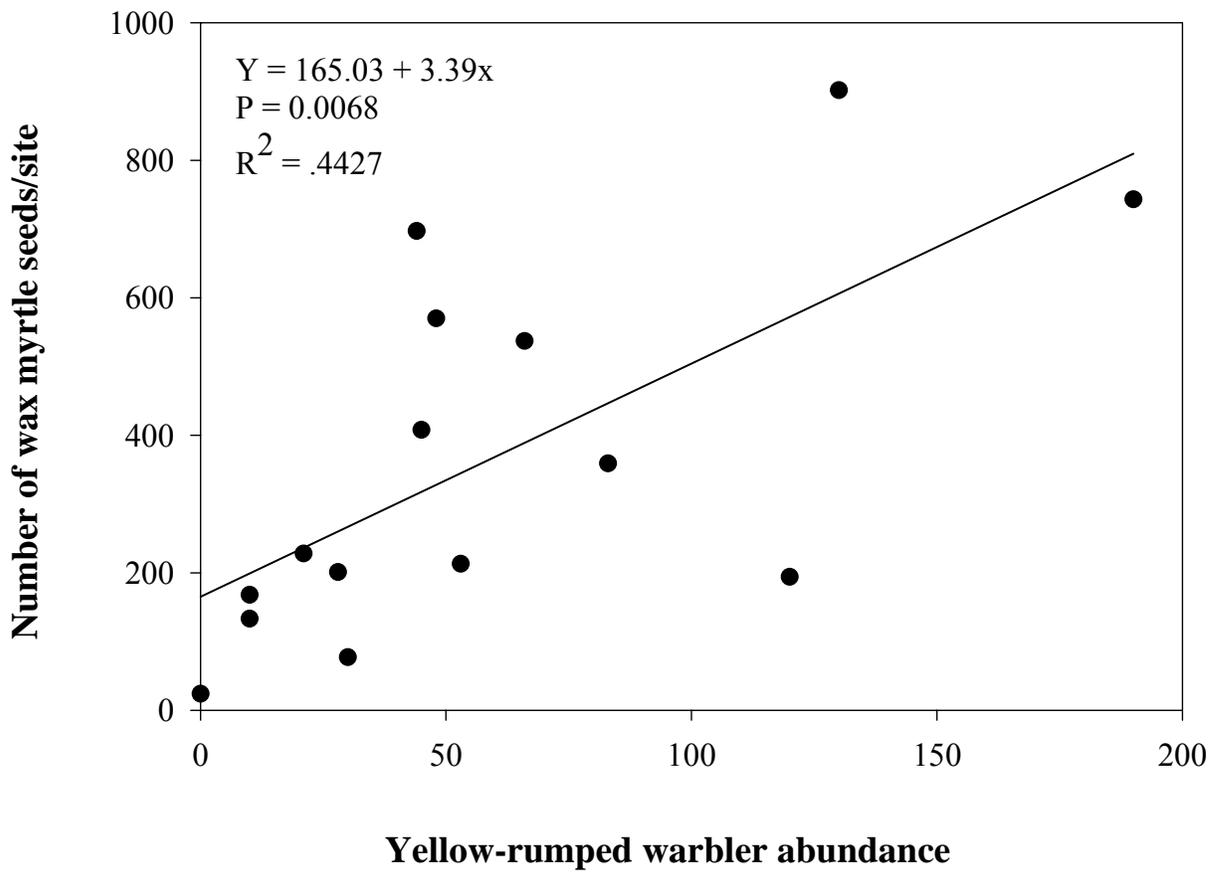
Figure 1-5. Relationship between the total number of wax myrtle seeds captured in seed traps in scrub habitat and the number of myrtle warblers detected at the same sites during the same period as seed capture. Data points represent individual counts.

Chapter 2: Spatial and temporal contributions of seed dispersal, seed predation and seedling survival to wax myrtle (*Myrica cerifera*) recruitment

Abstract

Recently have ecologists begun to investigate the multiple factors affecting plant recruitment rather than focusing on just one recruitment stage. However, the effect that time and habitat of deposition both have on recruitment of fruiting plants has received little attention. Here I present data on seed dispersal of wax myrtle (*Myrica cerifera*) during six months of a single seven and a half month long dispersal season on Assateague Island National Seashore and the seed predation and seedling survival rates associated with time and habitat of deposition (salt grass meadow, scrub, and forest). I indicate how microsite variables influenced the within habitat rates of deposition, seed predation and seedling survival. These data were then used to interpret the causes of that season's seedling recruitment in each habitat.

Wax myrtle seed was dispersed throughout the season and into all habitats. By the conclusion of the season, scrub sites received more seed than either of the other habitats. Seed dispersal in scrub and meadow was consistently influenced by the presence of fruiting conspecifics, but location of dispersal throughout the season was random in forests. Seed predation rates within and between habitats changed over time. Most notable was the significant reduction in seed predation rates of wax myrtle seeds after December in meadow habitat and the strong increase in predation rates in forests during the same time. Seed predation in scrub remained consistent and

was strongly associated with abundance of fruiting conspecifics. Seed germination and seedling survival in rodent exclosures were unaffected by time of experimental seed deposition. However, a greater percentage of seeds survived their first summer in scrub habitat. In spite of differences in seed rain and experimental seedling survival, natural seedling abundance did not differ between scrub and meadow habitats. Meadows had a significantly greater seedling:seed ratio because of spatial concordance between seed and seedling stages in meadows and spatial discordance in scrub. These data demonstrate that wax myrtle recruitment is increased by seed dispersal throughout its entire season and highlight the importance of considering multiple recruitment stages, multiple habitats and time periods when assessing seedling recruitment.

Introduction

Seed dispersal by avian and mammalian frugivores is considered central to the population dynamics of animal dispersed plants, determining the density, shape and extent of seed shadows (Howe and Smallwood 1982, Gorchov *et al.* 1993, Schupp 1993, Herrera *et al.* 1994, Wenny 2000, Garcia 2001, Howe and Miriti 2004), which are considered the template for future recruitment (Schupp and Fuentes 1995). Although seed rain may generally conform to a leptokurtic curve (e.g. Willson 1992, Clark et al. 1998), seed dispersal can occur at substantial distances from the parent plant (Erickson and Hamrick 2003, Fragoso 2003, Levin et al. 2003) and has been shown to be influenced by a wide array of microsite variables, varying in importance with disperser species (Sorensen 1981, Jordano 1992, Schupp 1993, Calvino-Cancela

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2002). The significance of seed dispersal is illustrated by the frequency of reports of

seed limitation in a wide variety of systems (Rand 2000, Turnbull et al. 2000, Dalling

et al. 2002, Jordano and Godoy 2002, Muller-Landau 2002), the positive correlation

between the number of seeds deposited and the seedlings appearing at a site (Hughes

and Fahey 1988, Debussche and Lepart 1992, Herrera et al. 1994, De Steven and

Wright 2002) and the evidence that deposition patterns can be responsible for the

distribution of adults (Fragoso 1997, Rand 2000, Aukema and Martinez del Rio 2002,

Svenning and Skov 2002).

However, plant recruitment is a multistage process and seed shadows can be

substantially altered by the subsequent impact of seed predators and of differential

survival of seedlings and juveniles (e.g. Willson 1989, De Steven 1991, Crawley

1992, Herrera et al. 1994, Rey and Alcantara 2000, Wang and Smith 2002).

Although some general patterns have emerged (e.g. Janzen 1970, Connell 1971), the

effect of these post-dispersal factors on recruitment frequently varies with seed

species, habitat, microhabitat and year (Janzen et al. 1976, Wellington and Noble

1985, Howe 1990, Bazzaz 1991, Gill and Marks 1991, Crawley 1992, Clark et al.

1999, Diaz et al. 1999, Hulme 2002). Nor are the habitats and microhabitats that best

contribute to the completion of one stage necessarily the best for another, an

uncoupling that can result in spatial discordance between seed and seedling stages,

with substantial implications for the numbers and spatial distribution of recruits (Gill

and Marks 1991, Herrera et al. 1994, Schupp 1995, Schupp and Fuentes 1995, Forget

1997, Rey and Alcantara 2000).

Therefore, only if the combined effects of seed dispersal, predator escape and seedling survival are considered is it possible to understand the workings of plant population dynamics and the relative importance of dispersal, escape and survival (Herrera et al. 1994, Jordano and Herrera 1995, Schupp and Fuentes 1995, see also Muller-Landau 2002). However, in spite of a growing trend to consider multiple variables when investigating the population dynamics of animal dispersed species and evidence that ecological conditions may change over time (Johnson 2004), relatively few studies (e.g. Willson and Whelan 1990, Forget et al. 1998) have addressed how time of dispersal impacts recruitment. The effect of habitat on the relative stages of recruitment has rarely been investigated by using large samples sizes at replicated sites (Clark et al. 1999, Nathan and Muller-Landau 2000).

The objective of this study was to determine the relative influences of seed dispersal, seed predation and seedling survival on the recruitment of wax myrtle, a shrub commonly found on barrier islands along the Atlantic coast of the United States. Although the population dynamics and ecology of this species have been investigated from a variety of perspectives (Sande and Young 1992, Young et al. 1995, Crawford and Young 1998, Shao et al. 1998, Wijnholds and Young 2000), no previous study has addressed which factors actually promote or limit recruitment. Because wax myrtle is found in different habitat types and because its seeds are dispersed during a seven and a half month period (late September – April), wax myrtle provides an opportunity to assess how the relative effects of post-dispersal stages are likely to change between habitat and time of deposition. A better understanding of the population ecology of this species is of further interest because

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of its role in vegetative succession on barrier islands (e.g. Levy 1983) and because its

fruits are an important food source for passerines wintering along the coast, in

particular the wax myrtle specialist, the myrtle warbler (Chapter 1). Further, only by

identifying the factors influencing wax myrtle recruitment is it possible to compare

the relative contributions provided by different disperser species (Herrera et al. 1994,

Jordano and Herrera 1995, Schupp and Fuentes 1995, Rey and Alcantara 2000) (see

Chapter 3). The specific questions addressed in this study are: (1) What are the

temporal and spatial patterns of seed deposition at both habitat and microsite scales?

(2) Do the time and/or habitat/microhabitat of deposition significantly affect the

likelihood of seed predation and of seedling survival? (3) Is there evidence of spatial

discordance between recruitment stages?

Methods

Natural History of Wax Myrtle

Wax myrtle, a frequent understory component of longleaf and slash pine

forests throughout the southeastern US (e.g. Pearson *et al.* 1987), is also a common

dioecious shrub on barrier islands along the Atlantic coast of the United States. This

woody pioneer of newly stabilized soils plays an important role in vegetative

succession (see also Morris 1974, Collins and Quinn 1982, Young et al. 1995, Day

1996, Crawford and Young 1998). Its establishment follows shoreline accretion

(Shao et al. 1998), and eventually develops into dense thickets. In concert with its

abundant actinomycete partner, *Frankia*, wax myrtle enriches nutrient-poor soils

(Levy 1983, Young et al. 1992, Wijnholds and Young 2000), and its branches provide

perches for avian seed dispersers (see McDonnell and Stiles 1983), aiding in both the

deposition and recruitment of other woody species. These subsequent, heterospecific

immigrants eventually replace wax myrtle and its recruitment in individual habitat

patches declines as thickets mature and senesce (Young et al. 1995). Eventually,

maritime forests dominate these patches where wax myrtle recruitment is rare (Levy

1983). Abiotic factors like freshwater availability and salinity also limit

establishment and survival of wax myrtle seedlings and adults (Young 1992, Young

et al. 1992, Shao et al. 1998, Day et al. 2001). Although adults may survive brief

pulses of salinity due to storm surge (Young et al. 1995), long-term elevation of soil

salinity frequently devastates wax myrtle in affected areas (Conner 1995, Tolliver *et

al.* 1997, Conner and Inabinette 2003). While there is little evidence of herbivory on

adults, herbivores may limit wax myrtle seedling distribution in some habitats

(Barimo and Young 2002).

Wax myrtle fruit is a wax-covered drupe and individual females on

Assateague Island commonly produce >1000 berries and sometimes >10,000 fruits.

These are persistent and seeds are dispersed on Assateague Island over seven and a

half months, between late September and late April (Chapter 1). Fruit quality does

not appear to decline during this period, although germinability declines 9 months

after fruit presentation (Erickson and Hamrick 2003), suggesting that seed banks are

not a significant source of recruits; pre-dispersal predators inflicted minimal damage

to crops prior to fruit removal (Lowe, pers. obs.). There is no evidence for masting or

substantial between-year variation in fruit abundance in this species.

General

I selected sites in three major habitat types on Assateague Island, representing three distinct seral stages (salt grass meadow, scrub, forest) to document the effect of time and habitat on wax myrtle seed dispersal as well as the rates of seed predation and seedling survival associated with deposition in these habitats and at different times. By pooling data from each habitat, I also measured the influence of microsite vegetative composition and structure on dispersal, predation and seedling survival. Each habitat type was replicated three times (a total of nine sites) and replicates were >2 km distant to promote independence. Sites were judged to be typical of each habitat type. However, given the highly patchy nature of vegetation communities on Assateague Island, no habitat location was uniform in its vegetative composition or structure. Meadow sites, containing the most recently stabilized soils and occasional woody pioneers, were characterized by abundant *Spartina patens*, interrupted by infrequent islands of wax myrtle and *Baccharis halimifolia*. Shrub habitats, an intermediate stage along the chronosequence, contained large numbers of wax myrtle adults interspersed with poison ivy (*Toxicodendron radicans*) , *B. halimifolia* and occasional loblolly pines (*Pinus taeda*). Loblolly pine dominated the overstory of the forest sites, the oldest seral stage, and *Smilax* spp. were abundant in the understory, occurring as both thickets and lianas; wax myrtle and *Vaccinium* were also present.

At each site, a 100 m X 100 m (1 hectare) grid was established. Seed traps (n = 100) were attached to the ground every 10 m on this grid. Seed predation and seedling survival experiments were placed within 10 cm of seed traps, allowing for prediction of the fate of seeds deposited at that particular location at different time

periods. Special care was taken not to disturb the vegetation structure of these sites.

To determine the influence that different microsite vegetation parameters had on

dispersal, predation and seedling survival, I recorded the number of wax myrtle

female individuals (Females) as well as the sum of the number of males and non-

Myrica shrubs (Other Shrubs) within a 1m radius circle centered around each trap at

all sites (hereafter Circles). I also estimated the vertical vegetative profile

(Vegetative Density) by placing a 2m pole vertically in the center of the trap and at 4

separate randomly determined locations along the circle perimeter. I recorded

whether or not vegetation touched the pole in 5 height strata (<0.5 m, 0.5 m - .99 m, 1

m – 1.49 m, 1.5 m – 2 m, >2 m). Strata where vegetation touched the pole received a

1, untouched strata received a 0, so each stratum in a Circle could have a score

ranging from 0 - 5 and total Vegetative Density scores of an individual Circle could

range between 0 – 25.

Seed Deposition

Seed traps (n = 100) at each site were constructed of a 28 X 56 cm flat with a

slotted bottom to facilitate drainage. A lining of plastic screen prevented seed loss

through the bottom and a hardware cloth top excluded rodents but allowed seed entry.

Seed traps were set in place on November 17, 2001. The number and species of all

seeds and all whole fruits were recorded at 6 different time periods, ranging between

22 and 30 days, until April 30, 2002. Only wax myrtle seed data will be presented

here. Because time between data collection periods varied, I calculated the number of

seeds deposited/day to allow comparison of seed deposition rates over time.

Although bayberry (*M. pensylvanica*) also occurs on Assateague Island, I assumed that all *Myrica* seeds recovered were wax myrtle because bayberry fruit abundance was negligible by early November due to fruit consumption and relatively low numbers of individuals (Chapter 1). After each trap inspection, all fruit and seeds contained in each trap were placed in a plastic bag and removed from the site, so as not to influence ongoing seed predation experiments.

To determine whether habitats differed in the total number of wax myrtle seeds received, I compared the sum of different habitat types with ANOVA, using square root transformed data to meet assumptions of normality and homoscedasticity; independent mean comparisons were made using Least Significant Difference (LSD) tests. I also tested whether habitats differed in the total number of traps that contained at least one seed by the end of the season, using ANOVA and LSD tests for subsequent multiple comparisons; no data transformation was necessary. I used repeated measures analysis (Proc Mixed, SAS Institute 1999) with a first-order autoregressive covariance structure [AR(1)] suitable for approximately equally spaced time periods (see Littell et al. 1996), to compare the numbers of wax myrtle seeds deposited over time in different habitats. These data were log transformed to meet assumptions. Multiple comparisons were made using the Tukey-Kramer test.

The influence of microhabitat composition on the number of seeds deposited within habitats was assessed by using stepwise logistic regression on seed trap data in each time period. Females and Other Shrubs were the independent variables in regression analyses used for all habitats. Vegetative Density was also added to regression models for forest habitat data because much of the understory structure

was due to *Smilax* whereas wax myrtle and other woody shrubs were the primary

determinants of structure in scrub and meadow habitats.

For this analysis, I assumed that the number of seeds deposited in any

individual trap was independent of the number deposited in other traps, and so pooled

all data from replicate sites. Such an assumption may be questionable if dispersers

maintained coherent flocks during the period of data collection or if individual traps

were close together. However, myrtle warblers, the primary disperser during this

time (Chapter 1), form only very tenuous, opportunistic associations (Lowe, pers.

obs.). Because the movement and foraging behavior of individuals appeared casually

influenced by other conspecifics and because individual traps were located at a

minimum distance of 10m, this assumption of independence seems reasonable.

Seed Predation

To determine the rate of predation of dispersed seeds, I placed screen cones

containing 10 manually depulped seeds at fifteen trap locations on each of the nine

grids in three time periods (every 50 days): December 19, January 28, and March 18.

Cones were located systematically on each grid. In December, cones were placed

next to each trap in the second column of the grid and next to every other trap in the

third column. Cones in January were placed beside each trap in the fifth column and

beside alternating traps in the sixth. This pattern was the same for seed cone

placement in March in the eighth and ninth columns. Because subsequent analysis

with Kruskal-Wallis confirmed that there was no significant difference in vegetative

variables between the columns used for the different time periods within habitats

(Lowe, unpub. data), I am confident that the test for a time effect is not confounded with either vegetation or edaphic differences associated with column location and this non-random methodology.

Screen cones were used because they were judged to be both less conspicuous than the frequently used Petri dishes or trays (e.g. Casper 1987, Kollman et al. 1998, Traveset et al. 2003) and less susceptible to flooding. Each cone was approximately 5 cm tall and had an opening with a diameter of approximately 2.5 cm. I placed each cone in a small depression that had been dug into the soil at least four days earlier so that the top of the cone extended approximately 6 mm above the lip of the depression. The cone was filled with soil so that soil level in the cone was comparable to the level outside and seeds were placed within. By digging depressions prior to placement of seed cones, I hoped to reduce the likelihood that rodents would associate soil disturbance with a food reward. All cones were planted within 10 cm of seed traps. Extra care was taken however to not disturb these sites during the subsequent collection of seed trap data.

On April 30, by which time wax myrtle seeds had germinated, I recorded whether seeds remained in each cone. Because rodent seed predators have been shown to consume the vast majority of seeds that they encounter (e.g. Webb and Willson 1985, Hulme 1996), I recorded only whether seeds were absent or present. Cones that were either trampled by horses or that had disappeared because of flooding were not included in the analysis. Otherwise, I concluded that missing seeds were the result of seed predators; intact cones without seeds were commonly surrounded by shell fragments indicating rodent predation.

To measure the effect of habitat and time of deposition on seed predation rates, I compared the percent of individual cones whose contents were uneaten, testing for the effect of habitat, time, and habitat X time interaction. These data, transformed by an arcsine-square root transformation, were analyzed as a split plot with ANOVA (Proc Mixed, SAS Institute 1999). Habitat was the whole plot and time periods were the subplots. Multiple comparisons were made using the Tukey-Kramer test.

I used stepwise logistic regression (SAS Institute 1999) to determine the effect of microsite vegetative variables on the likelihood of seed predation in different habitats, pooling all data from each habitat type; as above, I assumed that the fate of individual cones was independent because all cones were a minimum of 10m apart. Female abundance and Other Shrubs were the two microsite variables entered into the model in all habitats, and Vegetative Density was also used for forest site data.

Seedling survival

I tested the effects of habitat and of time of deposition on seedling survival by planting seeds in meadow, scrub and forest sites in three time periods (every 50 days): December 19, January 28 and March 18. Two days prior to planting, I collected fruits from 5 different individual females and manually removed the waxy exocarp covering the seed. Because there is no significant difference between the germination rate or time of manually depulped wax myrtle seeds and frugivore-voided seeds (Chapter 3), I assume that germination rates of these seeds are similar to those dispersed by frugivores. Seeds were then mixed in a paper bag to ensure

random assignment to the different habitats. On each day, I placed 50 seeds at 5

locations in each habitat replicate; in December seeds were placed beside every other

trap in column 3 of the grid, by traps in column 6 in January, in March by column 9.

As above, analysis indicated that there were no systematic edaphic changes associated

with columns along grids. Seeds were placed on the mineral soil to remove

previously deposited seeds and to anchor adequately the hardware cloth exclosure (3

X 4 X 3 inch) that prevented rodent access. No exclosure showed signs of rodent

entrance. The top and sides of the exclosure were covered with nylon screen to

prevent access by seeds subsequently dispersed by frugivores and to prevent seeds

from being washed away in the case of local flooding. Screen on the top of the

exclosure was removed in late April after the conclusion of the seed dispersal season.

The percentage of seedlings surviving in each exclosure was recorded in August

2002.

I tested the effect of habitat and time of deposition on percent of seedlings

surviving, by analyzing these data as a split plot, using Proc Mixed (SAS Institute

1999) as well as determining whether habitats differed in the number of circles in

which seedlings survived. I also tested the effect of microsite variables on percent

survival in all habitats by pooling data from each replicate and using stepwise logistic

regression. The explanatory variables used were those in the seed dispersal

regression above: Females, Other Shrubs for all habitats, and also Vegetative Density

for Forest sites. I assume that results from exclosures at individual sites are

independent due to the distance between exclosures ($\geq$15 m).

To determine the actual seedling abundance in each habitat, I surveyed seedling abundance in each Circle. Because wax myrtle can reproduce vegetatively via rhizomatous shoots (Thieret 1966), I confirmed seedling status by pulling up potential seedlings. I tested for differences in abundance between habitats by using ANOVA on log transformed data. I tested for microsite effect with stepwise logistic regression on data from scrub and meadow habitats, using the same variables employed above; seedlings appeared in too few Circles in forest habitat to perform analysis.

Results

Seed Deposition

Wax myrtle seeds were widely dispersed on Assateague Island, landing in all three habitat types (meadow, scrub and forest) throughout the entire period of data collection (November 7 - April 30), approximately 80% of the actual dispersal season. After relatively low levels of seed rain during the first dispersal period (November 7 – December 9) in all habitats, seed deposition rates remained high well into spring, dropping noticeably only in April (Figure 2-1).

Repeated measures analysis of the numbers of seeds deposited into meadow, scrub, and forest habitat over time showed a significant time X habitat interaction (Table 2-1). This interaction appears to be due to a very low rate of seed deposition in forest traps during the first time period. This was confirmed when a second repeated measures analysis was conducted without the November – December data, in which the interaction term was no longer significant and the main effects were

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highly significant ($P < 0.01$); contrasts of these data indicated that all habitats consistently received different ($P < 0.05$) numbers of wax myrtle seed: scrub > forest > grass.

Using the full data set, multiple comparison of seed rain between habitats indicated that with the exception of the first and last collection periods, wax myrtle seed rain was always significantly greater in scrub sites than in either of the other two habitats, which never differed significantly from each other (Table 2-2).

Within-habitat comparisons indicated that the number of wax myrtle seeds deposited in all habitats varied, but remained relatively constant throughout this period (Table 2-3). Significant differences among time periods most evident toward the end of the period of seed deposition in late April for both scrub and forest habitats. In contrast, there was no significant difference in the amount of wax myrtle seed that meadow habitats received between time periods.

The number of traps at forest and scrub sites receiving wax myrtle seeds changed among time periods (Table 2-4), yet regression analyses of the influence of microsite vegetation on the number of seeds deposited in individual traps appeared relatively consistent among time periods in all habitats (Tables 2-5, 2-6). Abundance of female wax myrtle individuals within one meter of the trap consistently had a significantly positive effect on deposition in meadow and scrub habitats; occasionally the presence of other shrubs was significant as well. In contrast, in only one period did any variable explain the presence of wax myrtle seed rain at forest sites. During April, Vegetation Density significantly increased seed deposition in forests ($X^2 = 4.02$, $P < 0.05$, Point Estimate = 1.13).

Habitats differed significantly in total numbers of seeds deposited ($F_{2,6}$ = 10.06, $P < 0.05$). Scrub habitats received significantly more seeds than either meadow ($P < 0.005$) or forest sites ($P < .05$), which did not differ significantly in their total seed rain (Figure 2-2). Analysis of the mean percentage of traps receiving at least one wax myrtle seed indicate that the seed rain differed spatially among habitats ($F_{2,6}$ = 30.47, $P < 0.001$) (Figures 2-3, 2-4, 2-5). Significantly fewer traps in salt grass meadows received any seeds than in either scrub or forest sites.

Seed Predation

Analysis of predation rates of experimentally dispersed seeds showed a highly significant time X habitat interaction (Table 2-7, Figure 2-6). Comparison of escape rates of wax myrtle seeds between habitats over time revealed no difference in survivorship for seed deposition in December (Table 2-8). However, rates did differ significantly between habitats in the two subsequent time periods.

Comparison of seed escape rates over time within habitats revealed two different trends (Table 2-9). Likelihood of avoiding predators in scrub habitats did not change significantly between times, displaying an overall rate of 60.9%. In contrast, the likelihood of escape from predators was dramatically different between time periods for seeds deposited in meadows and forests. Seeds deposited in December in both habitats differed significantly in probability of escape from those deposited subsequently, but the trends were opposite. Seeds deposited in forest habitats in December enjoyed an initial 88 ± 8.5 % escape rate, which dropped to 34

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± 4%. In meadow habitats, only 52 ± 7.8 % of seed cones deposited in December were not attacked, but 95 ± .4 % for seeds deposited in later months survived.

The influence of microsite vegetative variables on seed predation differed between sites (Table 2-10). Density of vegetation in forest habitats increased rates of wax myrtle seed predation while the presence of heterospecific shrubs reduced it to a lesser extent. In scrub habitats, the presence of female wax myrtle adults significantly increased predation rates. No microsite variable measured affected predation rates in meadow habitats.

Experimental Seedling Survival

The mean number of seeds that germinated and survived their first summer was very low in all habitats. The time of experimental deposition played no significant role in the likelihood of seeds germinating and surviving until August ($P >$ 0. 05). However, the habitat in which seeds were placed did significantly affect the likelihood of survival ($F_{2,6} = 8.37$, $P < 0.05$). A significantly greater percentage of seeds deposited into scrub habitats survived their first summer than those in either meadow or forest habitats. Survival rates were not significantly different between forest and meadow habitats (Figure 2-7). However, habitats did not differ in the number of Circles that contained at least one seedling ($P > 0.2$).

Although microsite vegetation had no significant influence on the likelihood of seeds to germinate and survive their first growing season in scrub or forest habitats, the presence of Other Shrubs significantly improved the likelihood of survival in meadow habitats (Wald $X^2 = 4.01$, P < 0.001, Point Estimate = 2.234).

Seedling abundance

Wax myrtle seedlings were relatively rare in all three habitats on Assateague Island, yet density of seedlings differed significantly between habitats ($F_{2,6} = 8.47$ $P < 0.05$) (Figure 2-8). Independent contrasts showed that forests had significantly fewer seedlings than either scrub or meadow habitats. Meadow and scrub habitats were also similar in that seedlings tended to have a clumped distribution (Figures 2-3, 2-4). Although no microsite variable was a significant explanatory factor in seedling abundance in either forest or scrub sites, stepwise logistic regression indicated that abundance of Females increased the likelihood of seedling presence significantly (Wald $X^2 = 11.91$, $P < 0.001$, Point Estimate = 1.24) in meadow habitat.

Seedling:seed ratios from the three habitats were significantly different ($X^2 = 205.3$, $P < 0.0001$). Subsequent pair-wise comparisons demonstrated that ratios from all three habitats differed significantly from each other (Table 11, Figure 2-9).

Discussion

Seed Dispersal

Seed deposition occurred throughout the entire study period in all habitats. After early December, a period characterized by low seed dispersal in all habitats, the differences in the number of seeds that each habitat received were consistent, suggesting constancy in relative habitat use over time by seed dispersers. Similarly, the number of seeds deposited in each habitat was relatively uniform over time after December, as well. This uniform rate of dispersal well into spring is consistent with

the relatively large number of myrtle warblers present and their heavy use of wax myrtle between autumn and spring (Chapter 1).

Although the number of traps containing wax myrtle seeds also changed significantly over time in both forest and scrub sites, the vegetation characteristics of the microsites into which seeds fell did not change substantially. Greater abundance of female wax myrtle individuals always increased seed deposition in scrub and meadow sites; the presence of heterospecific shrubs was also an occasional factor in both habitats, indicating the importance of perches to deposition. In contrast, seed deposition in forest sites was always random, unaffected throughout the study season by any of the understory variables measured, a result attributed to the abundance of perches provided by the nearly ubiquitous canopy cover. These trends are largely consistent with previous work that has emphasized the positive effect on seed deposition at a microsite level of both fruiting plant abundance (Herrera and Jordano 1981, Hoppes 1988, Murray 1988, but see Willson and Crome 1989, Izhaki et al. 1991, Debussche and Lepart 1992, Herrera et al. 1994, Alcantara 2000, Aukema and Martinez del Rio 2002, Traveset et al. 2003) and perch availability (McDonnell and Stiles 1983, Debussche and Isenman 1994, Wenny and Levey 1998, Alcantara 2000, Jordano and Schupp 2000, Rey and Alcantara 2000).

By the end of April, habitats differed significantly in the total numbers of seeds they had received and in the number of traps that had received seeds, as seen elsewhere (Jordano and Herrera 1995, Calvino-Cancela 2002, Muller-Landau 2002). Scrub habitats, characterized by high wax myrtle abundance, received significantly more seed than did either forest or meadow sites which both contained low levels of

wax myrtle adults. These results are consistent with previous studies that have reported a positive relationship between seed rain and fruiting plant abundance at a habitat scale (Hoppes 1987, but see Forget 1992, Jordano and Herrera 1995, Kollman and Pirl 1995).

Similarly, as seen elsewhere, habitats differed in the number of traps containing seeds (Clark et al. 1998, Muller-Landau 2002). Seed shadows in forest and scrub habitats were both more extensive than those in salt grass meadows. Although source limitation, resulting from low abundance of fruiting plants, can be responsible for limited seed dispersal (Clark et al. 1998, Muller-Landau 2002), regression analyses strongly suggest that limited dispersal, due to low perch availability, was the cause (Table 2-6, see also Dalling *et al.* 2002). Woody plants occurred in only 9% of Circles at meadow sites.

Together, these data indicate two important points. First, the relative consistency of the seed deposition patterns over time at the habitat and microhabitat scale, in conjunction with low interannual variability of fruit abundance (Chapter 1), suggest that the spatial patterns and quantity of wax myrtle seed rain may not vary widely between years (Schupp 1995, see Calvino-Cancela 2002, Traveset et al. 2003). One weakness of these data is the fact that deposition patterns were not measured in the first 6 weeks of the dispersal season. However, because myrtle warblers dispersed the vast majority of seeds in all months over 3 years and because their habitat use appears relatively consistent (Lowe, unpub. data), seed rain in this unmeasured period may not be substantially different. Second, at the end of the seed dispersal season, each habitat contained very different seed shadows. Wax myrtle

seeds in meadow habitats were rare and clumped beneath female adults and to a lesser extent around heterospecific shrubs. In scrub habitat, seeds were numerous, widely scattered, but concentrated beneath female plants (Table 2-5), while wax myrtle seeds in forest habitat were rare, widespread and randomly distributed, an artifact of the tendency of dispersers to perch in the abundant over story.

Seed Predation

Post-dispersal predation rates of wax myrtle seeds were significantly influenced by both time of deposition and habitat. In the absence of observations and rodent trapping, I can only speculate about the identity of wax myrtle's seed predators. However, only occasional evidence of wax myrtle consumption by several granivorous sparrows (e.g. *Melospiza georgiana*, *M. melodia*, *Zonotrichia albicollis*) and the high frequency of seed coat fragments observed near cones strongly suggest that rodents were the most important seed predator (Herrera et al. 1994, Garcia 2001).

The strong time X habitat interaction demonstrates that here, as frequently in other systems, escape from granivores has a temporal as well as spatial component (Schupp and Frost 1989, Forget 1992, Hulme 1994, Diaz et al. 1999, Yamashita et al. 2003). This demonstration that predation rates can change significantly over only 50 days on Assateague Island indicates that estimates of predation over even a short period that are based on a single sample in time are inadequate (e.g. Gill and Marks 1991, Herrera et al. 1994, Jordano and Herrera 1995, Hulme 1996, Rey and Alcantara 2000, Diaz 2001, Calvino-Cancela 2002).

Although post-dispersal predation rates may vary unpredictably (Whelan et al. 1991), the change in predation rates over time and habitats on Assateague Island presented clear patterns. Likelihood of predation within scrub habitats did not vary over time, but seed predation rates in both meadow and forest habitats changed dramatically after the first experimental deposition (early December). Seeds deposited in forests in late January and March were 40% less likely to escape than those in December, while later deposition at meadow sites led to the escape of over 90% of seed cones. Analysis of predation rates between habitats at different time periods showed that after no initial difference in predation pressure, seeds deposited in meadows always had the highest survival rate in January and March and forests the lowest. Predation rates in scrub habitats were not significantly different from forest sites in January or from meadow sites in March.

The trends in predation rates over time in both scrub and forest habitats appeared to be strongly affected by temporal changes in food abundance as frequently observed in other systems (Webb and Willson 1985, Willson and Whelan 1990, Forget 1992, Bowers and J. L. Dooley 1993, Hulme 1993, Kollman et al. 1998).

In scrub habitat, a relatively steady rate of seed deposition was matched by an unvarying rate of seed predation. The importance of wax myrtle seeds to granivores was indicated by the positive effect wax myrtle female abundance on predation likelihood (Table 2-10), suggesting that seed predators act in a density-dependent manner consistent with the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) and concentrate foraging activities in areas of greatest seed deposition (see also Janzen et al. 1976, Becker and Wong 1985, Webb and Willson 1985, Kitajima and

Augspurger 1989, Bustamante and Simonetti 2000), a pattern seen also in primate

dispersed seeds (Hallwachs 1986). Although post-dispersal predator satiation has

been documented under fruiting plants (De Steven and Putz 1984, Courtney and

Manzur 1985, Wellington and Noble 1985, Willson and Whelan 1990, Forget 1992,

Crawley and Long 1995, Alcantara 2000) and may be likely to occur in habitats

dominated by one species (Curran and Webb 2000, Hulme 2002), the high rate of

consumption of experimental seed depots suggests that predators in scrub habitat

were not satiated (see also Kwit et al. 2004).

In contrast, there was no relationship between rates of wax myrtle seed

deposition and predation rates at forest sites. Instead, the relatively low rates of wax

myrtle seed predation in this habitat, which coincides with the time of loblolly seed

deposition (Burns and Honkala 1990), appear to be due to the presence of an alternate

food source for granivores (Thompson 1985). Although the use of loblolly seeds by

granivores on Assateague was not investigated, loblolly seeds are a common food

source for granivorous rodents (DeSteven 1991), as are other conifer seeds elsewhere

(e.g. Abbott and Quink 1970, McCracken and Hunter 2001, Cote et al. 2003). The

increased rates of seed predation seen in late January and in March may thus be due

to a subsequent drop in pine seed abundance due either to depletion of the crop or to

the escape of the remaining seeds in litter (Crawley 1992, Myster and Pickett 1993,

Yamashita et al. 2003). Because interannual variation of seed production by loblolly

pines is not dramatic (Burns and Honkala 1990) and because rodent preferences

display little interannual variability (Kollman et al. 1998), I suspect that, as in scrub

habitats, predation likelihood associated with different time periods would be relatively constant between years.

Predation rates in pine forest microsites were significantly increased by vegetation density which itself had only a slight effect on seed deposition, suggesting that granivores favored these microhabitats which would provide the greatest protection from predators (Rood and Test 1968, Schupp and Frost 1989, Simonetti 1989, Gill and Marks 1991, Kollman and Pirl 1995, Hulme 1996, Diaz et al. 1999, Trejo and Guthmann 2003) – a sensible tactic because great horned owls are present in all forest sites (Comrich et al. 2002). The reduction in seed predation associated with heterospecific shrubs was likely due to the fact that these shrubs tend to grow in the less dense areas of the forest sites which are generally dominated by thickets of *Smilax* species.

Potential explanations for the decrease in predation rates in meadows are more problematic. Seed deposition rates were constant over time and seed rain was predictably concentrated beneath fruiting conspecifics. In contrast with forest habitat, the dominant plant species at these sites, *Spartina patens*, does not produce the large numbers of seeds that might be expected to produce such a drastic change. It is possible that seasonal changes in granivore abundance might account for observed changes (Kollman et al. 1998, Diaz et al. 1999). In the absence of small mammal trapping and surveys of granivorous birds, I am unable to evaluate this hypothesis.

Predation rates in meadow habitats were random with respect to microsite variables, demonstrating that the response of seed predators to seed shadows can differ between habitats (see also Schupp 1988). Relative rarity of both fruiting plants

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(present in only 10% of meadow vegetation circles) and low levels of seed rain in this habitat presumably made these foci of deposition both hard to find and relatively unrewarding when found for foraging rodents (Whelan et al. 1991, Hulme 1994).

Experimental Seedling Survival

Time of experimental deposition, which has influenced seedling survival in other systems (DeSteven 1991, Forget 1997), had no significant effect on the likelihood of wax myrtle seeds' germination and survival through their first growing season. This lack of a temporal effect indicates that the only impact that dispersal time has is on likelihood of escape from post-dispersal predators. Percent survival differed between habitats and was greater in scrub than either forest or meadow sites. However, because the density of seeds in exclosures was greater than the actual density of dispersed seeds at meadow and forest sites, these results must be interpreted with caution. In contrast, the number of exclosures containing at least one seedling also did not differ among habitats, indicating that the number of microsites suitable for germination and seedling survival do not differ among habitats. Given the very different conditions among habitat types, wax myrtle seedling establishment does not appear to be constrained by a narrow range of microsite requirements. Because exclosures were not monitored throughout the summer, it is impossible to determine the causes of seedling mortality during this period. I suspect, however that drought, which has been cited as a primary cause of seedling mortality in other temperate systems (DeSteven 1991, Traveset et al. 2003), was a major factor in summer mortality rates of this drought-intolerant species (Young 1992).

The low numbers of surviving seedlings in forest habitat were not surprising. Wax myrtle seeds can readily germinate in this habitat (Haywood 1994, Lowe pers. obs.), yet soils beneath a pine overstory on barrier islands tend to be poor in nutrients (Levy 1983). Further, in the understory of a pine forest, competition is likely to be intense as seedlings compete with established understory vegetation and adult pine trees for light and water. The role of pathogens in pathogens was not assessed. However, given the rarity of adult wax myrtle individuals, I suspect that the impact of pathogens was minimal. The lack of any microsite effect on survival suggests frequency of pine trees and their extensive cover created a uniformly hostile environment for seedlings throughout each site.

In contrast, the presence of heterospecific adults in meadows greatly improved the likelihood of seedling survival, presumably by ameliorating the potentially harsh conditions of salt marsh. Facilitation by heterospecifics is not uncommon (De Steven 1991, Gill and Marks 1991, Herrera et al. 1994, Pugnaire et al. 1996, Rey and Alcantara 2000). Heterospecific adults have been reported to improve seedling survivorship by reducing water loss and increasing surface water availability through "hydraulic lift" (Bustamente and Simonetti 2000). But in a salt grass meadow, a highly saline environment frequently flooded with salt water where salinity restricts recruitment (Bertness and Ellison 1987), heterospecific adults have also been shown to benefit seedlings by reducing local soil salinity through shading (Bertness 1991, Bertness and Shumway 1993). Because the recruitment (Young et al. 1994), growth (Graves and Gallagher 2003), survival (Conner and Inabinette 2003) and nitrogen fixing abilities (Young et al. 1992) of wax myrtle are all substantially reduced by soil

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salinity, this effect is likely to be of great value. Thus, the relatively low abundance of experimental seedlings in this habitat may be attributable to the low numbers of shrubs present at any site.

The fact that adult wax myrtle plants had no significant effect on seedling survival in meadow habitat is itself interesting. Numerous studies have reported a negative relationship between seedling density and proximity to adults, unrelated to seed predation (Howe 1984, Howe et al. 1985, Debussche and Lepart 1992, Herrera et al. 1994, Rey and Alcantara 2000). The absence of a negative effect on seedling survival suggests that any passive facilitative advantages adult conspecifics may have provided were countered by disadvantages associated with proximity to conspecific adults: changes in soil biota (Packer and Clay 2003), pathogen infection (Augspurger 1984, Masaki and Nakashizuka 2002) or by competition for nutrients (Clark and Clark 1984), a struggle that may be especially intense between mychorrhizal adult and seedlings (Kytoviita et al. 2003). Competition for light with adults, considered important elsewhere (e.g. De Steven and Putz 1984, Debussche and Lepart 1992, Forget 1997, Packer and Clay 2003), was not likely to be a limited resource in this habitat with low density of both conspecifics or woody heterospecifics.

Seedling abundance at scrub sites was unaffected by any microsite variable, suggesting that the relatively numerous adults in this habitat created uniform conditions (see Bustamante and Simonetti 2000). As in meadow sites, competitive disadvantages associated with proximity to adult conspecifics may have been balanced by passive facilitation.

Actual Seedling Demography

Although wax myrtle seedlings were rare at all sites, patterns of recruitment differed between habitats (see also Traveset et al. 2003). As above, habitats differed significantly in both the number of Circles containing seedlings and in mean seedling density. Seedlings occurred in a greater number of Circles in scrub than elsewhere, indicating that the spatially extensive seed shadow generated by frugivores was maintained to the seedling stage in this habitat but lost in forests. Seedling abundances between habitats were similar, except that both scrub and meadow contained more seedlings than did forest habitat – demonstrating that in this system, even large differences in seed deposition could be overcome in subsequent recruitment stages (see Jordano and Herrera 1995). This resulted in seedling:seed ratios that differed by an order of magnitude among the habitats: meadow > scrub > forest. These results are consistent with the population dynamics of wax myrtle previously reported (e.g. Young et al. 1995) and fit the expectation of lower recruitment in pioneer (meadow) than in established (scrub) habitats (Fleming and Williams 1990).

The low likelihood of seeds in forest sites to survive to become seedlings appears to be a product of the combination of high predation rates and low survivorship of escaped seeds. Yet, seed deposition in pine forests could substantially benefit parent plants in the event of tree-fall gaps or the reduction of the pine overstory via drought, beetle infestation (Lowe, pers. obs.), or fire. Although, I am unaware of any data on the effect of fire on the germination rates of dispersed seeds, wax myrtle adults are able to survive such events and to resprout vigorously (Terry

and White 1979, Taylor and Herndon 1981), but are unlikely to survive fires in successive years (Lay 1956). Seed banks, however, are unlikely to contribute substantially because germinability of wax myrtle seeds declines after nine months (Erickson and Hamrick 2003). Historically, fire may have played an important role in providing sites suitable for colonization. However, the effect of fire on wax myrtle colonization is context dependent, increasing rates in moist areas, suppressing it at more xeric sites (Richardson 1977, Bridges and Orzell 1989).

In contrast, the relative abundances of seedlings and the differences in the seed:seedling ratio between scrub and meadow habitats appear not to be determined by stage specific survival but by spatial concordance and discordance (Schupp 1995). Presence of seed rain and seedling abundance both rose with increasing wax myrtle abundance in meadow habitats, a positive relationship seen also for many other plant species, (Hughes and Fahey 1988, Herrera et al. 1994, Forget 1997, De Steven and Wright 2002). This concordance also demonstrates the importance of frugivore foraging behavior to the seedling shadow (Jordano and Herrera 1995).

At scrub sites, however, the relationship between seed rain and recruitment was negative (Augspurger 1986, Augspurger and Franson 1988, Houle 1992). This inverse relationship was caused by spatial discordance between seed rain and seed escape, both positively affected by the abundance of female adults (see also Traveset et al. 2003). Previous reports have documented spatial discordance occurring between a variety of recruitment stages (Schupp 1988, Huenneke and Sharitz 1990, Herrera et al. 1994, Houle 1998, Clark et al. 1999, Traveset et al. 2003).

Of course, spatial discordance between these stages does not necessarily impact the relative distribution of seedlings (e.g. Herrera 1984, Callaway 1992, Schupp and Fuentes 1995, Hulme 1996), especially if predators are satiated or alternate microsites are even more unsuitable. The extent to which this discordance reduces seedling recruitment in scrub is indicated by the fact that only 50% of all wax myrtle seedlings were found in the 281 circles containing a wax myrtle adult, the remaining 19 without wax myrtle contained the remainder – an effect that is due exclusively to predation and not to seedling survival. This indicates that predators play a substantial role in shaping seedling distributions, as is frequently reported in a wide variety of habitats (Bochert and Jain 1978, Inouye 1980, Davidson et al. 1984, Risch and Carroll 1986, Watkinson et al. 1989, Augspurger and Kitajima 1992, Crawley 1992, Forget 1992, Hughes 1994, Murray and Garcia-C. 2002). Escape is an important benefit of seed dispersal in this habitat (Howe and Smallwood 1982, Clark and Clark 1984, Howe 1993), but unimportant in meadows.

The primary limitation of this investigation is that these data were collected during only one seed dispersal season and so provide no measure of interannual variation (Clark et al. 1999). Although seed dispersal patterns may not display great interannual variability, seed predation patterns frequently do change between years (Ostfeld et al. 1997, Kollman et al. 1998, Traveset et al. 2003). Yet even if the relative likelihoods of escape associated with habitat, microhabitat and time of deposition reported here are not representative, they do testify to the need to sample predation rates over the course of even short seed dispersal seasons. Similarly, seedling survival and the factors affecting it can change annually (Titus and del Moral

1998, Bustamante and Simonetti 2000). However, because these results concur with the previous work on wax myrtle population dynamics, I speculate that they may be an adequate representation of what occurs in other years. Finally, it is clear that tracking the fate of seeds to the sapling stage provides more robust data on the factors affecting recruitment (Louda 1983, Schupp 1995, Balcomb and Chapman 2003). Nonetheless, conclusions drawn from seedling data may not be without value because the early stages of recruitment can be critical (Wellington and Noble 1985, Kitajima and Augspurger 1989, Rey and Alcantara 2000, Traveset et al. 2003).

Additionally, it should be noted that while these results may be describe how dispersal, predation and seedling survival affect wax myrtle recruitment on other barrier islands, different dynamics may determine recruitment patterns in inland longleaf and slash pine communities where fire has been shown to have an important impact. To determine this, further work is necessary.

Conclusion

Wax myrtle recruitment on Assateague Island benefited from seed dispersal in the 6 months that were considered in the two habitats where recruitment was most likely to occur. Seed rain was generally higher in scrub habitats than in either forests or meadows. Time of deposition influenced the likelihood of escape in forests, but less so in meadows, which provided the greatest likelihood of escape throughout the season. Seed germination and seedling survival were greatest in scrub habitats. But comparison of these data with seedling abundances indicated that meadow habitat provided the best possibility for successful seedling recruitment, due primarily to

spatial concordance between recruitment stages in meadow and spatial discordance in scrub.

The results of this study underscore the insufficiency of predicting recruitment from seed arrival and conversely the inadequacy of relying on seedling abundance to determine the recruitment potential of habitats. Understanding the mechanisms responsible for recruitment patterns requires the documentation of the spatial and temporal patterns of seed dispersal and their effect on seed predation and seedling survival when considering seedling recruitment. The results presented here also provide further evidence of the important impact that spatial discordance can have on recruitment.

Table 2-1. Repeated measures analysis of the number of wax myrtle seeds deposited per day in three different habitat types (forest, meadow, scrub) in 6 time periods of approximately 30 days (November 7, 2001 – April 30, 2002).

Effect	Numerator DF	Denominator DF	F	$P <$
Habitat	2	6.61	12.68	0.01
Time	5	29.7	11.78	0.0001
Time X Habitat	10	29.5	2.78	0.05

Table 2-2. Results from multiple comparisons of mean number of wax myrtle seeds deposited per day in individual habitat types at 6 different time periods. Traps were set out on November 7, 2001. Superscripts indicate that deposition rates/time period is significantly different ($P <$ 0.05) according to the Tukey-Kramer mean comparison test.

Time of Collection	Habitat	Mean	Standard Error
Dec. 9	Forest	0.64 [a]	0.33
	Meadow	0.71 [a]	0.69
	Scrub	7.56 [a]	2.07
Jan. 8	Forest	3.03 [a]	0.56
	Meadow	0.32 [a]	0.26
	Scrub	15.25 [b]	5.1
Feb. 3	Forest	4.94 [a]	1.58
	Meadow	0.69 [a]	0.65
	Scrub	14.71 [b]	4.1
Mar. 5	Forest	5.31 [a]	1.75
	Meadow	0.87 [a]	0.68
	Scrub	18.36 [b]	5.65
Apr. 3	Forest	3.39 [a]	1.39
	Meadow	0.71 [a]	0.70
	Scrub	18.07 [b]	7.65
Apr. 30	Forest	0.83 [a]	1.39
	Meadow	0.22 [a]	0.20
	Scrub	7.41 [a]	4.15

Table 2-3. Results from multiple comparisons of mean number of wax myrtle

seeds deposited per day in individual habitat types between time periods. Traps

were set out on November 7, 2001 and collected on April 30, 2002. Superscripts

indicate that deposition rates/time period are significantly different ($P < 0.05$)

according to Tukey-Kramer mean comparison test.

Habitat	Time of Collection	Mean	Standard Error
Forest	Dec. 9	0.64 [a]	0.33
	Jan. 8	3.03 [b, c]	0.56
	Feb. 3	4.94 [b, c]	1.58
	Mar. 5	5.31 [c]	1.75
	Apr. 3	3.39 [a, c]	1.39
	Apr. 30	0.83 [a, b]	0.29
Meadow	Dec. 9	0.71 [a]	0.69
	Jan. 8	0.32 [a]	0.26
	Feb. 3	0.69 [a]	0.65
	Mar. 5	0.87 [a]	0.68
	Apr. 3	0.71 [a]	0.70
	Apr. 30	0.22 [a]	0.20
Scrub	Dec. 9	7.56 [a, b]	2.07
	Jan. 8	15.25 [a, b,]	5.1
	Feb. 3	14.71 [a, b]	4.1
	Mar. 5	18.36 [a]	5.65
	Apr. 3	18.07 [a]	7.65
	April 30	7.41 [b]	4.15

Table 2-4. Results of repeated measures analysis indicating that the number of

seed traps receiving at least one wax myrtle seed changed significantly between

different time periods in two of the habitats sampled. The number of traps in

meadow habitat containing wax myrtle seeds did not differ significantly between

collection dates.

Habitat	Numerator DF	Denominator DF	F	*P*
Meadow	5	10	1.78	> 0.2
Scrub	5	10	11.88	< 0.001
Forest	5	10	6.08	< 0.01

Table 2-5. Results from analysis of the effect of scrub microsite variables on wax myrtle seed deposition at individual traps (n = 300) during different time periods (2001 – 2002) using stepwise logistic regression. The number of individual wax myrtle females and the number of heterospecific woody shrubs were the two explanatory variables entered into the model. Data collection began on Nov. 7, 2001.

Date	Variable	Parameter Estimate	Standard Error	X^2 Value	$P<$	Point Estimate
Dec. 9	Wax myrtle females	0.1187	0.0295	16.24	0.001	1.126
Jan. 8	Wax myrtle females	0.2068	0.0319	41.89	0.001	1.23
Feb. 3	Wax myrtle females	0.1635	0.0296	30.4616	0.001	1.178
Mar. 5	Wax myrtle females	0.1822	0.0321	32.46	0.001	1.20
	Other shrub	0.0697	0.0314	4.932	0.05	1.072
Apr. 3	Wax myrtle females	0.1717	0.0301	32.58	0.0001	1.187
Apr. 30	Wax myrtle females	0.1307	0.0279	21.91	0.001	1.14

Table 2-6. Results from analysis of the effect of meadow microsite variables on wax myrtle seed deposition at individual traps (n = 300) during different time periods (2001 – 2002) using stepwise logistic regression. The number of individual wax myrtle females and the number of heterospecific woody shrubs were the two explanatory variables entered into the model. Data collection began on Nov. 7, 2001.

Date	Variable	Parameter Estimate	Standard Error	X^2	$P <$	Point Estimate
Dec. 9	Wax myrtle females	0.3243	0.0812	15.94	0.001	1.383
Jan. 8	Wax myrtle females	0.1577	0.0769	4.203	0.05	1.17
	Other shrubs	0.2665	0.0834	10.22	0.01	1.303
Feb. 3	Wax myrtle females	0.3453	0.0863	15.99	0.001	1.412
Mar. 5	Wax myrtle females	0.1643	0.067	6.01	0.05	1.179
	Other shrubs	0.1465	0.053	7.618	0.01	1.158
Apr. 3	Wax myrtle females	0.3243	0.0812	15.94	0.0001	1.32
Apr. 30	Wax myrtle females	0.2773	0.107	6.695	0.01	1.32
	Other Shrub	0.3049	0.1118	7.43	0.01	1.357

Table 2-7. Analysis of the effects of time and habitat on the percentage of wax myrtle seeds depots escaping post-dispersal predation in three habitats (forest, meadow, scrub) at three different time periods (December 9, January 28, March 18) in 2001 – 2002 on Assateague Island.

Effect	Numerator DF	Denominator DF	F	$P <$
Habitat	2	6	2.33	0. 1
Time	2	12	3.58	0. 05
Time X Habitat	4	12	19.31	0. 0001

Table 2-8. Results of multiple comparisons of mean percentage of wax myrtle seed depots escaping post-dispersal predation (n = 15) between habitats at three different time periods on Assateague Island. Each habitat was replicated three times. Comparisons were made using the Tukey – Kramer test. Superscripts indicate significant differences ($P < 0.05$) between habitats within time periods.

Time	Habitat	% Mean Survival	Standard Error
Dec. 9	Meadow	52.2 [a]	7.8
	Scrub	63.9 [a]	9.3
	Forest	88.1 [a]	8.5
Jan. 28	Meadow	94.4 [a]	2.8
	Scrub	51.2 [b]	18.2
	Forest	30.2 [b]	8.4
Mar. 18	Meadow	95.2 [a]	4.8
	Scrub	67.6 [a, b]	11.8
	Forest	38.1 [b]	8.6

Table 2-9. Results of multiple comparison of mean percentage of wax myrtle seed depots that escaped post-dispersal seed predation between times in three different habitat types on Assateague Island. Each habitat was replicated three times. Comparisons were made using the Tukey – Kramer test and significance ($P < 0.05$) between time periods is indicated by superscripts.

Habitat	Date	% Mean Survival	Standard Error
Meadow	12/9	52.2 [a]	7.8
	1/28	94.4 [b]	2.8
	3/18	95.2 [b]	4.8
Scrub	12/9	63.9 [a]	9.3
	1/28	51.2 [a]	18.2
	3/18	67.6 [a]	11.8
Forest	12/9	88.1 [a]	8.5
	1/28	30.2 [b]	8.4
	3/18	38.1 [b]	8.6

Table 2-10. Results of stepwise logistic regression analysis of the influence of vegetative microsite variables on the percent of wax myrtle seed depots consumed by post-dispersal predators. No variables were significant in analysis of data from meadow sites.

Habitat	Variable	Estimate	Standard Error	Wald X^2	$P <$	Odds Ratio
Scrub	Wax myrtle Females	0.1449	0.0512	8.0065	0.005	1.156
Forest	Vegetation Density	0.1923	0.0797	5.822	0.05	1.212
	Heterospecific Shrubs	-0.3786	0.1819	4.3309	0.05	0.685

Table 2-11. Relationship of the number of wax myrtle seeds and seedlings from

three habitat types on Assateague Island. Data from all replicates of each

habitat type were pooled and analyzed using Chi Square. Superscripts indicate

significant ($P < 0.0001$) differences in the seedling:seed ratio between all

habitat types.

Habitat	Seed Number (%)	Seedling Number (%)	Seedling:seed
Meadow	289 (3)	38 (24)	0.13 [a]
Scrub	6845 (79)	115 (74)	0.016 [b]
Forest	1541 (18)	3 (2)	0.0019 [c]
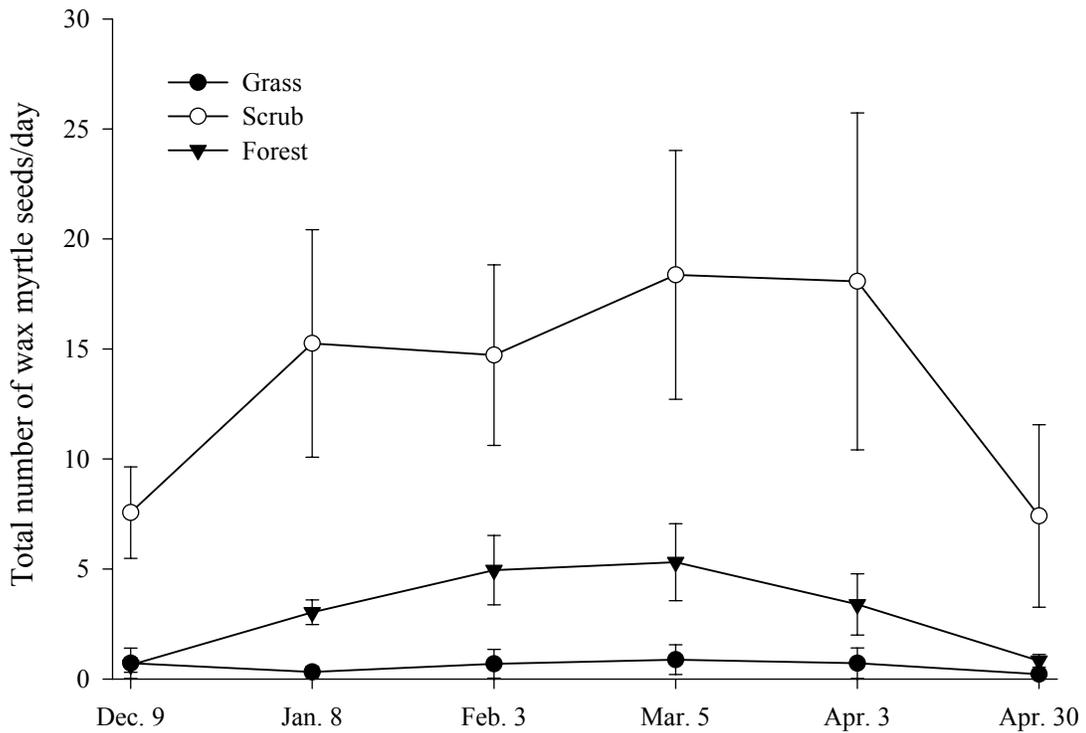
Figure 2-1. Number of wax myrtle seeds deposited per day into traps (n = 100) into

three different habitats on Assateague Island. Individual points represent the mean ±

SE number of wax myrtle seeds derived from the three replicates of each habitat.

Repeated measures analysis indicated a significant time X habitat interaction (*P* <

0.005).
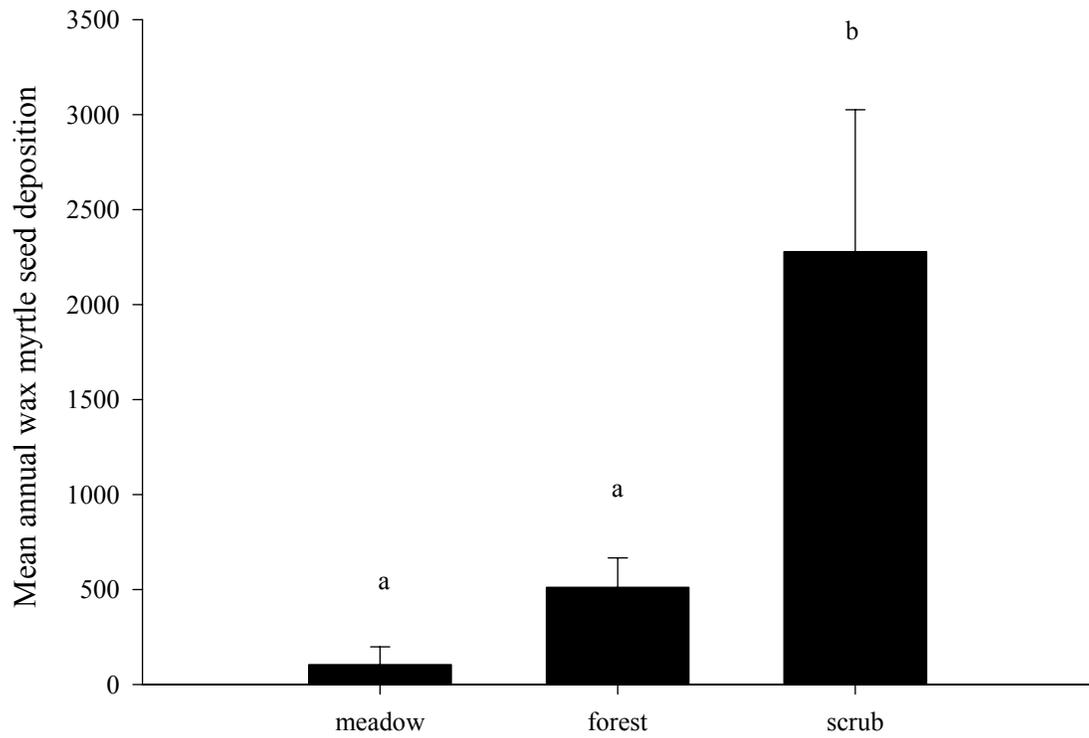
Figure 2-2. Mean ± SE number of the total number of wax myrtle seeds deposited in three different habitat types on Assateague Island over approximately six months. Each habitat type contained 100 seed traps and had three replicates. Letters indicate significant differences ($P < 0.05$) in the total number of seeds deposited.
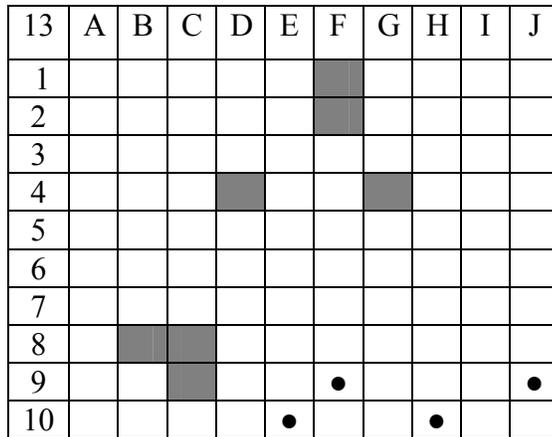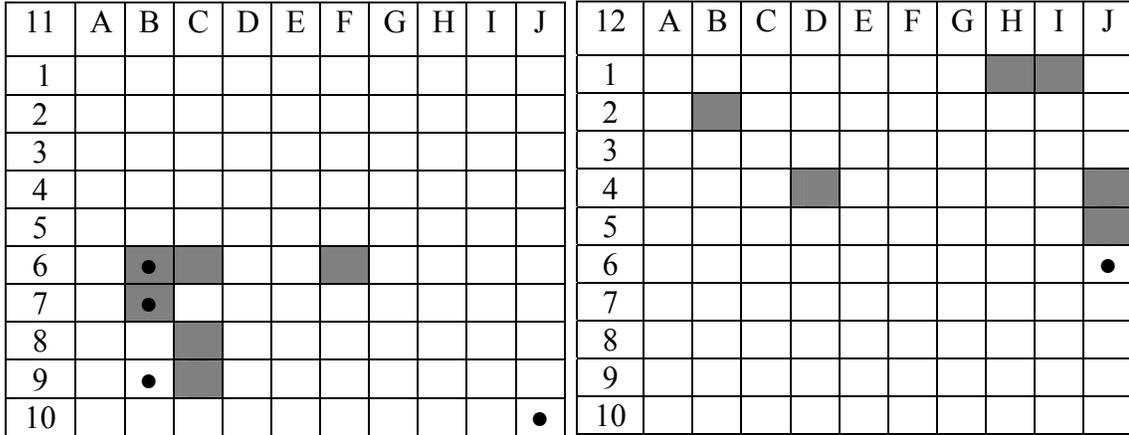
11	A	B	C	D	E	F	G	H	I	J
1										
2										
3										
4										
5										
6		●	▉			▉				
7		●▉								
8			▉							
9		●	▉							
10										●

12	A	B	C	D	E	F	G	H	I	J
1								▉	▉	
2		▉								
3										
4				▉						▉
5										▉
6										●
7										
8										
9										
10										

13	A	B	C	D	E	F	G	H	I	J
1						▉				
2						▉				
3										
4				▉			▉			
5										
6										
7										
8		▉	▉							
9			▉			●				●
10					●		●			

▉ At least one wax myrtle seed deposited in Circle

● Presence of wax myrtle seedling in Circle

Figure 2-3. Representation of the occurrence of wax myrtle seed deposition and subsequent presence of naturally occurring wax myrtle seedlings at three salt grass meadow sites (identified by number in top left corner). Individual rectangles represent Circles, which in the field were separated by at least 8m; at the center of each was located a single seed trap. Seedling surveys were conducted around each trap (see Methods for further details).

Site 21

21	A	B	C	D	E	F	G	H	I	J
1	■	●	●	■	■		■			
2	●	■	■	■	■	■	■	■	■	■
3	■	■	■			■	■	■	■	■
4	■	●	■			■	■		■	■
5	■	●	■	■	■	■	■	■		
6	■			■	■	■	■	■	■	■
7	■	■	■	■	■	■	■	■	■	■
8	●	■	■	■	■	■	■		■	■
9	■	●	■	■	■	■	■	■	■	■
10	●	■	■	■	■	■		■	■	■

Site 22

22	A	B	C	D	E	F	G	H	I	J
1	●	■		■		■	■	■		■
2		■	■	■	■		■	■		
3		■	■		■	■	■			
4		■	■	■		■	■	■		
5		■				■	■			
6	■		■	■	■				■	■
7		■		■	■	■				
8	■	■	■	■	■	■	■			
9	■	■		■		●	●			
10	■	■		●	●	■				

Site 23

23	A	B	C	D	E	F	G	H	I	J
1		■		■	■	■	■	■	■	■
2		■	■	■	■	■				■
3		■	■		■	■				■
4		■	■		■	■	■			
5		■		■	■	■	■			
6	■	■	■		●	■	■	●	■	■
7		■	■	■	■	■	■		■	■
8	■	■	■		●	■		■	●	
9	■	■	●	■	■	■				
10	■	■		■	■			●		
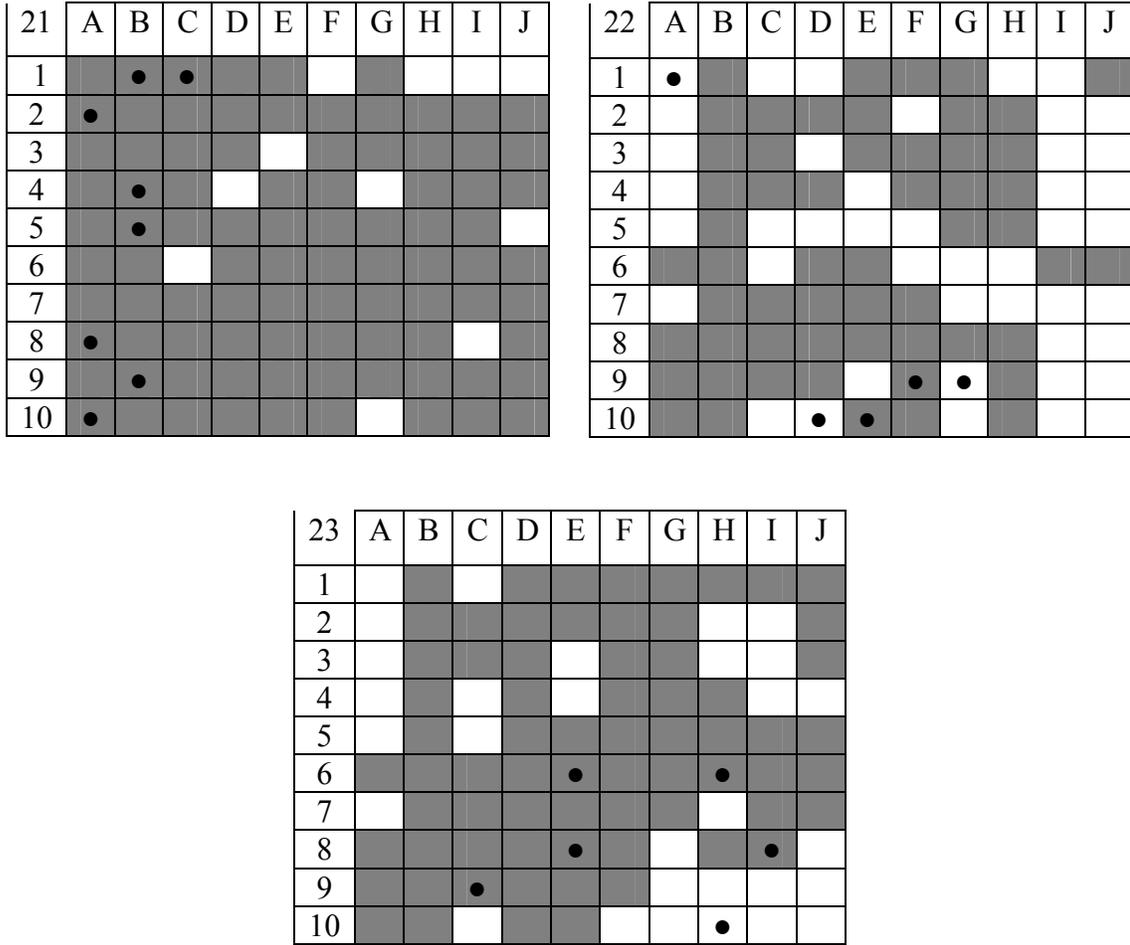
■ At least one wax myrtle seed deposited in Circle

● Presence of wax myrtle seedling in Circle

Figure 2-4. Representation of the occurrence of wax myrtle seed deposition and subsequent presence of naturally occurring wax myrtle seedlings at three scrub sites (identified by number in top left corner). Individual rectangles represent Circles, which in the field were separated by at least 8m; at the center of each was located a single seed trap. Seedling surveys were conducted around each trap (see Methods for further details).
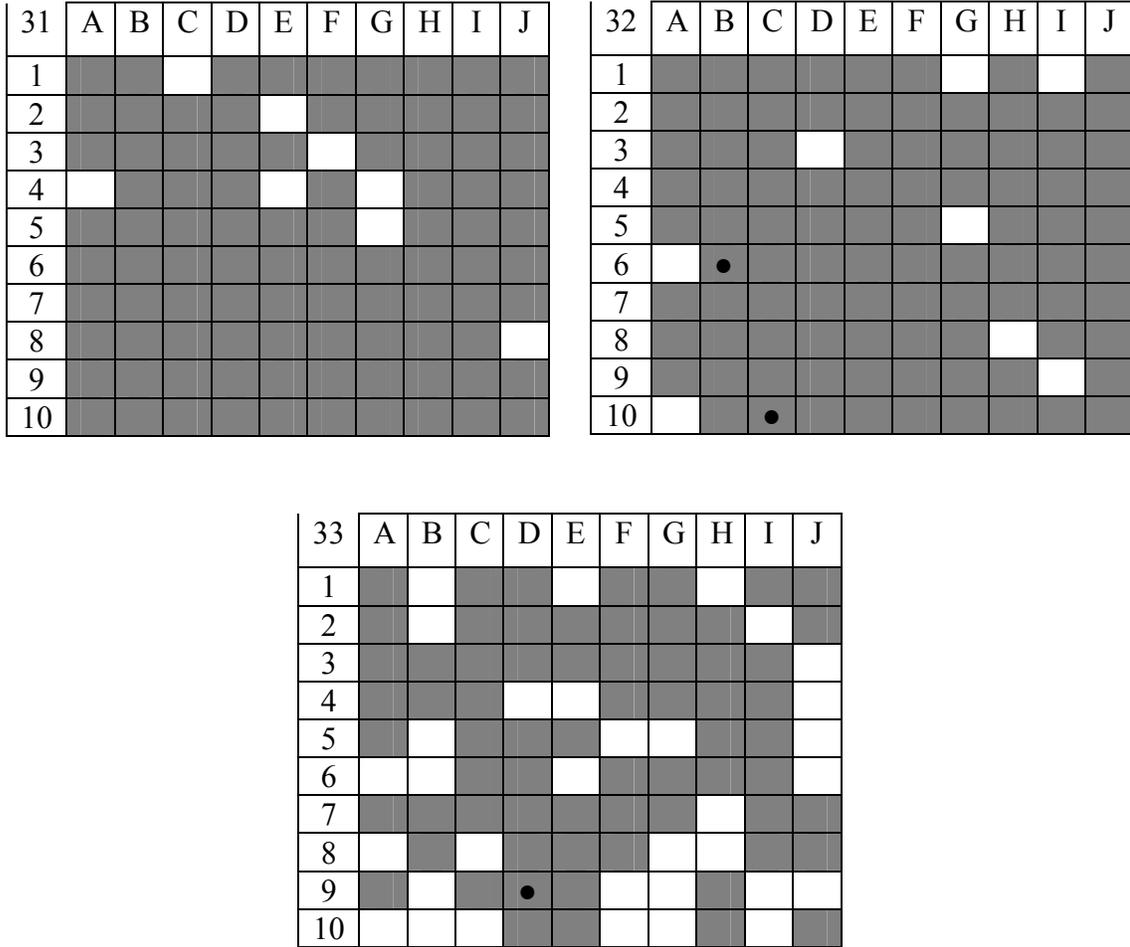
At least one wax myrtle seed deposited in Circle

●   Presence of wax myrtle seedling in Circle

Figure 2-5. Representation of the occurrence of wax myrtle seed deposition and subsequent presence of naturally occurring wax myrtle seedlings at three forest sites (identified by number in top left corner). Individual rectangles represent grid location of Circles, which in the field were separated by at least 8m; at the center of each was located a single seed trap. Seedling surveys were conducted around each trap (see Methods for further details).
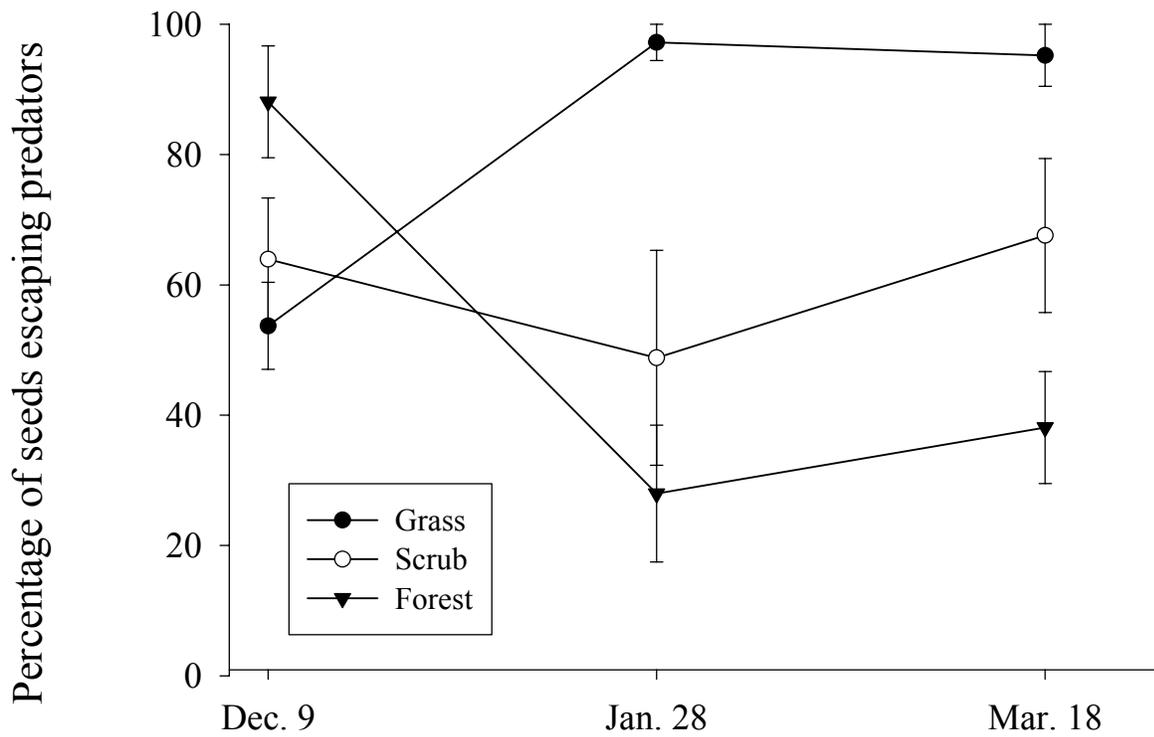
Figure 2-6. Survival rates of wax myrtle seeds experimentally deposited in three habitats on different dates on Assateague Island, 2001-2002 demonstrated a significant habitat X time interaction ($P < 0.0001$). Survival data was collected on April 30, 2002. Individual points are the mean ± SE survival rate of three replicate sites.
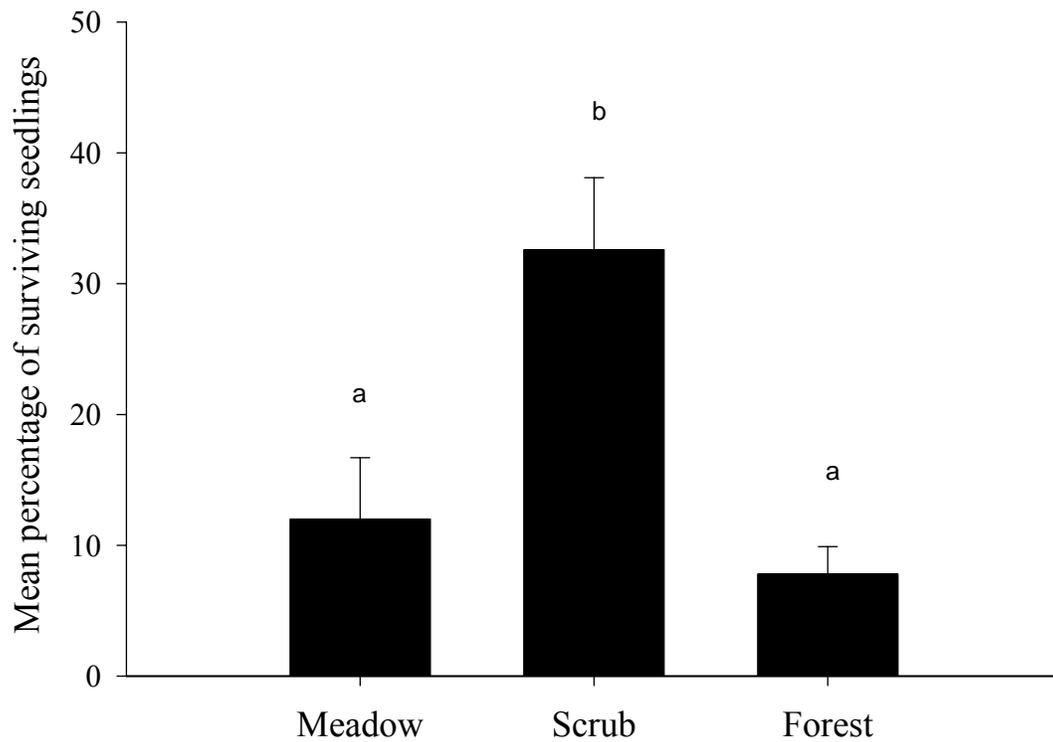
Figure 2-7. Comparison of the mean percentage (± SE) of wax myrtle seeds that germinated and survived until the end of the first summer from seeds experimentally planted at three different dates and in three habitats on Assateague Island. Time effect was not significant, but habitat exerted a significant effect ($P < 0.05$). Letters above column indicate significant differences between habitat treatments.
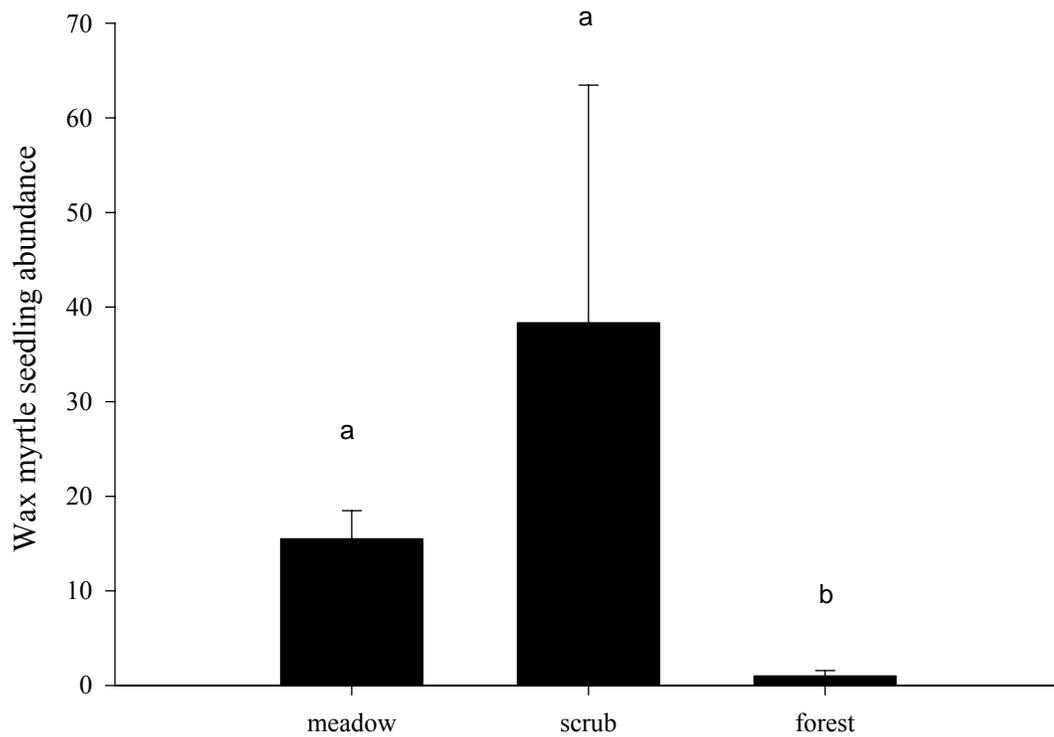
Figure 2-8. Mean ± SE number of wax myrtle seedlings detected per Circle in August 2002 in three different replicated habitat types on Assateague Island. Letters indicate significant differences ($P < 0.05$) in seedling abundance.
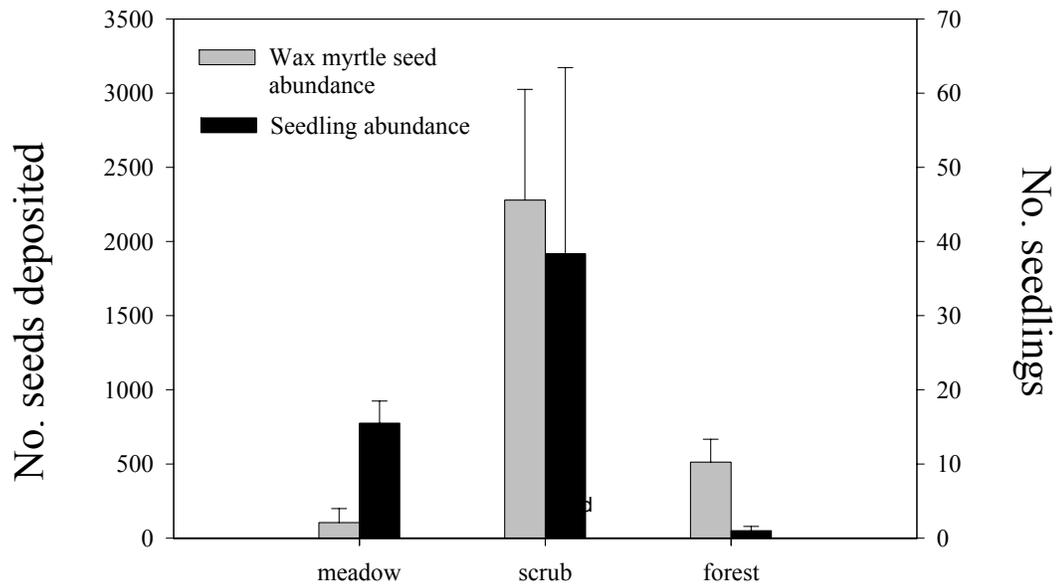
Figure2-9. Comparison of the mean (±SE) number of wax myrtle seeds dispersed into three different habitats (n = 3) and mean (±SE) number of seedlings subsequently detected within 1m of seed traps. All habitats differed in seedling:seed ratio (*P* < 0.0001). Columns are presented in order of magnitude of seedling:seed ratio.

Chapter 3: Qualitative and quantitative contributions of seed dispersers to wax myrtle (*Myrica cerifera)* recruitment on Assateague Island

Abstract

Frugivorous seed dispersers are assumed to play an important role in plant population dynamics, although few studies have considered simultaneously both the quantitative and qualitative contributions of individual disperser species. The impact of dispersers is especially important for a pioneer plant like wax myrtle (*Myrica cerifera*) whose recruitment and population viability on a barrier island are ultimately contingent on colonizing new sites to avoid more competitive species and on avoiding encroachment of the ocean due to island erosion and overwash. In this study, I document the quantitative and qualitative contributions that wax myrtle receives from its primary dispersers: gray catbirds (*Dumatella carolinensis*), tree swallows (*Iridoprocne bicolor*) and, the wax myrtle specialist, myrtle warblers (*Dendroica coronata coronata*). Over three years, myrtle warblers dispersed a substantially greater proportion of wax myrtle seeds than all other species combined, both within and between years.

Because seed trap data indicated that there was no difference in the number fruits falling from parent plants and dispersed seeds, I also tested the reproductive potential of seeds encased in fruit. Seed germination experiments revealed that wax myrtle seed germination rates are not affected by disperser identity and that seeds that passed through dispersers were as likely to germinate as those in fallen fruits.

However, median germination date of seeds in fruit was significantly later than the dates of those depulped or ingested. Post-foraging observations of all three avian dispersers suggested that in scrub habitat where recruitment was determined largely by escape from post-dispersal predators, seed shadows generated by myrtle warblers and gray catbirds were likely to be similar. However, myrtle warblers were the primary agent of emigration for seeds produced in scrub, a clear benefit especially for seeds produced in mature thickets where survival and establishment were contingent on colonization of new sites. Tree swallows contributed little to recruitment since their primary defecation sites were located on beaches and primary dunes, a highly saline habitat devoid of both wax myrtle adults and seedlings. This study demonstrates that fruiting plants may benefit from the focused attention of specialist frugivores, that the contribution of dispersers can be contextual and that members of a disperser assemblage should not be assumed to be functionally redundant.

Introduction

Seed dispersal by birds and mammals is widely accepted as a major influence on plant recruitment (Fleming and Heithaus 1981, Hallwachs 1986, Jordano 1992, Gorchov *et al.* 1993, Rey and Alcantara 2000, Calvino-Cancela 2004), by enabling the escape from density-dependent mortality around the parent, colonization of new sites, and directed dispersal to sites especially suitable for seedling establishment (Howe and Smallwood 1982, Augspurger 1984, Wenny 2001). Seed dispersal for fruiting plants is commonly accomplished by assemblages of endozoochorous frugivores; the physiology and behavior of which have been shown to impact

substantially plant recruitment and population dynamics (Estrada and Fleming 1986, Fleming and Estrada 1993, Levey *et al.* 2002). Because fruit has been shown to be an important resource, successful establishment of fruiting plants ultimately has important consequences for the life histories of breeding, migrating and over-wintering frugivores (Greenberg 1981, Herrera 1981, Wheelwright 1983, Parrish 1997).

Coevolution was at the heart of the first models proposed to explain how different disperser species affect plant recruitment.   These models rested on two assumptions: that a sizeable proportion of interactions were specialized and that specialist frugivores, i.e. those with an annual diet largely composed of fruit, provided predictable benefits to the plants whose seeds they dispersed (McKey 1975, Howe and Estabrook 1977). Both of these assumptions have largely been rejected, however (Wheelwright and Orians 1982, Herrera 1985, Jordano 1993, but see Howe 1993). The current consensus is that interactions between fruiting plants and frugivores are mostly generalized (Wheelwright and Orians 1982, Wheelwright et al. 1984, Gautier-Hion et al. 1985, Jordano 1987, Fuentes 1995, but see Chapter 1). Similarly, the effect of dispersers is no longer considered a constant primarily determined by disperser identity. Instead, as in other mutualisms (e.g. Cushman and Whitham 1989, Cushman 1991, Bronstein 1994), the benefit a plant receives is contextual, influenced by the biotic environment (Howe and Primack 1975, Herrera 1984, Gautier-Hion et al. 1993, Kaplan and Moermond 1998), variability in the abundance of disperser species (e.g. Parrish 1997, Herrera 1998) and the vagaries of their fruit use (Malmborg and Willson 1988). The current consensus is that most

interactions are examples of diffuse mutualisms in which no individual avian

frugivore consistently provides greater benefit than does the entire disperser

assemblage as a whole (Howe 1984, Herrera 1985, Jordano 1987, Herrera 2002),

although results from investigations of myrmechores are more ambiguous (e.g.

Hughes and Westoby 1992, Gorb and Gorb 1999, Garrido *et al.* 2002).

Yet conflating generalized interactions with diffuse mutualisms is problematic

because here generalized refers to the strength of association whereas diffuse refers to

the result of the interaction (Cushman and Beattie 1991). In fact, in other

mutualisms, generalists can provide substantial benefits to their partners (Motten *et

al.* 1981). Not only is the current understanding of the impact of frugivores on plant

recruitment limited (Sun *et al.* 1997, Bohning-Gaese *et al.* 1999, Jordano and Schupp

2000, Herrera 2002), but data on the relative contributions of specialist and generalist

frugivores are sparse and come almost exclusively from systems where mistletoe is

the fruiting plant (e.g. Reid 1989, Murphy *et al.* 1993, Larson 1996, but see also

Calvino-Cancela 2002, Calvino-Cancela 2004). However, understanding the

dependence of fruiting plants on any disperser, especially a specialist frugivore, may

have significant implications for conservation as well as for community dynamics

(Loiselle and Blake 1999, Loiselle and Blake 2002, McConkey and Drake 2002).

The most convincing assessments of the value of avian and mammalian

frugivores to plant recruitment are based on considerations of how dispersal by

frugivorous species differs quantitatively and qualitatively (Schupp 1993, Kaplin and

Lambert 2002) and how these differences correspond with a particular plant species'

dispersal needs (Herrera and Jordano 1981, Howe and Smallwood 1982, Willson

1989, Schupp 1993). Quantitative dispersal is simply the number of seeds removed by each species. Although this can be influenced by a variety of factors, including degree of frugivory (e.g. Jordano 1982, Herrera 1984, Malmborg and Willson 1988, Schupp 1993), fidelity to a particular fruiting species (Boddy 1991, Ladley and Kelly 1996) and feeding rate (Schupp 1993, Sun *et al.* 1997), the number of visits by each species frequently appears to have the greatest effect (Schupp 1993). Qualitative dispersal, or the likelihood of a seed surviving to adulthood, is determined by the location and time of deposition (Schupp 1993), although the latter has rarely been addressed (but see Chapter 2), as well as by the effect of gut passage on germination time and rate.

Assessing all three of these parameters (quantitative and qualitative dispersal, and how individual plant species benefit from dispersal) is important for several reasons. First, an investigation focusing on just quantity or quality may produce erroneous conclusions since the two are not necessarily of equivalent importance to a plant (Reid 1989, Schupp 1993, Loiselle and Blake 1999, Calvino-Cancela 2002, Godinez-Alvarez *et al.* 2002, Calvino-Cancela 2004), nor is their relative importance absolute. One disperser may remove more fruit than another, but ultimately contribute less to recruitment if it deposits seeds in sites less suitable for establishment (e.g. Howe 1981, Schupp 1993, Compton *et al.* 1996, Calvino-Cancela 2002, 2004). For example, resplendent quetzals (*Pharomachrus mocinno*) deposit up to 90% of seeds beneath the parent plant (Wheelwright 1983), which is not typically optimal for recruitment. Conversely, the value of the superior deposition and treatment of seeds produced by one frugivore may be outweighed by substantially

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greater quantitative contribution of another species (Reid 1989, Godinez-Alvarez et al. 2002, see also Motten et al.1981). Second, considering both quantity and quality provides ecologists with an opportunity to add to the limited understanding of the mechanisms influencing fruit-frugivore mutualisms (Sun *et al.* 1997, Bohning-Gaese *et al.* 1999, Jordano and Schupp 2000), and also to predict the effect of frugivore population fluctuations on plant population viability, especially since quantitative dispersal can be heavily dependent on disperser abundance. Understanding the relative importance of these types of dispersal may be a valuable tool when modeling the possible impacts of habitat fragmentation and destruction as well as global warming. Finally, by determining the way in which a fruiting plant actually benefits from dispersal allows for an accurate prediction of how disperser species will affect recruitment. A species relying on colonization of tree fall gaps, for example, is more likely to benefit from a disperser providing an extensive seed shadow (Murray 1986, Hoppes 1988) than plants requiring very specific establishment conditions (Wenny 2001) or those surrounded by inhospitable habitat (Watkinson 1978).

In this paper, I consider the quantitative and qualitative contributions to wax myrtle (*Myrica cerifera*) recruitment on Assateague Island of the three most common dispersers: gray catbirds (*Dumatella carolinensis*) and tree swallows (*Iridoprocne bicolor*), myrtle warblers (*Dendroica coronata coronata*) and fallen fruit.

In this study I posed three questions. 1) Is there a significant difference in quantitative dispersal provided by dispersers and is any observed difference consistent between years? 2) Is there a significant difference in the quality of dispersal provided, and is the ranking of qualitative dispersers equivalent to rankings

of quantitative dispersers? 3) Is wax myrtle recruitment dependent on any particular species or does it, indeed, benefit from a diffuse mutualism?

Study Site and Species

Assateague Island is a dynamic barrier island located off the coast of Maryland and Virginia, approximately 45 kilometers in length, totaling approximately 16, 066 hectares.   This study was conducted primarily in scrub, which of all habitats was most dominated by wax myrtle.

Wax myrtle is a common, dioecious woody pioneer of newly stabilized soils and an important link in vegetative succession on the barrier islands stretching south along the mid-Atlantic coast of the United States (Young et al. 1992, Young et al. 1995). Individual females commonly produce vast crops (> 1000) of wax-covered drupes with no sign of interannual variation. On barrier islands, wax myrtle seedling establishment does not appear limited by *Frankia*, its nitrogen-fixing bacterium which is abundant (Young et al. 1992), but by edaphic conditions, especially soil salinity (Conner and Inabinette 2003) and fresh water availability (Shao et al. 1995). Actinorhizal wax myrtle thickets develop rapidly after establishment and facilitate subsequent heterospecific colonization of these sites by increasing soil nitrogen content (Permar and Fisher 1983, Young 1992, Young et al. 1992, Young et al. 1995), and by providing perches for seed dispersing birds (see McDonnell and Stiles 1983, Hoppes 1988, Holthuijzen 1993).

In the early stages of thicket development, wax myrtle seedling recruitment can be relatively high (Young et al. 1995, Chapter 2). In these patches, proximity to

plants does not increase mortality (Chapter 2) in contrast to other systems (e.g. Janzen 1972, Clark and Clark 1984, Dirzo and Dominguez 1986, Howe 1986, Crawley 1992).

Wax myrtle recruitment halts within patches as thickets mature and other more competitive species arrive, eventually dominating the community (Levy 1983, Young et al. 1995, Crawford and Young 1998). Thus in the absence of a major disturbance like fire which can create open sites for colonization and which adults can survive (Richardson 1977, Terry and White 1979, Taylor and Herndon 1981), the emigration to new sites becomes increasingly important in these later stages of thicket development. While colonizing fruiting plants in other systems may benefit if dispersed only a short distance (Levey 1988), wax myrtle seeds in such a context are unlikely to survive if dispersed only short distances. Due to the patchy availability of freshwater and suitable edaphic conditions, illustrated in the defined mosaics of vegetation communities seen on Assateague Island (Higgins et al. 1971, NBS-NPS Pilot Veg Map1995, Shao et al. 1995, see also Snow 1984), the nearest safe site for seeds may be located across large stretches of unsuitable habitat (Chapter 2, NBS-NPS Pilot Veg Map Project 1995). Because barrier islands are highly dynamic (Clark 1986, Stalter and Lamont 1990), colonization via dispersal also benefits wax myrtle by allowing it to retreat from areas currently or soon to be exposed to the lethal effects of salinity levels due to overwash and island erosion (Dolan et al. 1977, Levy 1983, Clark 1986, Ehrenfeld 1990, Conner and Inabinette 2003) and to colonize new open sites.

Methods

Quantitative Dispersal

The relative quantitative contributions of fallen fruit and frugivore-dispersed seeds to seedling recruitment were determined by comparing the numbers of entire fruits and voided seeds in seed traps located in three habitat types: forest, scrub, and meadows (see Chapter 2 methods). Data collection began approximately 45 days after the start of the seed dispersal season, on November 17, 2001. Trap contents were collected approximately every 30 days subsequently until the final day of trap inspection, April 30, 2002. To determine the relative quantitative contribution of frugivores and fallen fruits, I compared the total number of wax myrtle fruits and seeds collected in each habitat using Proc Mixed (SAS Institute 1999). I used Spearman rank correlation (Proc Corr, SAS Institute 1999) to examine the relationship between fallen fruits and seeds over time.

To measure the relative numbers of wax myrtle fruit consumed by myrtle warblers and gray catbirds, I collected fecal samples from birds captured in mist nets in the Off Road Vehicle section of Assateague National Seashore from late September – April, 1997 – 2000 and 2001-2002 (see Chapter 1 methods for further details). Data from the first year will not be presented here because no gray catbirds were mist netted in 1997 – 1998. Fecal samples of all birds were collected by using fecal bags, which were labeled with each bird's date, location and time of capture, and unique U.S. Geological Survey band number. Fecal bags were made from athletic socks that have had the toe removed and replaced with hardware cloth. A re-sealable plastic bag was suspended from the body of the sock to catch all voided

contents. Samples were frozen, thawed, placed in methanol solution, broken apart with forceps, and examined under a dissecting scope (0.7X – 3X).

Identification of *Myrica* seeds on Assateague Island where bayberry (*M. pensylvanica*) and wax myrtle are sympatric was accomplished by measuring seed diameter, which is an effective way to distinguish between these species. In 1998, I measured the diameter of 327 *Myrica* seeds (22% of all *Myrica* seeds recovered from fecal samples), 72% of which met the diameter criterion of wax myrtle. In 1999, 72% of all *Myrica* seeds from myrtle warbler fecal samples were measured, 87% of which were wax myrtle. All *Myrica* seeds from gray catbirds were measured; 85% were identified as wax myrtle. I did not collect these data from gray catbirds in 1998 or 2001 and so assumed that this proportion in 1998 was similar to the proportions in the previous and subsequent years. Because data on seed diameter were not collected in 2001 from myrtle warbler fecal samples, I used the mean of the two previous falls, 79.5%, to estimate the percentage of all *Myrica* seeds made up by wax myrtle. All *Myrica* seeds collected after October were assumed to be wax myrtle since fruit censuses indicated that bayberry fruit levels were negligible (Chapter 1).

I relied on fecal samples for these data rather than reporting the number of each species visiting focal plants and the number of fruits removed per visit because the latter method restricts data collection to a limited number of trees (e.g. Herrera and Jordano 1981, Howe and Vande Kerckhove 1981, Bronstein and Hoffmann 1987) and because the dense habitat at my site made thorough assessment of visitor foraging behavior difficult (see also Blake and Loiselle 1992). However, fecal data can be biased if the target species differ in their habitat preferences or ability to be captured.

Although gray catbirds appeared slightly more confined to areas of denser vegetation than were myrtle warblers, there was a large degree of overlap in habitat use (Lowe, pers. obs.). Mist nets were located to maximize capture rates of both species. There was no indication that these species differed in their ability to avoid mist nets.

Relative abundances of myrtle warblers and gray catbirds were calculated by comparing the numbers captured/100 mist net hours per month during the months that catbirds were caught on the island. The data were analyzed using repeated measures (Proc Mixed, SAS Institute, 1999) and the covariance structure within subjects was modeled using compound symmetry (CS).

Tree swallows avoided all mist nets, rendering impossible any direct comparison of their quantitative contribution with myrtle warblers'. However, I tested whether tree swallows were likely to remove as much fruit during their three months residence as myrtle warblers did during their seven months stay, by estimating the amount of fruit removed by warblers and considering whether tree swallow abundance was sufficient to remove a similar amount. To accomplish this, I used the following calculations:

Total number fruit removed by myrtle warblers = (Monthly mean ± SE myrtle warbler abundance) x (Mean ± SE number fruit eaten/day) x (Number of days/Month) x (Total area of scrub habitat/area of transect)

Monthly warbler abundance was estimated by using survey data for warblers in scrub habitat (see Chapter 1 for details regarding survey methods). Because transects were established in scrub habitat and because the vegetative composition and structure were not uniform but reflected heterogeneity observed throughout wax

myrtle dominated scrub, I assumed that myrtle warbler abundance on these transects was representative of the abundance found in this habitat elsewhere on the island. Surveys were not conducted in every month during the season (October – April) in each year. However, monthly means were based on data from at least two years, and each year's monthly mean was based on at least one survey of five transects.

The estimated number of fruits removed/day by myrtle warblers was based on the number of wax myrtle fruits consumed by captive warblers in *ad libitum* fruit preference experiments in 1999 (see Chapter 1 for details regarding fruit preference methods). My estimate of the total area of habitat containing wax myrtle was based on the estimated area of vegetative communities in which wax myrtle was a major component. These data were collected by the National Park Service in conjunction with the Nature Conservancy as part of a survey of vegetation communities on Assateague Island National Seashore (NBS-NPS Pilot Veg Map Project 1995).

Estimates of tree swallow abundance were collected opportunistically in 1997-1999 and 2001-2002 by observers within an approximately 14 km stretch of the Maryland portion of Assateague Island. This location was visited approximately six days a week between late September and mid- December each year, when tree swallows were most common. Between late December and April, this area was visited at least one week per month. The length of the study site was traversed on most days observers were present. Observers reported the presence of tree swallows and estimated flock size to the nearest 100 and to the nearest 1,000 with flocks composed of <1,000 and >1,000 individuals, respectively. I extrapolated island

abundance by increasing monthly estimates by 66%, because my study site occupied only 33% of Assateague Island National Seashore's total length.

The validity of these estimates rests on important assumptions. I assume that the amount of fruit consumed by captive warblers in autumn approximates the number consumed in the field throughout the entire seven-month fruiting season. This assumption appears justified, if not conservative, for several reasons: wild birds can be expected to experience greater energetic costs and so to consume greater amounts of food than captive individuals; wax myrtle fruit is abundant and a major food item and energy source for warblers throughout their entire seven-months of their residence on Assateague (Chapter 1); warblers respond to reduced fruit availability with facultative migration rather than diet switching and fecal samples provide no indication of decreased consumption (Chapter 1). In fact, using fruit consumption of birds in autumn likely underestimates daily fruit consumption of warblers in the winter, since consumption of wax myrtle fruit by myrtle warblers increases as temperatures decline in winter (Kwit et al. 2004).

I also assume that tree swallows were consistently detected when present, although systematic surveys of their abundance were not conducted. The conspicuous nature of tree swallow flocks renders it unlikely that flocks went systematically undetected. Rather I suspect that tree swallow abundance was overestimated, making the overall comparison conservative. While the double-counting of warblers during surveys was rigorously avoided, daily estimates of swallow abundance were frequently comprised of swallows observed at multiple locations, all of which were assumed to be different individuals.

Because tree swallows are up to 33% heavier than myrtle warblers (Robertson *et al.* 1992), I assumed that they could eat up to 33% more fruit (see Howe and Primack 1975, Herrera and Jordano 1981, White and Stiles 1990). This assumption again conservative since myrtle warblers are substantially more frugivorous than tree swallows (Bent 1963, Yarbrough and Johnston 1965). Tree swallows on Assateague Island more commonly foraged as aerial insectivores than as frugivores, in contrast with heavy and consistent use of wax myrtle by myrtle warblers (Lowe unpub. data, Chapter 1). Further, the rarity of tree swallows on Assateague after November, when wax myrtle fruit is still abundant (Chapter 1) but flying insect populations are dramatically reduced (pers. obs., see also Parrish 1997), further indicates the relative importance of fruit and insects in the swallow diet.

Qualitative Dispersal

Germination

I used greenhouse experiments to determine the effect of the following treatments on the rate (%) and time (median date) of wax myrtle seed germination: (1) the presence of pulp (fruit encased seeds vs. ingested and manually depulped seeds); (2) exposure to gastric acids (ingested vs. manually depulped seeds); (3) frugivore identity (seeds defecated by myrtle warblers vs. gray catbirds); (4) mode of voiding (seeds regurgitated by gray catbirds vs. those defecated by gray catbirds); and (5) presence of feces accompanying seeds defecated by both species.

One hundred control fruits were removed from each of five randomly selected female wax myrtle individuals on November 3, 1999. Wax was manually removed from 250 randomly selected fruits. The remaining fruits remained intact. All fruits

and seeds were stored in paper bags outdoors until planting. Seeds voided by myrtle warblers (n = 5) and gray catbirds (n = 5) were collected from the fecal trays of captive gray catbirds and myrtle warblers in fruit preference experiments (late October/early November 1999, see Chapter 1, fruit preference methods for details). Seeds defecated by individual gray catbirds and myrtle warblers were randomly assigned to be accompanied (n = 50) and unaccompanied by feces (n = 50). All seeds in the former group were covered by a slurry of rehydrated feces recovered from the fecal trays of the appropriate avian species. The amount of gray catbird feces applied to these seeds (0.0075 g) was based on the mean amount of fecal material accompanying each seed for all catbirds (n = 9). The mean amount of myrtle warbler feces was not calculable with the scale in use because its mass, <0.01 g, was less than the scale could register. Instead, the total amount of warbler feces was added to the seeds, an overestimation of the actual amount associated with each seed since not all seeds defecated by warblers were used. Seeds (n = 50) regurgitated by catbirds (n = 3) were separated from those defecated. Although the captive birds were not observed when processing fruit, regurgitated seeds were identifiable since they were free of fecal material and tended to roll to the edge of the trays. Seeds whose method of voiding was ambiguous were not included.

On November 7, all seeds were placed on a mixture of 50% sand and 50% topsoil in flats that were divided into narrow, separate compartments to reduce the likelihood of any contamination of non-fecal treatments. All treatments, except for regurgitated seeds and seeds defecated by warblers and planted with feces, were replicated in 5 flats of 50 seeds each. Regurgitated seeds were replicated 3 times,

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warbler defecated seeds with feces were replicated 4 times. Flats were then covered

and subjected to a 131 day cold stratification treatment at 5 º C. (Barton 1932). On

March 17, flats were removed from cold treatment and put in the greenhouse at the

University of Maryland under misters (mist for 14 seconds every 8 minutes),

experiencing natural photoperiod and temperature. Data were collected weekly for

three weeks and a final determination of germination was made after a total of 38

days. Observations were discontinued at this point since no remaining seed showed

any sign of germination. Viability of these remaining seeds was not determined.

However, because seeds were randomly assigned to treatments, I have no reason to

suspect that the frequency of non-viable seeds differed between treatments, biasing

the results.

The data were analyzed with ANOVA, using Proc Mixed (Institute 1999).

Although this experiment was designed as a randomized incomplete block (RIBD),

the data were analyzed as a completely randomized design (CRD), since the block

effect did not account for any variation. These experiments were not repeated for

fruits collected at different times within a year, since wax myrtle germinability

remains constant for 9 months (Erickson and Hamrick 2003, see also Chapter 2).

Seed Deposition

Comparison of the actual seed rain generated by gray catbirds and myrtle

warblers was not logistically possible, due to the distance at which these species were

observed and to their highly vagile nature. Instead, I used observations to determine

whether they differed in post-foraging flight patterns.

Foraging observations were conducted in 1998 between early October and mid-December in scrub habitat in the study area. This habitat is composed of discrete thickets of wax myrtle separated by large open areas of *Spartina* grasses and mixed occasionally with *Baccharis halimifolia*, *Vaccinium*, and occasional *Pinus taeda* and *Acer rubrum* saplings (see Chapter 1 for a more complete habitat description). Forest habitats were not surveyed since these areas contain very few fruiting females and myrtle warblers were largely found in the pine canopy (Lowe, unpublished data). Observers moved opportunistically throughout scrub habitat, and halted upon encountering either a myrtle warbler or gray catbird. Using binoculars and a stopwatch, observers recorded the number of fruits ingested from each wax myrtle plant, the number dropped, and the time spent on each plant.

To determine post-foraging habitat selection of these species, observers recorded the movements of all individuals after consuming fruit. Observations were concluded when the focal individual disappeared. Observers recorded where each individual frugivore was lost, then assigned the bird to one of three categories: (1) the frugivore retreated into the fruiting plant or thicket in which they had been feeding, (2) flew to another location within the same habitat patch, or (3) left the patch altogether. No data were included when there was any indication that the frugivore's behavior was altered by observer presence. Since myrtle warblers were present in very large numbers and since this species showed no sign of territoriality, the likelihood of pseudo-replication was considered to be minimal. Gray catbirds were far less numerous, but care was taken to avoid repeating observations on the same individual during that day's observations.

As with tree swallow abundances, seed deposition patterns by tree swallows were collected opportunistically and without established survey protocol. The location of all resting swallow flocks was recorded; voided *Myrica* seeds were abundant at all such sites upon later inspection, consistent with previous studies reporting that after bouts of frugivory, foragers tend to rest until ingested seeds are either defecated or regurgitated (see McDonnell and Stiles 1983, Hoppes 1985). I assume that observations are not biased since, during the period of tree swallow presence at my site, each of the island's gross habitat types (beach, dune, scrub, forest, marsh, salt flat) was visited approximately six days a week, in the course of conducting warbler surveys and collecting fecal data. All swallow resting sites were revisited by July of the following year and surveyed for wax myrtle seedlings.

Results

Quantitative Dispersal

Seed trap data indicated that there was no significant difference in the total number of voided seeds and fallen fruits present in traps in the meadow ($P > 0.5$) and scrub habitats ($P > 0.1$). In contrast, seeds were significantly more numerous than fruit in forest traps ($F_{1,4} = 53.94$, $P < 0.01$). There was a significant correlation ($P < 0.001$) between the number of fruits and seeds in traps over time in both meadow ($r = .76$) and scrub ($r = 0.74$) habitats.

Among the three major consumers of wax myrtle fruit, myrtle warblers made the greatest quantitative contribution to wax myrtle seed dispersal in all four years (1997-2000, 2001-2002) on Assateague Island. The total number of wax myrtle seeds

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recovered from myrtle warbler fecal samples each year was far greater than the number recovered from gray catbirds both in late September and October (Figure 3-1A), when catbirds were most abundant, and throughout the remaining 6 months of fruit presentation (Figure 3-1B). There was no significant difference in the number of seeds per fecal sample of warblers and gray catbirds ($P > 0.05$). But myrtle warblers were significantly more numerous in all months that gray catbirds were present ($P < 0.01$) (Table 3-1). These data indicate that the relatively slight impact of gray catbirds on wax myrtle seed removal was influenced by both their comparatively short residence time as well as their limited abundance (Figure 3-2).

In contrast to catbirds, tree swallows could achieve very great abundance. Tree swallow flocks frequently numbered more than 1,000 individuals (Lowe pers. obs.). However, these flocks were highly sporadic in their occurrence and generally were present in only three (late September – December) of the seven months of wax myrtle fruit presentation. Only in 2002 were swallows (a flock of eight individuals) spotted after December.

During their seven-month residence on Assateague Island, I calculated that myrtle warblers annually removed between mean (±SE) 483 X 10^6 (± 147 X 10^6) (Table 3-2). Removal of a comparable amount of fruit in three months by tree swallows would require the a monthly abundance at my study site of flocks of at least 160,000 individuals eating 360 fruits/day (a weight adjusted estimate of 33 % more fruit than myrtle warblers are estimated to consume) between the end of September and the end of November. However, observations indicate that monthly totals of swallow abundance were never present in such numbers (Table 3-3). The mean

monthly total abundance of swallows observed throughout late September and October was approximately 14,500. For November the mean was 8,100 and 167 for December. This comparison strongly suggests that although tree swallows may provide superior fruit removal services than do gray catbirds by virtue of greater abundance, myrtle warblers remove far greater numbers of fruit than tree swallows. The quantitative contribution of tree swallows appears to have been limited not only by their short residence time relative to myrtle warblers, but also by the high variability in their presence on the island (Lowe, unpub. data).

Qualitative Dispersal

Germination

Germination rates of wax myrtle were not significantly affected by any treatment ($P > 0.1$): presence of fruit pulp, exposure to gastric acid, disperser identity, method of voiding, presence or absence of feces. The median date of germination did differ significantly between treatments, however ($F_{6,19.7} = 3.74$, $P > 0.05$). Independent multiple comparisons using test for Least Significant Difference (LSD) revealed that seeds encased in waxy pulp had a significantly later germination date ($P < 0.001$), by approximately 4 days, than seeds whose wax had been removed, whether by digestive processes of either frugivore or by hand (Figure 3-3).

Seed Deposition

Both myrtle warblers and gray catbirds were frequently observed resting in wax myrtle thickets. Similarly, both species commonly left fruiting shrubs after fruit consumption, sometimes flying as far as 25 m to another fruiting shrub. However,

not infrequently after foraging, warblers would leave a shrub, rapidly ascend to a height of > 4m, and leave the habitat patch altogether; catbirds were rarely observed leaving the habitat patch after foraging. Myrtle warblers (n = 283) and gray catbirds (n = 21) differed significantly in their post-foraging behavior (X^2 = 6.2889, $P <$ 0.05). Multiple comparisons using a Bonferroni adjustment indicated that myrtle warblers were significantly more likely to leave a habitat patch after consuming wax myrtle than gray catbirds (Fisher's exact test, $P < 0.05$) (Figure 3-4). There was no significant difference in their likelihood, however, to remain in the fruiting plant after fruit consumption.

Tree swallows, in contrast, invariably left wax myrtle plants shortly after foraging on fruit (Lowe, pers. obs.) and so seed deposition in the immediate vicinity of the maternal plant was considered to be minimal. Unlike warblers and catbirds, however, flocks of resting tree swallows were highly conspicuous. The majority of such flocks were observed most commonly resting on the beach and primary dunes. Less frequently tree swallows settled on salt pannes. Only once were swallows observed resting in scrub habitat (Table 3-4). Inspection of all sites confirmed that resting swallow flocks defecated *Myrica* seeds in large numbers. Although some seeds were presumably defecated in flight, these observations suggest that large numbers of *Myrica* seeds ingested by swallows were ultimately deposited in this habitat. No seedlings were ever observed growing in these sites on subsequent surveys.

Discussion

Results from this study indicate that myrtle warblers in all years contributed more to wax myrtle recruitment than did either of the two more generalist dispersers considered here or than did fallen fruit. This is in agreement with previous work showing that dispersers differ in their impact on recruitment (e.g. Schupp 1993), that individual disperser species can provide significantly better services to plants (Godinez-Alvarez *et al.* 2002) and that specialist dispersers can provide the most valuable services to a fruiting plant (Reid 1989, Murphy *et al.* 1993, Larson 1996).

Quantitative Dispersal

Fruit removal is only the first of many steps that need to be accomplished for a seed to reach adulthood (Herrera 1985, Herrera et al. 1994). Because subsequent variables can substantially influence recruitment, the most important quantitative disperser does not always provide the largest benefit to its plant partner (Snow 1962, Howe 1980). Nonetheless, its importance to recruitment should not be discounted (Murray 1988, Jordano and Schupp 2000, McConkey and Drake 2002). Recruitment, especially among early successional species, is frequently seed-limited (Turnbull et al. 2000). Further, frequently all fruits are not removed from fruiting plants (e.g. Howe 1980, e.g. Burger 1987, Snow and Snow 1988, Englund 1993, Herrera 1995).

In all years (1997-2000, 2001-2002), myrtle warblers were clearly the most important quantitative dispersers of wax myrtle seeds. While it is common for disperser species to differ widely in their abundance (e.g. Jordano 1982, e.g. Skeate 1985, Parrish 1997) and for the relative quantitative contribution of frugivores to be highly skewed (Murray 1988, Schupp 1993, Parrish 1997, Jordano and Schupp 2000),

the within and between year consistency reported here contrasts with other systems in which the identity of the primary disperser varied within a fruiting season (Holthuijzen and Sharik 1985, Bronstein and Hoffmann 1987, see also Boddy 1991) and between years (Jordano 1984, Malmborg and Willson 1988, Loiselle and Blake 1990, 1994, Herrera 1998). Also worthy of note is the finding that myrtle warblers are the only major disperser of wax myrtle seeds on Assateague Island after December when tree swallows and gray catbirds have for the most part left for their more southerly wintering grounds (Robertson *et al.* 1992, Cimprich and Moore 1995), but when a large proportion of the fruit crop remains undispersed (Chapter 1) and when post-dispersal predation is especially low in colonization sites (Chapter 2).

The total number of seeds recovered annually from myrtle warbler fecal samples was at least one order of magnitude greater than those recovered from gray catbirds in all years. Even when only those fecal samples collected between late September and the end of October were considered, the period of greatest and most consistent catbird abundance, myrtle warblers dispersed a substantially greater number of seeds.

These results are not unexpected given the difference in the frequency of warbler and gray catbird fecal samples containing evidence of *Myrica* consumption (Chapter 1). It should be noted, however, that the magnitude of difference between the percentages of wax myrtle seeds removed by warblers and catbirds indicated by these data is a substantial underestimation, since fecal samples were collected only sporadically between mid-December and April each year – a period when gray catbirds were largely absent but warblers were highly abundant and consistently

consuming wax myrtle (see also Whittle 1922, see also Borgman et al. 2004, Kwit et al. 2004, Kwit et al. 2004). The primary cause of the difference in the quantity of fruit removed by myrtle warblers and gray catbirds appears to be the far greater warbler abundance (see also Jordano and Schupp 2000), since there was no difference in the number of seeds per fecal sample. This is in agreement with other studies that illustrated the importance of the number of visitations for quantitative dispersal (e.g. Schupp 1993).

Fecal data provide only a rough assessment of the relative contribution of these two species, however, since they do not account for the cost of dropped fruit and further may not include seeds dispersed via regurgitation. Forty-five percent of warblers observed foraging in the field dropped approximately an average 18% of the fruit that they handled (Lowe pers. obs.), a clumsiness they also displayed when foraging on fruit in other systems (Willson and Whelan 1993). Gray catbirds, on the other hand, were observed to be always successful in their handling. Similarly, these species differed in their tendency to regurgitate wax myrtle seeds. Myrtle warblers in captivity only defecated seeds. In contrast, 3 out of 4 captive gray catbirds regurgitated a mean 33% of ingested wax myrtle seeds (Lowe, unpub. data). Comparison of the percent of all the fecal samples from these two species containing evidence of *Myrica* consumption (either seeds or bractioles) that also contained seeds, strongly suggest that gray catbirds commonly regurgitate wax myrtle seeds in the field as was observed. This suggests that reliance on fecal samples may underestimate the number of wax myrtle seeds removed. However, given the large percentage of the annual wax myrtle crop removed by myrtle warblers relative to gray

catbirds, even increasing the number of seeds removed by gray catbirds by 33% does not change the conclusion that myrtle warblers are the most important quantitative disperser. But they do illustrate that reliance on fecal samples alone may not provide a complete picture of the relative costs and benefits associated with each disperser.

In contrast to catbirds, whose abundance was always relatively low, tree swallows could be present in very large numbers between late September and November. When frugivorous, a flock of several thousand swallows were able to strip a thicket's fruit crop during a single, spectacular foraging bout (Lowe pers. obs.). Yet, tree swallows occurred very sporadically, a pattern displayed by other flocking frugivores (Holthuijzen and Sharik 1985, Greenberg *et al.* 2001), whereas warblers were consistently present. Indeed, the number of tree swallows required to remove an amount of wax myrtle fruit equivalent to the number consumed by myrtle warblers exceeded the swallow abundance actually observed by more than a factor of ten. Even though the calculations presented here are rough, they clearly illustrate the relative importance of these two species as quantitative dispersers.

Other investigations of the relationship between wax myrtle and myrtle warblers suggest that these findings are not anomalous and likely are typical of the quantitative effect of myrtle warblers at other sites containing wax myrtle (Whittle 1922, Skeate 1985, Borgman *et al.* 2004) or its congener bayberry (Wiltz and Giampa 1978, Parrish 1997). If true, such a geographic consistency would be highly unusual (Howe and Kerckhove 1979, Guitian 1992, Vander Wall 1994, Ladley and Kelly 1996, Carlo *et al.* 2003) and suggests a dependence rare in fruit-frugivore interactions.

The most surprising finding was that a substantial portion of the fruit crop was never ingested by frugivores, but fell to the ground beneath the parent plant. The significant correlation between the number of bird-passed seeds and the number of fruits in traps located in scrub and meadow habitats strongly suggests that such fruits fell as a result of frugivore activity and not because of abiotic factors like gusting winds. The lack of a relationship between these two variables in forest habitat, I imagine, is due to the low density of wax myrtle plants growing in these areas. Because these data were collected when warblers were largely the only disperser present at my site (November – April), I suspect that myrtle warblers are the principal cause of the observed relationship between voided seeds and fallen fruits in scrub and meadow habitats. The tendency of these frugivores to drop wax myrtle fruit (Lowe, unpub. data, Willson and Whelan 1993) may be a factor. Since a cursory inspection of whole fruits in traps revealed no obvious sign of infestation or rot, dropping fruit appears to be more a matter of dexterity than actual rejection. Though these data were collected in only one year, the relatively large numbers fallen or dropped fruit indicate the importance of determining whether such propagules are likely to contribute to plant recruitment.

Qualitative Dispersal

Germination

Greenhouse experiments testing the effects of pulp removal, seed coat abrasion by gastric acids, disperser identity, method of voiding, and the influence of feces on germination suggest that dispersers provide no benefit to the plant in terms

of germination likelihood. However, these results should be interpreted with some

caution since such treatments could produce important effects later in the seedling

stage (Soto-Gamboa and Bozinovic 2002).

The most unexpected result was the high germination rate of wax myrtle seeds

encased in fruit. Because wax myrtle fruits are surrounded by a waxy exocarp that

presumably inhibits water absorption (see Meyer and Witmer 1998) and because *M.*

faya germination rates improved with fruit removal (Walker 1990), I expected these

fruits to germinate at much lower rates than manually depulped or voided seeds as

reported by Fordham (1983).   However, the comparatively low germination rates

that he reported in other trials suggest that our results may not be comparable.

Similarly, the presence of pulp has been shown to depress germination in a variety of

species, whether dispersed by birds or ants (McDiarmid *et al.* 1977, Hickey *et al.*

1999, Pizo and Oliviera 2001, Godinez-Alvarez *et al.* 2002), sometimes even

rendering it impossible (Izhaki and Safriel 1990, Ladley and Kelly 1996, Yagihashi *et*

al. 1998). For example, only 1.2% of Virginia creeper seeds (*Parthenocissus*

quinquefolia) remaining within pulp germinated, while manually depulped seeds

exhibited a mean germination rate of 80% (Lowe unpub. data).

Avian and mammalian ingestion, and consequent seed coat abrasion (Barnea

et al. 1990), also commonly produce an increase in germination rates, as shown in

the recent, comprehensive review by Traveset and Verdu (2002) and work by Motta-

Junior and Martins (2002). For example, germination rates of *Juniperus virginiana*

seeds improved nearly 40% after ingestion by myrtle warblers (Holthuijzen and

Sharik 1985). As with fruit removal, seed scarification is assumed to increase water

and oxygen absorption (Mayer and Plojakoff-Mayber 1989), breaking down a seed

coat evolved to be thick enough to withstand the rigors of digestive processes. It is

possible, however, that these results (and those herein), obtained in a greenhouse

where water was plentiful, may not be applicable to habitats like barrier islands where

fresh water is limiting (Young et al. 1992, Shao et al. 1995) and where efficiency in

water use may be critical (see Rey and Alcantara 2000).

Although the effect of disperser identity is perhaps less important than

initially expected (see Snow 1971, McKey 1975), conspecific seeds passed through

different disperser species commonly display significantly different rates of

germination success (Krefting and Roe 1949, Holthuijzen and Sharik 1985,

Lieberman and Lieberman 1986, Izhaki and Safriel 1990, Murphy *et al.* 1993,

Godinez-Alvarez *et al.* 2002, Calvino-Cancela 2004). Indeed, specialist frugivores

improve germination likelihood in mistletoe (Reid 1989, Murphy *et al.* 1993, Larson

1996). The cause of these differences are as of yet unclear (Lieberman and Lieberman

1986, but see Murphy *et al.* 1993), though differential passage times (McKey 1975,

Murray et al. 1994, but see Wahaj 1998) and species-specific bacterial composition of

feces (Crossland and Kloet 1996) seem likely causes.

In contrast to the treatments above, the relative effects of method of voiding

(regurgitation versus defecation) and the presence and amount of feces on

germination rates are largely unexplored. *Corema album* seeds had significantly

higher viability when regurgitated by gulls (Calvino-Cancela 2002), whereas Meyer

and Witmer (1998) found that the method of voiding had no impact on germination

on seeds from three temperate fruiting plants. The presence of mammalian and avian

feces has been shown to depress germination (Dinerstein and Wemmer 1988, Meyer and Witmer 1998, Hickey *et al.* 1999, but see Rogers 1998, Balcomb and Chapman 2003, Calvino-Cancela 2004). Any fertilizing effect, I suspect, would be negligible given the size of the defecation.

In contrast, the timing of germination was significantly slowed by the presence of the waxy exocarp (see also Traveset *et al.* 2001), but did not differ between species or depulped seeds (Greenberg et al. 2001). This suggests that seeds in fallen fruit are less likely to survive the seedling stage if earlier emergence date increases seedling survivorship as commonly assumed (Murray 1988, Izhaki and Safriel 1990, Loiselle 1990, Traveset et al. 2003), especially in nutrient poor communities (Hutchings *et al.* 2003). Although the ecological significance of different germination dates for wax myrtle seedling establishment was not explicitly tested in this study, a speedier emergence would not only reduce exposure time of seeds to predators, but also provide an advantage when competing for water with neighbors over the course of the summer (see Shao et al. 1995).

Seed Deposition

Observations of the post-foraging behaviors and habitat preferences of frugivores have proven to be a useful means of assessing the value of seed shadows generated by avian and mammalian dispersers to fruiting plant recruitment (Howe and Primack 1975, Herrera and Jordano 1981, Sorensen 1981, Hoppes 1987, Malmborg and Willson 1988, Fuentes *et al.* 2001, Calvino-Cancela 2002, Kaplin and Lambert 2002, Calvino-Cancela 2004). While the effects of tree swallow post-

foraging behavior on wax myrtle are relatively clear, results presented here strongly suggest that those of myrtle warblers and gray catbirds are stage dependent (Bronstein 1994).

The lack of a significant difference between the within patch post-foraging movements of warblers and catbirds suggests that they generate similar seed shadows with respect to distance from the parent plant. In younger, but established thickets patches where seedling recruitment is limited largely by escape (Chapter 2), both species could therefore be expected to provide equivalent dispersal services. Although post-foraging microhabitat preferences of dispersers have been shown elsewhere to influence seedling recruitment (Herrera 1984, Herrera et al. 1994, Calvino-Cancela 2002, 2004), vegetation analysis indicates that those microhabitat variables perceptible to dispersers had no effect on seedling recruitment in scrub habitat (Chapter 2).

Yet for seeds produced in a mature thicket in scrub habitat, where local recruitment is highly unlikely and establishment is contingent on either emigration to a younger patch or on colonization of a new site altogether (Young et al. 1995), only deposition outside the patch's boundaries can be expected to improve the likelihood of establishment (Murray 1986, Hoppes 1988). Although the value of within-patch dispersal could increase if followed by a fire that removed heterospecifics, the effect of fire on dispersed seeds is as yet unexamined. In the absence of such data I conclude that myrtle warblers, with their significantly greater tendency to leave patches after frugivory, provide greater benefit to wax myrtle. While these data do not provide information on the likelihood that departing warblers fly to patches

suitable for colonization, they do suggest that myrtle warblers are the most likely

agent of seed deposition beyond the boundaries of a particular patch. Additionally,

unlike catbirds, these warblers were commonly observed in a variety of habitats in

addition to wax myrtle thickets. For example, myrtle warblers were observed in

Spartina meadows many meters away from scrub patches, potential sites for wax

myrtle colonization (see Chapter 2). Catbirds were never observed in these open

grasslands.

Other studies suggest that the observed behavior of both species on

Assateague is typical at other locations. In Illinois, myrtle warblers left fruiting

plants after foraging more often than expected, while gray catbirds did not

(Malmborg and Willson 1988). Elsewhere, both species also have been reported to

differ in their habitat use. While gray catbirds are generally associated with shrubby

habitats (Hoppes 1987, Cimprich and Moore 1995), myrtle warblers are highly plastic

in their habitat selection during the non-breeding season (Parnell 1969, Wiltz and

Giampa 1978, Zeller 1995, Hunt and Flaspohler 1998, Suthers et al. 2000), increasing

the number of potential sites in which they might deposit seeds.

Tree swallows were the only disperser for which direct observation of

defecation sites was possible. Unlike myrtle warblers, which form casual and loose

flocks on Assateague Island, tree swallow flocks have highly cohesive even when

processing a fruit meal. This cohesion, in combination with a generally large flock

size and relatively short tarsi, restricts swallows to relatively large and dry expanses

when food processing. Flocks of tree swallows were most commonly observed

resting on beaches and primary dunes and less so in dry salt pannes along

Assateague's western flank; very few flocks were observed resting in scrub habitat. Inspection of these areas after flocks had departed confirmed that these were sites of heavy *Myrica* seed deposition.

Seeds deposited either in the highly saline environment of beaches or salt pannes were highly unlikely to survive (Miller and Egler 1950, Salter and Lamont 1990, Young et al. 1995). Neither wax myrtle adults nor seedlings were observed on subsequent surveys of these locations. These data clearly demonstrate the pitfalls of estimating contributions of disperser species to plant recruitment without considering qualitative factors (e.g. Moran et al. 2004). However, even if their seed shadow does not contribute substantially to the recruitment of wax myrtle, tree swallows may be adequate dispersers of bayberry seeds indicated by adults commonly found on Assateague Island's primary dunes (Ehrenfeld 1990). Although observations of their seed deposition sites were collected opportunistically, these observations provide a clear trend to post-foraging habitat preferences. It is quite possible, however, that tree swallows did provide higher quality seed shadows previously prior to the removal of power lines in 1999 that stretched south along the length of Assateague Island and traversed suitable habitat for wax myrtle recruitment.

Conclusion

Seed dispersal is essential for the population viability of wax myrtle on Assateague Island, allowing seeds to escape high mortality beneath fruiting plants in young thickets and those in older thickets to colonize new sites, thus outrunning both woody heterospecifics and the encroaching ocean. Myrtle warblers were both the

primary and the best disperser of wax myrtle. These frugivores provided the greatest

quantitative contribution of any disperser in all years and also appeared to provide a

seed shadow most consistent with wax myrtle's ecological needs. Although gray

catbirds may provide similar qualitative benefits to fruiting individuals in younger

patches, seed shadows generated by catbirds are not likely to be as broad as those

produced by myrtle warblers and are therefore less likely to include distant sites

available for colonization. Since seeds encased in fruits germinated at the same rate

as and appeared to be far more numerous than those removed by gray catbirds, fallen

fruits in areas of local flooding could *in toto* potentially contribute more to

recruitment than seeds dispersed by catbirds. However, any benefit from fallen fruit

is likely to be restricted to younger thickets since it is improbable that fruit-encased

seeds falling in more mature thickets could float a sufficient distance to reach a new

site. In contrast, the tendency of tree swallows to defecate on beaches and primary

dunes, suggests that tree swallows, whatever their quantitative contribution,

ultimately act more as predators in this interaction than as mutualists.

Wax myrtle does benefit in part from a diffuse mutualism on Assateague

Island in the sense that gray catbirds are likely contributors to recruitment. However,

there is no evidence of functional redundancy of dispersers given the myrtle warblers'

vastly superior quantitative dispersal, especially in winter and springs when predation

rates are lowest in salt grass meadows (Chapter 2), and the fact that their qualititative

contribution is not stage dependent. These data suggest that decreases in the number

of myrtle warblers would severely impact wax myrtle recruitment (see Howe 1984,

Loiselle and Blake 2002, Moran et al. 2004), paralleling the converse changes

discussed in Chapter 1. Whether myrtle warblers play an equivalently significant role in wax myrtle recruitment in other locations with different ecological conditions and a potentially different dispersal assemblage is unknown, however. Future research might profitably examine the effect of dispersers on wax myrtle elsewhere as well as investigating other relationships that have the suggestion of specialization (e.g. Bates 1992, Greenberg et al. 1995).

Acknowledgements

Table 3-1. Repeated measures analysis of the relative monthly abundance of myrtle warblers and gray catbirds on Assateague Island during the months in which both were present (late September/October, November and April.) Autumn data were collected in three years (1998, 1999, 2001), spring data were collected only in 2001.

Effect	Numerator DF	Denominator DF	F	*P*
Species	1	3.01	90.13	< 0.01
Month	2	22.5	26.39	<.0001
Month*Species	2	22.5	2.88	0.770

Table 3-2. Estimate of both monthly and annual total number of wax myrtle fruits consumed by myrtle warblers. Estimates are the product of monthly mean warbler abundance and on the number of fruits eaten in captivity (Chapter 1). Warbler abundance for the Maryland portion of the island was calculated by multiplying the expected fruit consumption of the number of birds sampled by the total area of wax myrtle scrub on Assateague Island.

Month	Mean ± SE warbler abundance	Mean ± SE fruit/day	Area (ha) of *M. cerifera*	Upper estimate consumed/ month	Lower estimate consumed/ month
Oct.	100.3±33	174 ± 21.4	178	143×10^6	568×10^5
Nov.	83.1±18	174 ± 21.4	178	105×10^6	530×10^5
Dec.	91.8±8.9	174 ± 21.4	178	109×10^6	698×10^5
Jan.	89.7±8.6	174 ± 21.4	178	106×10^6	698×10^5
Feb.	69.7±7.5	174 ± 21.4	178	751×10^5	472×10^5
Mar	56.0±12.1	174 ± 21.4	178	734×10^5	370×10^5
April	11.5±2.7	174 ± 21.4	178	148×10^5	740×10^4
Estimate of total wax myrtle fruit consumed per year				627×10^6	339×10^6

Table 3-3. Monthly totals of tree swallows observed on Assateague Island National Seashore in multiple years. Observations were not collected during late September – October 1997 nor in 1999.

Month	Year	Total No. swallows observed
Sept/Oct	1998	15,680
	2000	13,300
Nov	1997	3700
	1998	20,600
	2000	0
Dec.	1997	500
	1998	0
	2000	0

Table 3-4. Frequency of the occurrence of resting tree

swallow flocks in three gross habitat types on Assateague

Island. All flocks were observed between late September and

mid-November.

| Year	Beach/Dunes	Scrub	Low marsh/panne
1998	5	1	2
1999	6	0	1
2001	7	0	1
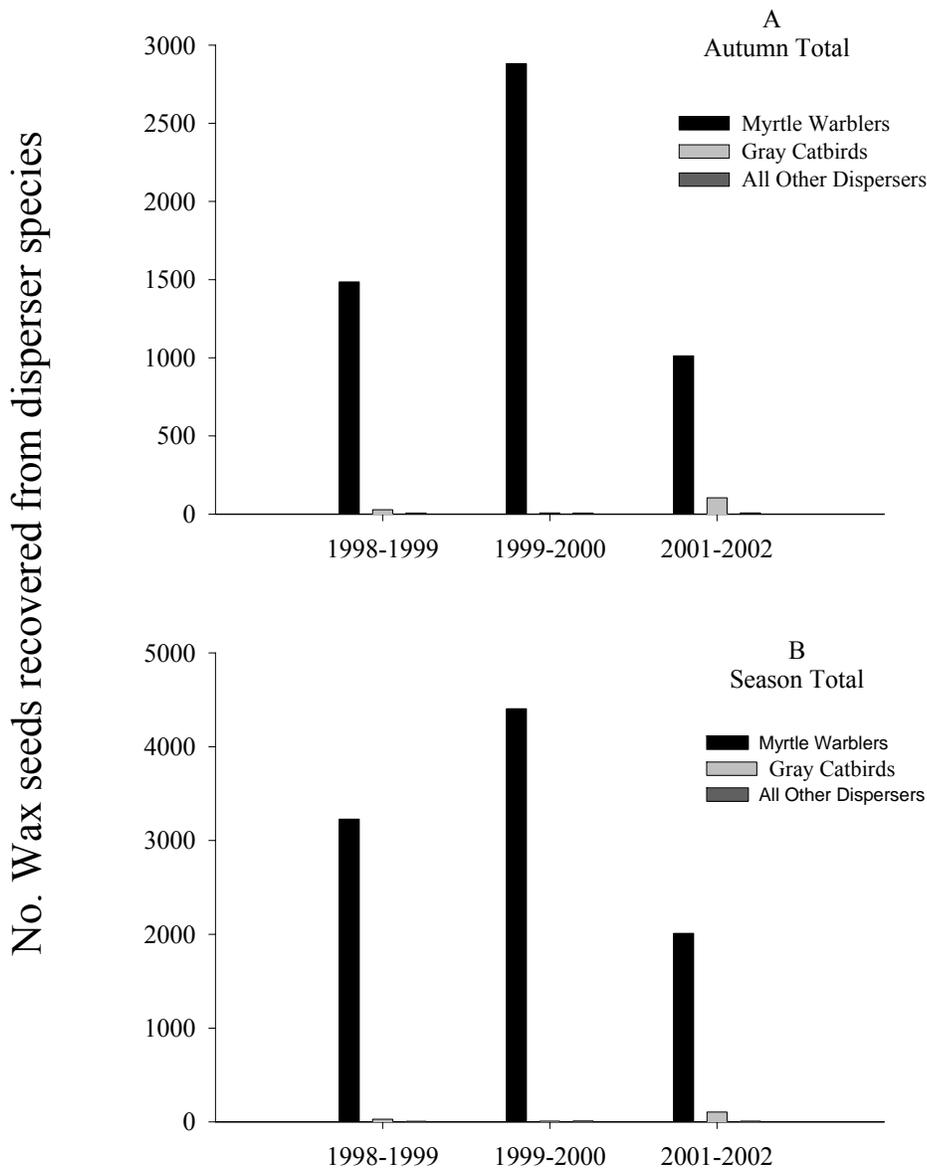
Figure 3-1. Number of wax myrtle seeds recovered from the fecal samples collected

from mist netted birds on Assateague Island National Seashore in multiple years.

Figure 3-1A presents data collected between late September and the end of October.

Figure 3-1B presents total number of seeds removed that dispersal season (late

September –April). These data do not include percentage of wax myrtle seeds

removed by tree swallows (see text).
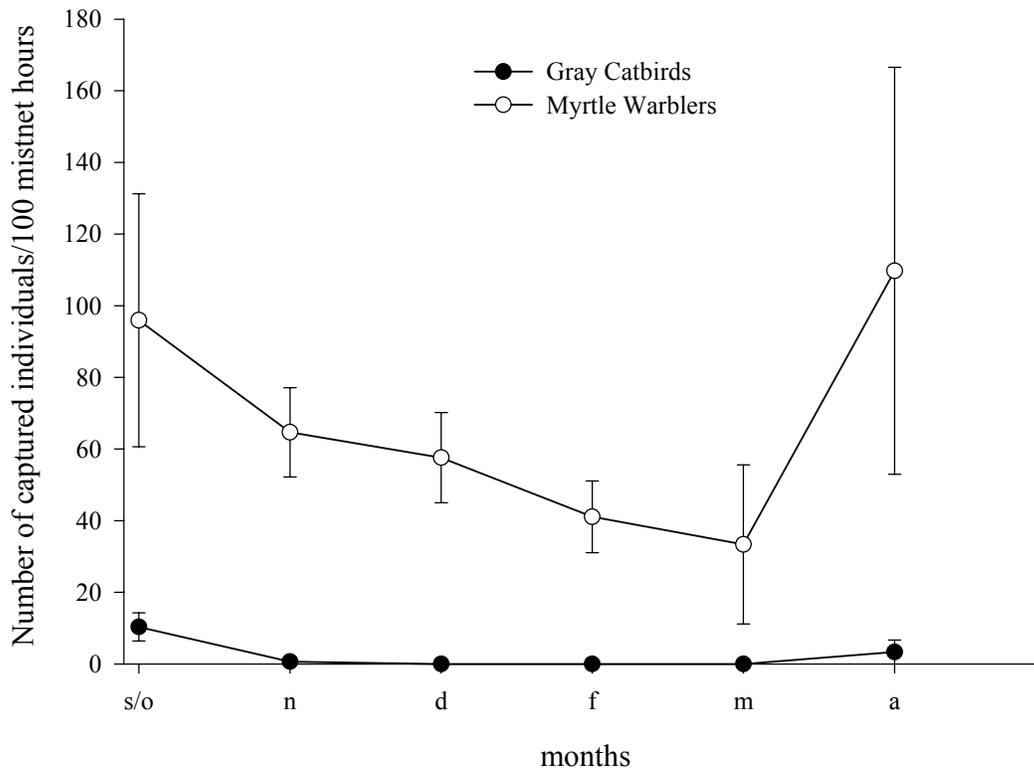
Figure 3-2. Comparison of the numbers of myrtle warblers and gray catbirds captured/100 mist net hours each month. Data points are the monthly means (± SE) of capture rates from 1998 – 2000, 2001-2002. The only exception is data from April, which are only from 2002.
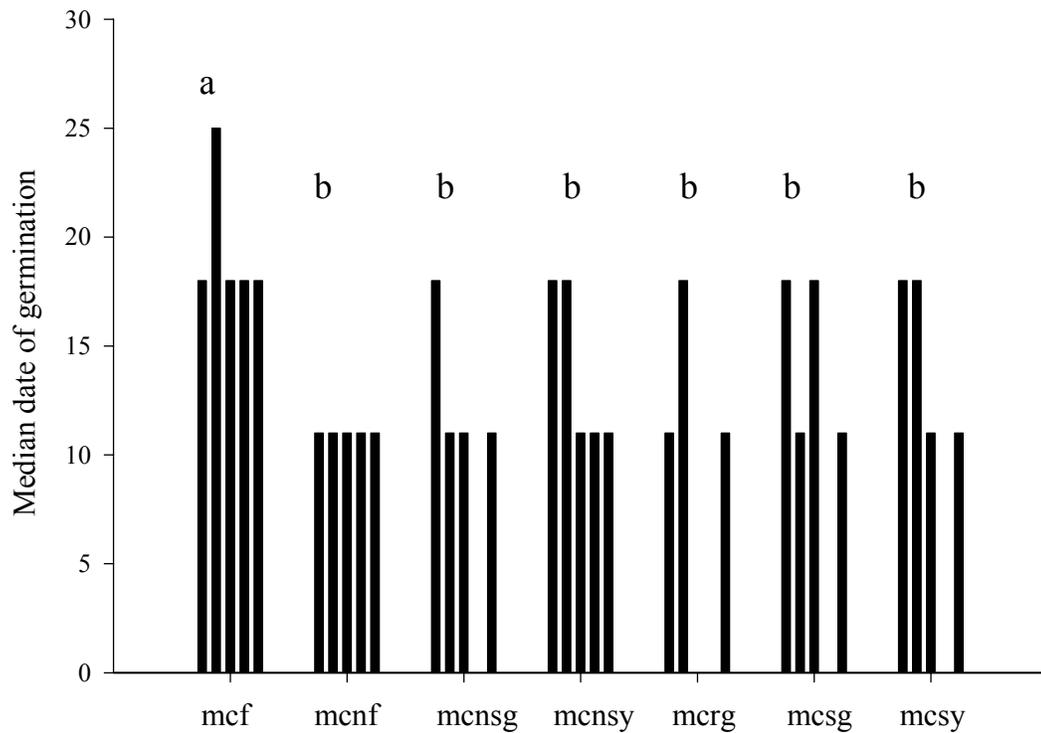
Figure 3-3. Effect of fruit pulp, gastric acid exposure, species identity, presence of feces and mode of voiding on the median germination date of wax myrtle seeds. Seeds encased in waxy pulp germinated significantly more slowly than other treatments ($p < .001$). Each line represents data from an individual seed flat. The treatments are abbreviated as follows: mcf = seeds in wax myrtle fruit, mcnf = manually depulped seeds, mcnsg = catbird defecated seeds without feces added, mcnsy = warbler defecated seeds without feces added, mcrg = catbird regurgitated seeds, mcsg = catbird defecated seeds with feces added, mcsy = warbler defecated seeds with feces added.
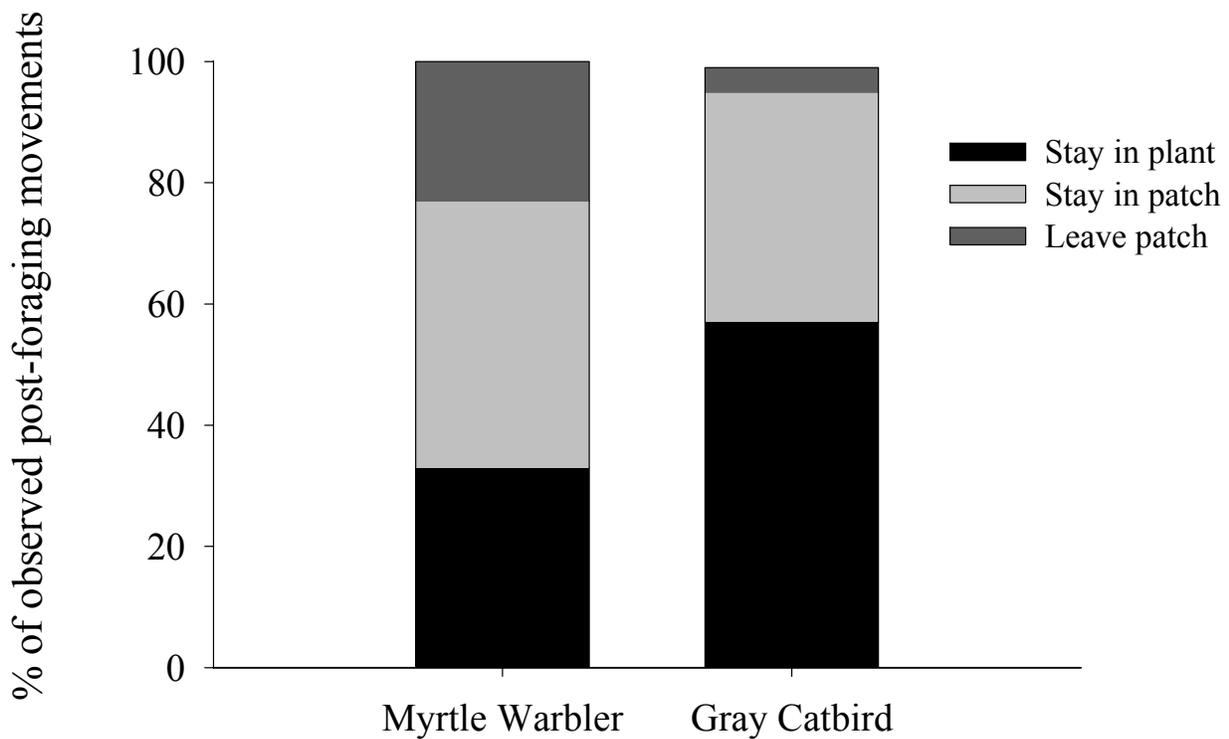
Figure 3-4. Comparison of the post-foraging movements of myrtle warblers (n = 283) and gray catbirds (n = 21) after consumption of wax myrtle fruit in scrub habitat. Columns represent relative frequency of species to remain in the fruiting plant after frugivory, leave the parent plant and fly to another location in the habitat patch or to leave the patch altogether prior to defecation of ingested seeds. Myrtle warblers significantly more likely to leave habitat patches after foraging (see text). Data were collected in scrub habitat in 1998.

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