2012

Prairie Warbler Nest-site Selection, Nest Survival, and Demographic Response to Management in a Pitch Pine-Scrub Oak Barren

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PRAIRIE WARBLER NEST-SITE SELECTION, NEST SURVIVAL, AND DEMOGRAPHIC RESPONSE TO MANAGEMENT IN A PITCH PINE-SCRUB OAK BARREN

A Thesis Presented

by

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Submitted to the Graduate School of the

University of Massachusetts Amherst in partial fulfillment

of the requirements for the degree of

MASTER OF SCIENCE

September 2012

Wildlife and Fisheries Conservation

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DEDICATION

To my family.

ACKNOWLEDGMENTS

The U.S. Forest Service, Northern Research Station provided the funding for the project, and I thank MASSWildlife and Dr. Bill Patterson for conducting the management treatments and allowing us to conduct work in the MPWMA. I would like to thank all the field technicians for their tireless work and countless hours of help in the field. These technicians include Carly Chandler, Jen Glagowski, Tyler Maikath, Deysha Rivera, Sam Roberts, Matt Smith, Greta Turschak, Mattie VandenBoom and Jesse Wampler. I am especially grateful to Brodie Kramer for working multiple summers and helping out with related work in the wintering grounds. I'd like to thank my advisor Dave King for his support and the opportunity to conduct this project, as well as his guidance throughout the project. Thanks to my committee as well, Bob Brooks and Bruce Byers, who also provided support and guidance throughout the project. I'm grateful to my lab mates and fellow graduate students in the Environmental Conservation department who were very helpful with feedback and stats guidance with this project. Thanks to my family, friends, and Bethany for your unwavering support.

ABSTRACT

PRAIRIE WARBLER NEST-SITE SELECTION, NEST SURVIVAL, AND DEMOGRAPHIC RESPONSE TO MANAGEMENT IN A PITCH PINE-SCRUB OAK BARREN

SEPTEMBER 2012

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Early successional forests occur in a "shifting mosaic", in which available shrubland habitat changes both spatially and temporally in response to disturbance. Due to suppression of natural disturbances, most shrubland habitat currently consists of habitat deliberately created and maintained in various forms by management: newly created shrubland habitat that matures over time (e.g., clearcuts), habitat that is persistent but disturbed on a periodic basis (e.g., scrub oak barrens), or habitat that is persistent yet minimally disturbed through time (e.g., power line corridors). As shrubland bird populations decline, there is a critical need to understand the effects of habitat creation, succession, and disturbance, and to acquire knowledge of basic demographic parameters such as habitat-specific fecundity and dispersal that are keys to shrubland bird conservation. I studied a population of color-banded prairie warblers (*Setophaga discolor*) between 2008-2011 in a shifting mosaic 'meso-landscape' within a Massachusetts inland,

pitch pine-scrub oak barren consisting of persistent, newly created, succeeding, and disturbed habitats. In Chapter One, I present data showing that the abundance and population structure at this site appears to be a function of colonization of newly created habitat by second-year birds, which are likely excluded from mature early-successional habitat by site-faithful older birds. Breeding season fecundity did not differ significantly between newly-created and mature habitats. Birds displaced by mowing or fire dispersed to nearby suitable habitat the following year. These displaced individuals did not negatively affect pairing or reproductive success for birds in adjacent areas. My findings that newly created habitat is colonized by second-year birds who enjoy similar reproductive success as older-birds in mature habitat, and that reproductive success was similar for birds displaced by habitat disturbance are novel. Furthermore, these findings show that the short-term effects of shrubland management on shrubland birds are minimal and beneficial in the long-term by maintaining ephemeral shrubland habitat.

Understanding nest-site selection and nest survival of declining shrubland birds is important for management as nest survival is considered one of the biggest determinants of passerine reproductive success. Many studies have examined the ways in which birds are adapted to select nest sites that increase nest survival, yet few studies have empirically taken into account interactions with plant leafing phenology. In Chapter Two, I examined nest-site selection and nest survival for a conservation-priority shrubland bird, the prairie warbler, in a managed pitch pine-scrub oak barren in Montague, Massachusetts. I found prairie warblers selected more dense vegetation at the preferred nest heights between 0.5-1.5 m and selected nest sites close to roads and fire breaks. Frost tolerant plant species were selected as nest substrates early in the season, as late frosts in the study site delayed oak species leaf-out dates. After oak species leaf-out, there was a predominant switch to using oaks as nest substrate in habitats in which oaks were a major component. Nest

survival rates differed among years, decreased with nest age and distance to road or fire break, increased with nest concealment, and in a delayed leaf-out year, survival rates were lower before leaf-out of the dominant nest vegetation. Few variables significantly affected cowbird parasitism rates. I conclude that nest-site selection is adaptive in the sense that it increased nest survival. Plant phenology influenced nest-site selection and nest survival in this system; its effects on birds should be considered as a potential mechanism by which bird communities can be affected by global climate change.

TABLE OF CONTENTS

Page

ACKNOWLEDGMENTS v

ABSTRACT vi

LIST OF TABLES xi

LIST OF FIGURES xii

CHAPTER

1. DEMOGRAPHIC RESPONSE OF A SHRUBLAND BIRD TO HABITAT CREATION, SUCCESSION, AND DISTURBANCE IN A 'SHIFTING MOSAIC' LANDSCAPE 1

Introduction 1

Methods 7

Study Site 7

Bird Sampling 9

Habitat Sampling 11

Statistical Analysis 12

Results 17

Discussion 20

Management Implications 27

2. PLANT PHENOLOGY AND OTHER FACTORS AFFECTING NEST SITE SELECTION AND NEST SURVIVAL FOR PRAIRIE WARBLERS IN A PITCH PINE-SCRUB OAK BARREN 41

Introduction 41

Methods 44

Study Site 44

Sampling 46

Statistical Analysis 49

Results 59

Discussion 63

Management Implications 75

APPENDIX: PHENOLOGY INDEXES 102

LITERATURE CITED 104

LIST OF TABLES

Table Page

1.1. Vegetation characteristics in prairie warbler territories in different years since treatment in treated pitch pine habitat in the MPWMA between 2009-2011 29

1.2. Vegetation characteristics in prairie warbler territories in four habitat types in the MPWMA, during 2009-2010 32

1.3. Prairie warbler seasonal fecundity among habitats, years, years since treatment(YST) of treated pitch pine, and male age classes in 2009-2011 34

1.4. Return rates and site fidelity of male prairie warblers by year since treatment in treated pitch pine, among bird ages, and among habitat types during 2008-2011 36

2.1. Covariates and their notation used in the nest survival and cowbird parasitism analyses. 77

2.2. Number of nest substrates by plant species and habitat type for prairie warbler nests found in 2008-2011. 79

2.3. Estimated percentage amounts of the most used nest substrates in prairie warbler territories, in relation to amounts of all vegetation and ground cover in the territories. 81

2.4. Vegetation characteristics between the nest location, nest patch, and random points within a territory in 2009-2011 82

2.5. Model selection results for the top models from nest depredation and nest parasitism analyses. 83

2.6. Parameter estimates from the best model of each subset analysis. 89

LIST OF FIGURES

Figure Page

1.1. Map of the MPWMA, located in Montague, MA 37

1.2. Prairie warbler density in newly created and maturing treated pitch pine in the MPWMA by years since treatment. 38

1.3. Prairie warbler density in power line corridor and scrub oak plots in the MPWMA between 2008-2011 39

1.4. Proportion of ASY prairie warbler males in treated pitch pine by years since treatment 40

2.1. Leaf length averaged per stem by year, day, and vegetation species in 2009-2011 92

2.2. Leaf length of scrub oak averaged per sampling point by day and habitat type in 2009 93

2.3. Nest-site selection of frost tolerant versus frost intolerant species over time in three habitat types during 2008-2011 94

2.4. Nest-site selection of frost tolerant versus frost intolerant substrate in relation to the complex leaf length index of a frost intolerant species (scrub oak) at the nest initiation date. 96

2.5. Distances to roads/fire breaks (RFB) and forest edges (FE) of nests found between 2009-2010, compared with mean distances of random points within territories to RFB and FE 97

2.6. Prairie warbler nest daily survival rates (DSR) relationships with significant covariates 101

CHAPTER 1

DEMOGRAPHIC RESPONSE OF A SHRUBLAND BIRD TO HABITAT CREATION, SUCCESSION, AND DISTURBANCE IN A 'SHIFTING MOSAIC' LANDSCAPE

Introduction

Early-successional habitat and associated wildlife are declining dramatically in the eastern United States and this decline is widely considered a critical conservation challenge (Trani et al. 2001, Oehler 2003). The area of early-successional forest, defined as seedling-saplings or non-stocked-size timber, has declined in the last half century (Trani et al. 2001, Brooks et al. 2003), and wildlife that predominantly use early-successional forests have been declining as well; the majority of avian species breeding in early-successional habitats are currently at their lowest populations ever recorded (Litvaitis 1993, Schlossberg and King 2007). Historically, early-successional forest was maintained by natural and Native American started fires, flooding due to beaver dams, and tree mortality and windfall due to occasional insect outbreaks and infrequent, large-scale hurricanes (Naiman et al. 1988, Litvaitis 2003, Lorimer and White 2003). However, currently wildfire is actively suppressed for human safety, beaver flooding is controlled to reduce landowner damages, and development has arisen in areas that historically afforded shrubland forests such as coastal areas and pitch pine-scrub oak barrens (Motzkin et al. 1999, DeStefano and Deblinger 2005, Lorimer and White 2003). The ecological effect of this decline of early-successional forest is striking—biological diversity in the region is decreasing as a large number of early-successional dependent plant, insect, and vertebrate species are now endangered, threatened, or of conservation concern (Clark and Patterson 2003, Wagner et al. 2003, Schlossberg and King 2007).

To prevent the decline of shrubland habitat, there has been a regional effort to create and maintain early-successional forests through management activities and forestry (Thompson and DeGraaf 2001, Clark and Patterson 2003, Oehler 2003). Silvicultural practices such as large-scale clearcuts are excellent for creating large areas of core shrubland habitat (King et al. 2009b), however clearcuts only provide shrubland habitat for 10-15 years before they become unsuitable for shrubland birds (Schlossberg and King 2008). Another method to create and maintain early-successional habitat has been through wildlife openings, which are managed areas that are regularly maintained by burning, mowing, applying herbicides, or by other means (Chandler et al. 2009a). These openings are punctuated by periodic disturbance and provide a distinct composition of shrubland birds relative to clearcuts (Chandler et al. 2009a, King et al. 2009b). Power line corridors maintained by utility companies can create persistent shrubland habitat, as the selective herbicide applications often used can maintain a relatively unchanging shrubland habitat that is dominated by low-growing, shrubby vegetation (Dreyer and Niering 1986, Confer and Pascoe 2003, VMP 2004-2009, Folsom 2008, King et al. 2009a). Managers have also created and maintained xeric early-successional habitat in pitch pine-scrub oak barrens, to reduce the risk of catastrophic wildfires and to promote biodiversity (Clark and Patterson 2003, Gifford et al. 2010).

Early-successional habitats are by their nature ephemeral and require constant management to preserve their distinctive ecological characteristics, however shrubland management can be costly (Oehler 2003). Shrubland management can also be controversial to people who view management as anathema to their values of maintaining mature forest (Gobster 2001). Indeed, public outcry has led to a decline in even-aged forestry practices in the northeast (Trani et al. 2001). Because management is associated with financial costs and social conflicts, care must be taken to ensure expenditures are efficient and

management activities are defensible. Detailed information on how wildlife is affected by management practices is critical to allocating scarce resources to conserve species dependent on shrubland habitats.

An important feature of shrubland habitats that has received little attention is how ephemeral habitats, and by extension the species that depend on them, persist on the landscape. One way past researchers have conceptualized this is with a shifting mosaic landscape concept in which available habitat occurs in patches that change spatially and temporally depending on the frequency, intensity and scale of disturbance (Watt 1947, Clark 1991). Shrubland birds may be influenced by a shifting mosaic habitat (Lent and Capen 1995, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Donner et al. 2010), as management practices and forestry create shrubland habitat that varies spatially and temporally at a landscape scale (Thompson and DeGraaf 2001, Brotons et al. 2005, Donner et al. 2010). Shrubland birds do appear to follow a pattern of colonization and abandonment of patches over time and space (Schlossberg and King 2009, Donner et al. 2010). Different shrubland bird species colonize newly created habitat at different years since initial treatment, and then follow a unimodal or negative directional trend as the habitat succeeds into mature forest (DeGraaf and Yamasaki 2003, Schlossberg and King 2009). Moreover, shrubland birds appear to colonize and abandon patches in relation to spatial characteristics, such as patch connectivity and size (Brotons et al. 2005, Donner et al. 2010).

Despite this knowledge, the mechanisms underlying these patterns remain poorly understood. Historically, researchers have considered early-successional birds to be 'fugitive' species characterized by low site fidelity; species that disperse from senescing habitat to colonize newly created patches only to become extirpated in habitat patches as they mature (Hutchinson 1951, Lent and Capen 1995), However a meta-analysis of site

fidelity studies showed adult male shrubland birds exhibited levels of site fidelity similar to those of forest birds in relatively static habitats (Schlossberg 2009). This finding suggests that the idea of shrubland birds as 'fugitive' species at the individual level thus needs to be re-examined and furthermore even the most basic demographic parameters remain to be established in these dynamic habitats.

Age-specific differences in dispersal behavior could provide a resolution as to how shrubland birds could exhibit high site fidelity as adults yet still colonize newly created habitats. Other studies have found that juvenile birds exhibit low natal philopatry and high dispersal distances (Greenwood and Harvey 1982, Lehnen and Rodewald 2009, Schlossberg 2009) leading Schlossberg (2009) to propose that newly created habitat would be colonized by second year (SY) males, as SY birds would be more inclined to disperse and find newly created habitat. After second year (ASY) males of shrubland birds typically arrive earlier on the breeding grounds and may outcompete SY males for the most suitable breeding territories in existing habitat (Fretwell and Lucas 1970, Zack and Stutchbury 1992, Petit and Petit 1996), making newly created habitat the only available habitat for SY males to colonize.

An understanding of these processes underlying the patterns of habitat use by shrubland birds can have important implications for population dynamics and habitat management. If SY birds are unable to colonize mature habitats occupied by ASY birds, yet have similar reproductive output as ASY birds (King et al. 2001b), this can increase reproductive output for the population and be beneficial for managers trying to conserve declining shrubland birds. Conversely, some studies have observed that younger males are less likely to acquire mates and can have lower reproductive success compared to older birds (Nolan 1978, Nol and Smith 1987, Lozano et al. 1996). If the majority of colonizing

birds are SY males that do not produce young, then the population benefits of habitat management are going to be characterized by a time lag of unknown duration as the habitat and the birds within it mature to the point where their reproductive potential is realized.

Another less-studied facet of shrubland bird demography relevant to the conservation and management of these species is the origin of individuals colonizing newly created habitat. Current conservation initiatives focused on creating habitat assume that if habitat is suitable, a newly created habitat patch will be colonized (DeGraaf and Yamasaki 2003). However, whether these colonizing birds originate from within the site or beyond its borders is poorly understood (Lehnen and Rodewald 2009). If the latter, than it is possible that management practices that fail to consider the availability of habitat at a landscape scale might be less effective for conserving shrubland birds (Dunning et al. 1995, Brotons et al. 2005).

In addition to studying mechanisms of colonization of newly created habitat and the abandonment of habitat patches as they mature beyond a condition useable to shrubland birds, it is also potentially important to consider the implications of shrubland habitat management on the individuals occupying the site prior to mowing or burning. Some studies have proposed that birds disperse to adjacent habitat after disturbance of mature forest sites (Hagen et al. 1996, Schmiegelow et al. 1997, Brotons et al. 2005), while at least one study noted birds remaining in newly created shrubland habitat after disturbance (Chandler 2006). To my knowledge only one study has tracked individually marked, displaced birds (n=2) (Betts et al. 2006). In addition to the effects of management on birds within the treated patch, dispersing individuals following disturbance may affect bird populations in adjacent areas. For example, Hagan et al. (1996) found an increase in forest birds in adjacent, non-disturbed habitat following the disturbance of forest sites by logging,

which then resulted in decreased pairing success and productivity in adjacent habitat, perhaps as the result of crowding. Few studies have examined if this also occurs with shrubland birds, despite disturbance playing a contingent part of habitat maintenance for these species.

Although the majority of shrubland habitat is ephemeral or periodically disturbed, some shrubland habitat is persistent over time without large-scale disturbance; understanding population dynamics in these habitats provides an interesting contrast to populations influenced by a shifting mosaic structure. Power line corridors in the northeast resemble this type of shrubland habitat, in which areas with selective herbicide application can resist tree invasion for as long as 50 years (Niering and Goodwin 1974, Neiring et al. 1986). Since these shrubland habitats are persistent, one might predict older males to dominate younger males and hold the majority of territories, if in fact adults exhibit high site-fidelity as shown by Schlossberg (2009) rather than exhibiting the low fidelity characteristic of "fugitive species" (Lent and Capen 1995). The age structure of these habitats could therefore contrast with the age structure of more ephemeral habitats. From the perspective of habitat management, maintaining persistent shrubland habitats could be more effective than periodic treatment that results in habitat passing through an earlier successional state, if there is lower bird abundance or reproductive success in newly created habitat than in more mature habitats (Confer and Pascoe 2003, Folsom 2008).

To address these knowledge gaps, I studied a population of color-banded prairie warblers (*Setophaga discolor)* in a managed, inland pitch pine-scrub oak barren with mosaic of newly created, maturing, mature and persistent habitats. Specifically, I studied bird abundance, age structure, reproductive output, return rates, and site fidelity as a function of

time since treatment to address the patterns, mechanisms and consequences of colonization of habitat for shrubland birds.

Methods

Study Site

The study took place in the Montague Plains Wildlife Management Area (MPWMA), an approximately 607 ha (1500 acre), actively managed reserve located in Franklin County, Massachusetts (N 42° 34', W 72° 31'). The MPWMA consisted of a mosaic of pitch pine and scrub oak (PPSO) stands, power line corridors, and transition hardwoods (Figure 1). The PPSO stands were managed by the Massachusetts Division of Fisheries and Wildlife (Clark and Patterson 2003), while the utility rights-of-way were managed by the Holyoke Water Power Company, Holyoke Power and Electric Company, and the Western Massachusetts Electric Company (a subsidiary of Northeast Utilities) (VMP 2004-2009).

The MPWMA, like most PPSO barrens, is located on nutrient-poor xeric soils. Plant communities in PPSO barrens are highly flammable and community retention is dependent on frequent fires (Motzkin et al. 1999). Due to the sandy soils, PPSO barrens tend to have extreme climatic fluctuations, in which killing frosts can occur in any month of the year (Motzkin et al. 2002). Within the MPWMA, wildfires occurred frequently in the early 20th century, with two fires burning parts of the nearby village of Lake Pleasant (Clark and Patterson 2003). The current PPSO stand distribution in the MPWMA has arisen greatly due to historic fire and human use; land cultivated in the 18th and 19th centuries grew back as pitch pine stands, while scrub oak stands remained in areas that were not historically plowed (Motzkin et al. 1996, Motzkin et al. 1999, Clark and Patterson 2003).

In 2000, the Massachusetts Division of Fisheries and Wildlife started a program of habitat restoration and fuels reduction to reduce fuel loads and wildfire risk and promote biodiversity (Clark and Patterson 2003). As a result, scrub oak stands during the study were comprised of a mosaic of burned, mowed or untreated areas, with relatively small treatment patches that were less than 1.5 ha (DFW Staff 2008). Scrub oak stands in the northern section of the study area were last burned in a wildfire in 1986, including plot 8 (Motzkin et al. 2002). I delineated this plot as untreated scrub oak. The scrub oak stands on the western side of the study site (named the Bitzer tract or plot 2) consisted of a mosaic of treatment plots. Some initial treatments were conducted in these treatment plots in 2000, while in other plots initial treatment occurred in later years (DFW Staff 2008). Most plots were mowed and/or burned twice between 2000-2005, while some treatment plots were treated just once since 2000. During the study, some treatment plots within plot 2 were then treated again primarily by large scale mowing (and some high-intensity burning as well), thus dramatically altering the habitat.

Active cutting of pitch pine stands has occurred since 2004, in which 70% of the basal area of overstory pitch pine was removed (Clark and Patterson 2003). There was also some post-harvest burning, mowing and selective cutting of grey birch and red maple in treated pitch pine (DFW Staff 2008), however, most of these treatments were relatively small-scale and low intensity. At present, approximately 50 % of the closed canopy pitch pine forests in the MPWMA have been cut. Power line corridors in the study plots were managed primarily by selective or broadcast herbicide application, and this effectively maintained a persistent early-successional habitat (VMP 2004-2009). Plot 1 had broadcast herbicide applied and plot 7 had selective herbicide applied in the winter of 2010-2011. Besides the power line corridors used as study plots, another power line corridor existed

through the study site from the southeast to the northwest; parts of this corridor have been burned repeatedly since 2000 and thus this corridor was maintained as a grassland.

Bird Sampling

I estimated bird abundance by mapping male prairie warbler territories using GPS locations, treatment maps, and field markers in the area (Franzreb 1981, Oelke 1981, DFW Staff 2008). Intensive territory mapping was done in 8 plots: 2 plots in scrub oak (1 managed and 1 unmanaged plot), 4 plots in treated pitch pine, and 2 plots in power line corridors. The treated pitch pine plot 6 was initially thinned in 2004, plot 5 in 2006, and plots 3 and 4 in 2007 (Figure 1). A small section of plot 5 was also partially thinned (more than 30 % canopy cover) in 2004 (MASSGIS aerial photo), however I ignored this partial thin in my analyses. The power line corridor plots (1 and 7) selected were within the PPSO barrens and consisted of a similar sandy soil type. I visited plots and mapped territories multiple times over the course of the breeding season, approximately every week in 2008 and every 2-4 days in 2009-2011. Birds were included in the final territory maps if they were confirmed breeders or if they were observed twice in a given territory over a period greater than 10 days (Bibby et al. 1992, Villard et al. 2007), although most birds were observed on many occasions over a longer period of time.

In order to delineate individuals, males were captured and color banded (72% of the males within extensively surveyed plots between 2009-2011). Territories for birds that I was unable to color band were determined by a bird's consistent presence in a given area and the presence of neighboring color banded males. I target mist-netted birds using prairie warbler songs and a decoy. All captured birds were banded with a United States Geological Survey aluminum band and a unique color combination of 2-3 plastic color bands. Birds

were identified by age and sex using plumage, breeding condition, feather wear and molt limits (DeSante et al. 2008).

I determined if birds fledged young by monitoring nests within territories and systematically searching for fledglings in territories where I did not locate a successful nest. Nests were found by observing parent behavior and conducting systematic searches (Martin and Geupel 1993). Nests were marked with flagging placed 10-15 m from the nest and monitored at intervals of 2-4 days until the nestlings fledged or the contents of the nest were gone (Martin and Geupel 1993, Weidinger 2008). Territories successful in fledgling young were classified as having fledged at least one prairie warbler young. The latest fledging date recorded (n=315 nests) during 2008-2011 was July 25th, which is a similar date found by Nolan (1978) in a long-term study. Using this date, I stated that a given territory did not fledge young if 1) a known nest in the territory failed on or after June 30th (given a 26-day nesting interval including a short building stage), or 2) I did not see or hear fledglings or observe parents carrying food during visits to the territory between June 10th and July 25th. In addition to passive surveys, at the end of the breeding season I also played prairie warbler and Eastern screech owl (*Otus asio*) callbacks to determine if birds were still present or breeding.

Between 2008-2011 at successful nests, I color banded prairie warbler nestlings when they were approximately 8 days old. In 2010 and 2011, in addition to re-sighting prairie warblers within the survey plots, I also surveyed for returning banded-as-nestling and dispersing adult birds outside the plots. These surveys were conducted within the general area of the study site in areas with suitable early-successional habitat. This allowed us to estimate what percentage of the total population at the entire study site was made up of returning natal birds banded from the previous year, assuming I banded the majority of

fledglings within the study site the previous year. I estimate that I banded approximately 85 % of nests that fledged young within the study plots in 2009, based on surveys of fledglings in territories where I did not find a successful nest. In 2010, bird densities increased, and I approximate that I banded 50 % of nests that fledged young in the entire study site. This 2010 approximation was based on observations of fledglings in territories where we did not find a successful nest, as well as estimating seasonal fecundity in known territories in which we could not extensively survey for fledglings, by using the proportion of territories that fledged young in 2010.

Habitat Sampling

To quantify vegetation structure and composition among habitats, I used point-intercept vegetation surveys (King and DeGraaf 2000, Chandler et al. 2009b). Vegetation surveys were located within mapped territories of male prairie warblers. Vegetation points within a territory were determined by creating 20 equally spaced locations along a transect spanning the length of a given male's territory. From these equally spaced locations, I selected a random direction, right or left, from this transect and paced out a random distance (using a random numbers table) between 0 and the width of a given territory. I then conducted the vegetation point surveys at these random points. At each point, overstory substrate and height, understory substrate and height, and vegetation structure were recorded. Overstory and understory levels were defined at greater than or less than 3-m in height respectively. Vegetation structure was measured using a density pole, in which I recorded the number of times vegetation contacted a 3-m pole at 0.5-m intervals.

Statistical Analysis

The 20 data points from each point intercept vegetation survey in the territories were combined per territory. Overstory height, understory height, and structure were computed by taking the average of the 20 data points per territory. For canopy cover, I took the number of times overstory substrate was recorded divided by the 20 point surveys tallied for every territory. I grouped vegetation species and genera into eight categories: ground (includes bare ground, leaf litter, dirt roads, moss, and brush piles), low woody vegetation (blueberry and dewberry), forbs and ferns, graminoids (grasses and sedges), conifers, scrub oak, *spiraea* sp., and all other woody vegetation in the last group. I also examined the amount of nest substrate in each territory, with vegetation species classified as nest substrate based on nests found in the study site. Frosts in the study site made certain nest substrates unsuitable for nesting early in the season, so I also examined the amount of frost intolerant (all oak sp.) and tolerant woody shrub and tree species in each habitat. As with canopy cover, I computed the percentage of the 20 points in each vegetation category for each territory. I used Analysis of Variance to compare vegetation height, composition and structure among territories in different habitats and used linear regression for comparisons in treated pitch pine over time. I log-transformed all vegetation data to improve normality and equality of variances before analysis. To reduce family-wise error rates I adjusted p-values by using the Bonferroni-Holm method (Holm 1979).

I computed bird density by calculating the number of territories per ha within intensively-mapped plots. Study plots were adjacent to each other, and bird territories were occasionally located in more than one plot. When this happened, I placed the bird in the plot where the majority of his territory was located. To examine bird abundance and stand age in treated pitch pine, I calculated the years since the initial harvest of each plot. For

example, for a plot harvested in the winter of 2003-04, in 2008 this was deemed 5 years old. Despite some post-harvest burning and selective cutting of grey birch and red maple in treated pitch pine, these post-harvest treatments tended to be small and irregular treatments that did not encompass large parts of a territory and did not appear to affect bird abundance or dispersal. One area in treated pitch pine was heavily burned and was an exception, and in this area I deemed a territory as being disturbed in my analysis.

To analyze bird density as a function of treatment age I conducted a linear mixed model, with birds per ha as the response variable and time since treatment as the predictor variable, including plot as a random effect. Including plot as a random effect effectively takes into account the interdependence of sampling the same plots over multiple years, consistent with a repeated-measures design. I used the "lmer" function in the "lme4" library in R, version 2.13 (Bates and Maechler 2010, R Development Core Team 2011). Because this modeling approach does not produce p-values because of ambiguities of the number of degrees of freedom in the model, I defined significant parameters if the mean parameter estimate (β) $\pm$ 1.96*SE was greater or less than 0. I present parameter estimates and standard errors.

To compare newly created treated pitch pine with regularly disturbed and persistent habitat, I examined bird density over time in scrub oak and power line corridors habitats as well. Since birds often used trees along the edges of power line corridors for singing perches and foraging, I included in the power line corridor area a 7.5 m buffer into the adjacent habitat on each side of the corridor to account for this. I did not include data from power line corridors in 2011, since the plots had been applied broadcast or selective herbicide management the previous winter. Treatment plots in treated scrub oak habitat were often times smaller than a bird's territory, and birds would use multiple treatment

plots that were treated at different times. I grouped together these relatively small treatments of scrub oak into one plot. Due to the few number of power line corridors and scrub oak plots I *a priori* decided to not create a statistical model, but visually examined the bird density data.

I also used data from 2008-2011 to examine differences in age classes. I examined the proportion of older males in each plot by tallying the number of banded ASY males divided by the number of banded ASY and SY males. Since I did not color-band the entire male population, the proportion of ASY birds in plots in 2009-2011 may be biased high by returning ASY birds captured the previous year, as unbanded birds could consist of mostly SY birds immigrating into the study site. Despite this possible bias, I banded the majority (>50 %) of males in each plot every year; I excluded one plot in 2008 in which the majority of birds consisted of unbanded birds. To examine bird age proportions, I conducted and presented a linear mixed model to examine male age proportion in treated pitch pine plots over time, including plot as a random effect.

I tallied the number of territorial males paired with females in each intensively studied plot between 2009-2011. I deemed a male paired if I saw a female, nest, or fledged young with a male in his territory. I did not include the number of non-territorial, floater males however (those observed for less than 10 days in a given location).

To examine reproductive success, I used fledging success (whether or not a territory fledged young) instead of fecundity, with individual territories as the sample. Most territories (89%) fledged 0, 3, or 4 young, and fledging success was analyzed because the number of fledged young data was highly non-normal and indicative of seasonal fecundity as there was not much variation in the number of young produced. I conducted 4 separate generalized linear mixed models of fledging success as a function of male age, habitat type,

years since treatment (only treated pitch pine plots), or year, and in all models included a random effect of plot. These mixed models fit to binomial distributions do produce p-values, and I presented these p-values as well. I did not use an AIC modeling approach because each model consisted of a different dataset. For instance, only 72% of the males were banded to use in the bird age model, and years since treatment only consisted of territories in treated pitch pine. Approximately 5 % of the territories in which I recorded fledgling success data consisted of birds that defended a territory only for half of the season (defined as arrived after June 1st, or left the study site after June 15th). These birds possibly could have dispersed within the season and fledged young in a different location (Nolan 1978), but it is also possible these birds did not find a new mate or territory so I kept them in the analysis. I was unable to determine fledging success for approximately 10 % of territories with certainty, and excluded these birds from the analysis. I also excluded the few birds in which I believed were unmated. I only included fledging success for three treated pitch pine plots in 2011, the power line plots were disturbed by herbicide applications and I was unsure if I determined fledgling success adequately in the other plots in 2011.

I determined return rate and between-year breeding dispersal for marked color-banded birds by examining territory maps and GPS points among years. Each year a bird returned was identified as a separate sample in the analysis – in that I included two samples for a bird that returned in consecutive years (Payne and Payne 1993). I stated that a bird did not disperse (had site fidelity) if the male overlapped its territory from the previous year. As in bird abundance, I only included birds that I observed breeding or observed twice over 10 days, and did not include 'floater' males that I caught but did not re-sight as territorial males. There was some with-in season dispersal of birds (Nolan 1978), as I observed some banded males move within the study site during the season, banded males disappear from the study site halfway through the season, or banded males arrive in the

study site late in the season. Movement within the study site was observed often in May when birds were selecting territories, and occasionally short distance territory shifts were observed within the study site after May. Despite this, I did not examine with-in season movement and only focused on dispersal among seasons.

I used logistic regression to examine if birds' return rates or site fidelity differed among variables. I ran two sets of models, 1) if a bird returned or did not return to the study site, and 2) did the bird exhibit territory (site) fidelity if it did return. I first subset the data to include just birds in treated pitch pine habitat, and then ran models with the dependent variable as return rate or site fidelity, and included independent variables of time since treatment and age of bird. I then ran similar models with all habitat types included, and when including variables replaced the time since treatment variable with habitat type. When conducting these analyses on return rates and site fidelity, I did not include birds that were in heavily disturbed habitat (including herbicide) the previous year. These birds could have been forced to disperse from their old territory and represent different samples.

I examined return rates and site fidelity in disturbed territories (territories in which the majority of the vegetation within a territory had been mowed or burned). I also compared the pairing and reproductive success of males whose territory was disturbed the previous year with the pairing and reproductive success of all other birds. Moreover, I examined the seasonal fecundity in the plot in which the most known displaced birds dispersed into, compared with other plots in the same year.

I also tallied the number of territorial SY males in intensively studied plots each year, in an attempt to determine the number of territorial SY birds entering the study site every year, regardless of treatment age. This would be a relative estimate, as in each year a considerable number of unbanded birds were not aged. Due to this possible bias, I also

tallied the proportion of SY birds over the number of SY and unbanded birds, to account for this. In all statistical analyses I used the program R, version 2.13 to conduct analyses (R Development Core Team 2011).

Results

I found vegetation structure, composition, height, and cover to significantly vary among years since treatment in treated pitch pine and among habitat types (Table 1.1 and 1.2). As treated pitch pine matured, canopy cover, the amount of woody vegetation, understory height and structure (number of vegetation contacts) above 1.5 m increased, while overstory height and the amount of graminoids decreased (Table 1.1). Scrub oak habitat had more structure, higher vegetation, more nest substrates, and more frost intolerant species than treated pitch pine and power line corridors (Table 1.2). Power line corridors had more *spiraea*, low woody vegetation, and grasses compared with treated pitch pine and scrub oak habitats.

There were approximately 285 male prairie warbler territories counted and mapped within the study plots during the 4 years. Newly created treated pitch pine had low bird densities that significantly increased over time until treatments were approximately 4-5 years of age (β=0.18, SE=0.038). Bird densities appeared fairly constant in plots between 4-8 years of age (Figure 1.2). In contrast, the treated scrub oak plot had fluctuating bird densities due to disturbance during the study. Untreated scrub oak habitat had low densities of birds, while persistent power line corridors had relatively high, somewhat stable bird densities over time (Figure 1.3).

Treated pitch pine habitat was first colonized by mostly SY males, and some dispersing ASY males. After the initial creation of habitat, the age proportion of males significantly switched from a majority of SY birds to mostly ASY birds as treated pitch pine matured over time (β=0.14, SE=0.023), Figure 1.4). In older treated pitch pine, males that were initially SY birds returned in later years, and I also captured new ASY birds dispersing into the plots. Persistent power line corridors and treated scrub oak habitat predominantly consisted of older males (85% and 81% ASY males respectively).

I recorded pairing success and fledging success for 157 territories in 3 habitat types during 2009-2011. Approximately 97 % of territorial males were paired, although some non-territorial males were observed and captured in all plots. Average seasonal fecundity was 1.91 fledglings per territory, with 61 % of territories fledging at least one prairie warbler young in all years and habitats combined. Fledging success did not differ significantly within treated pitch pine over time, among habitat type, between male age classes, or among years (p-values>0.05). Nevertheless, there did appear to be some variation among these variables (Table 1.3).

Of the 119 undisturbed territories of banded males in 2008-2010, 67 % males returned in the study site the following year, and 73 % of returning birds remained on their previous territory. Examining the subset sample of birds in treated pitch pine, I found as treated pitch pine matured there was no significant difference in return rates (β=0.19, SE=0.22, p-value>.1), but birds in younger treated pitch pine had marginally lower site fidelity (β=0.55, SE=0.32, p-value=0.08) (Table 1.4). In treated pitch pine, younger birds had similar return rates as older birds (β=0.01, SE=0.53, p-value>.1), but had marginally lower site fidelity compared with older males (β=-1.18, SE=0.67, p-value=0.08). There was no difference in return rates or site fidelity among habitats (p-values>0.1). In all habitats, age

class did not affect return rates (β=-0.08, SE= 0.46, p-value>1), but younger birds significantly had lower site fidelity compared with older males (β=-1.22, SE=0.57, p-value=0.03).

I observed 17 territorial males in habitat that was disturbed by management the following year. Of the 12 of these males that were color-banded, 58 % returned to the study site in a following year, yet all of these 7 males moved their territory location in a following year. Most returning birds were re-sighted the following year, with the exception of one displaced bird in 2008 that was not seen again until 2011. For birds that returned to the study site the year following dispersal, the average distance moved from the territory centers was 278 m (standard deviation of 294 m). Three of these returning 7 birds were observed arriving and singing in their previous, disturbed territory early in the season before dispersing and defending a new territory in the same season. All displaced males paired with females in a following year. Since all territorial males were paired in adjacent areas as well, the influx of displaced males did not alter pairing success. Birds that were disturbed by management had similar reproductive success the following year compared with all other birds (67 % of displaced birds fledged young). Although 3 displaced birds dispersed into new territories in treated scrub oak habitat in 2010, this plot had very high productivity relative to other plots during this year (Table 3).

I found an extremely high natal return rate of 15 %, with 34 banded-as-nestling birds returning in 2009-2011. Of these 34 birds, 41 % were returning males. Birds that were banded-as-nestlings in 2009 constituted about 6 % of the entire population (males and females) surveyed in the study site in 2010. In 2011, 8 % of the entire population was banded-as-nestlings from 2010, and another 3 % of the population was surviving birds banded-as-nestlings in 2009. In the examination of returning natal birds, 88 % were either

re-captured or re-sighted with unique color-band combinations, while 4 returning birds were only banded and re-sighted with a service band, but were presumed to be natal returns from my study site. Also, one natal return was captured in the study site as a juvenile bird in July 2008 and I included this bird in my analysis. Most returning natal birds were seen multiple times or re-captured, although 15 % of returning birds, all females, were only re-sighted once. Also, 3 returning males in 2011 did not maintain a territory throughout the summer.

In intensively studied plots, I tallied 10 territorial SY males in 2008, 13 in 2009, 17 in 2010, and 10 in 2011. As a proportion of the captured number of SY males over the number of unbanded males and SY males, this was 0.27 in 2008, 0.37 in 2009, 0.43 in 2010, and 0.35 in 2011.

Discussion

My study is the first to illustrate the demographic processes of a disturbance-dependent species within a shifting mosaic habitat. I found similar colonization rates as past studies, with prairie warblers colonizing at low densities after initial logging and increasing in the first ten years after treatment (Schlossberg and King 2009, King et al. 2011). Colonization and bird densities in new habitat 1-2 years of age appeared to correspond to prairie warblers' habitat preference. Prairie warblers prefer habitat with low canopy cover and an abundance of low woody shrubs that provide suitable nesting sites and food resources (Nolan 1978, Folsom 2008, Schlossberg et al. 2010). I observed that newly created habitat lacks shrub cover for nesting which develop 1-2 years after disturbance, at which point prairie warblers occupy habitat, albeit in lower densities than in more mature habitat. Average shrub height in the first 1-2 years after thinning was often lower than the

height range of most selected nest sites (below 0.5 m) (MA unpublished data). Bird density in 2-year old plots often increased mid-season as shrubs grew and became suitable for nesting (M.A. unpublished data). These results suggest that young habitat may be less suitable for prairie warblers due to the lack of available nesting sites above 0.5 m. Although past studies have found bird density can be related to food resources (Marshall and Cooper 2004), young stands appeared to have similar food resources than in older treatment areas, as nestlings' body condition were similar among young and slightly older habitat (MA unpublished data). Interestingly, despite suitable nesting habitat I also observed prairie warbler densities to be slightly lower in plots 3-4 years of age than 4-8 years of age. One possible explanation is conspecific attraction (Ward and Schlossberg 2004, Hahn and Silverman 2006); prairie warblers may be gradually increasing in abundance over time in newly created plots as more birds inhabit and are attracted to returning singing males. Another plausible explanation that past studies have noted is the lack of knowledge of suitable habitat can also restrict bird densities and colonization of newly created habitat, even for long-distance migratory birds (Villard and Taylor 1994, Dunning et al. 1995, Belisle et al. 2001, Hames et al. 2001, Brotons et al. 2005, Groom and Grubb 2006). I found more SY birds arrived into the site in 2009 and 2010, possibly because new treated pitch pine habitat was already colonized and more SY birds were returning after being born on site and had identified this new habitat the previous year.

My results support the Schlossberg (2009) hypothesis that newly created sites are being colonized mostly by dispersing SY males. I propose that differences in age structure I observed between newly created and mature habitats are due to a combination of site fidelity of established males and competitive interactions between them and SY birds for occupancy of more mature habitat. Site fidelity of adult males affects colonization rates and age structure in new habitats as it limits the number of ASY males dispersing into new

habitat. Theoretical and empirical studies have found that when site fidelity is high and dispersal distance is low, colonization rates will be reduced (Gaston and Blackburn 2002, Matthiopoulos et al. 2005, Donner et al. 2010). In an analysis of the long-term study of the Kirtland Warbler (*Dendroica kirtlandii*) metapopulation, Donner et al. (2010) found older males had strong site fidelity, even on patches that are maturing into less suitable habitat. Indeed, I found high adult male return rates and relatively short dispersal distances within the study site and correspondingly low colonization rates of ASY males in newly created habitat. Also, my findings of high return rates did not vary as a function of time since treatment or habitat type, although younger birds and birds in younger treated pitch pine had slightly lower territorial fidelity. In a number of avian species, ASY males arrive earlier than SY males and outcompete younger males for territories in preferred habitats (Lozano et al. 1996, Petit and Petit 1996, Cooper et al. 2009). Cooper et al. (2009), found that earlier arriving ASY male Eastern Kingbirds (*Tyrannus tyrannus*) outcompeted SY males for high quality breeding territories, and SY males exhibited delayed breeding due to unavailability of high-quality breeding sites. In my study, younger males did arrive later on the study site (M.A. unpublished data) and colonized newly created habitat, as ASY birds dominated older treatment sites. Overall, addressing shrubland birds as a 'fugitive' species could be misleading given the high adult site fidelity and other possible dispersal limitations of shrubland birds (Schlossberg 2009).

Site fidelity and preemption of the preferred, older habitat are plausible explanations for the differences in age structure of prairie warblers in newly created habitats. Further research on the colonization and age structure of other shrubland bird species, especially those that have peak densities in the first years following disturbance (Schlossberg and King 2009), would be useful for examining this relationship. For instance, for shrubland species that prefer habitat that is 1-2 years of age, one may expect more

dominant, ASY birds to attempt to hold the best territories in this younger habitat. Adult site fidelity of these species may be expected to be lower, as ASY birds continually disperse to acquire habitat that is 1-2 years of age. Therefore, the stand age that shrubland birds peak in abundance could help explain site fidelity variation among shrubland species. On the other hand, because shrubland habitat is ephemeral and hard to find, 'early peak' species could have similar adult site fidelity as prairie warblers (Schlossberg 2009), and the peak densities observed in stands 1-2 years of age could be made up of all SY birds. Examination of colonization patterns and consequences of other shrubland species would be beneficial for understanding population dynamics and management.

My results are consistent with other studies indicating that productivity in newly created habitats do not differ with time since disturbance (Chandler et al. 2009a). Some studies have found reproductive success to be lower for SY birds due to later arrival and egg-laying dates (i.e. Nolan 1978, Nol and Smith 1987). I also found a slight difference in reproductive success among age classes, although this was not statistically significant. Despite this slight difference observed, newly created habitat appears to allow for a segment of the population, SY males, to acquire territories and breed. Reproductive output was similar among the treated pitch pine stand ages between 3-8 years of age and I also observed birds nesting and fledgling young in plots 2 years of age; in 2008 I found a successful nest in treated pitch pine that was 2 years of age, as well as many successful nests found in 2010 and 2011 in sections of the treated scrub oak that were 2 years of age. Since reproductive output was the same between new and mature habitat I suggest that site fidelity and site preemption by established males is more likely the cause of differences in age structure than actual habitat quality (e.g. food or nesting opportunities) (Donner et al. 2010).

Although studies on shrubland birds have documented natal and adult return rates to an established breeding site (Nolan 1978, Payne 1991, Lehnen and Rodewald 2009), few studies have data on the origin of specific individuals that colonize newly created habitat. I observed a very high natal return rate, with a proportion of the incoming SY population in newly created habitat consisting of local returns. Although other immigrating SY birds may be dispersing from as far as 350 km from their breeding sites (Payne 1991, Studds et al. 2008), my results still highlight the possible importance of landscape connectivity and dispersal limitations of shrubland birds. For adult birds, return rates to the study site appeared to be just slightly lower than estimated prairie warbler annual survival rates (Nolan 1978, Slay 2010), therefore possibly only few adult male birds dispersed outside of the study area. Past studies have found that birds use prior knowledge of nearby available breeding locations and quality, so being site unfaithful and dispersing farther outside of the study site may have increased costs of finding suitable habitat (Doligez et al. 2002, Betts et al. 2008). Other studies have noted short dispersal distances for adult shrubland birds, even in landscapes where suitable habitat is less clustered together as in my site (Holmes and Sherry 1992, Lehnen and Rodewald 2009). Historically, xeric, early-successional habitat was created by large-scale hurricanes or wildfires started by Native Americans (Lorimer and White 2003). Early-successional habitat was most likely highly disparate along space and time; birds may be adapted to have high site fidelity to reduce the risk of not finding an equally suitable breeding territory in a given year (Schlossberg 2009).

This is the first study to document color-banded shrubland birds dispersing from occupied territories following complete removal of their habitat. Return rates of birds in disturbed habitat were similar but slightly lower than the overall return rate, and returning birds dispersed relatively small distances. Unlike Hagan et al. (1996), birds that dispersed from disturbed territories in my study did not appear to affect bird densities, pairing or

reproductive success in adjacent areas. In comparison, past studies have found increased densities of forest birds when adjacent forest is destroyed (Darveau et al. 1995, Hagan et al. 1996, Schmiegelow et al. 1997). My study differs from these previous studies in that the patches of disturbed habitat in my study were smaller, disturbance was conducted over a few years, and the adjacent habitat was extensive relative to the size of disturbance. As a result, in my study fewer birds were displaced into the adjacent habitat, which was large and thus able to absorb more dispersing birds.

Previous studies on shrubland birds have found continually disturbed shrubland habitat affords different population densities of shrubland birds relative to ephemeral clearcuts (Bulluck and Buehler 2006, Fink et al. 2006, King et al. 2009b); this is the first study to examine this in relation with age structure and seasonal fecundity. In my study, both regularly disturbed scrub oak habitat and new treated pitch pine habitats were rapidly changing as they matured or were disturbed, and making inferences on bird densities was difficult. Bird density fluctuated as birds dispersed when sections of the treated scrub oak plot were disturbed, and bird densities were low and then increased as treated pitch pine matured over time. When the plots were both older, bird densities appeared relatively similar. Just after treated scrub oak habitat was disturbed in 2008 and 2009, birds re-colonized the plot relatively quickly, with bird densities in 2011 only slightly lower than original 'capacity' of 2008. Past studies have noted that vegetation structure and composition lead to differences in bird abundance between regularly disturbed and more ephemeral shrubland habitat (Fink et al. 2006, King et al. 2009b). This may be occurring in my plots as well, with periodically disturbed scrub oak a few years after treatment having more dense vegetation structure and more birds compared with young, newly created treated pitch pine (Tables 1.1 and 1.2, Figures 1.2 and 1.3, MA personal observation). Perhaps bird densities a few years after treatment also differed in these two habitat types

because of birds' previous knowledge of existing habitat, resulting in a higher number of birds in regularly disturbed habitat after disturbance. Recently disturbed scrub oak was re-populated by other ASY birds moving in from adjacent habitat, and one recently disturbed area occupied by a displaced bird from a previous year's disturbance in the scrub oak. Thus, an older age structure was maintained in the treated scrub oak plot, even in recently treated habitat (note 2010 did have a slightly lower age proportion of 0.6). Bird densities and age structure may vary in landscapes with different patch sizes and connectivity of disturbed versus available habitat, as the number of displaced ASY birds after a disturbance can alter population demographics in surrounding areas. Consistent with King et al. (2009b) who examined shrubland birds' nest success in clearcuts and regularly disturbed wildlife openings, I found productivity between newly created treated pitch pine and regularly disturbed scrub oak was similar. Further research at a larger landscape scale examining how size and proximity of newly created and disturbed habitats affects colonization rates, age structure and productivity is needed (Donner et al. 2010).

As past studies have observed, power line corridors resemble a distinct shrubland habitat and bird population dynamics are different compared with more ephemeral habitats (Confer and Pascoe 2003, Bullock and Buehler 2006). I found prairie warbler density remained relatively constant in these habitats, and ASY males appeared to prefer these habitats and predominate over SY males. Seasonal fecundity, return rates, and site fidelity were similar compared to other habitats. Although broadcast and selective herbicide applications may affect bird densities the year after treatment, the bird densities still appeared to be fairly constant in the power line corridors, with a slight reduction after the broadcast herbicide application in one plot (MA unpublished data). Houlihan (2000) observed a similar density of prairie warblers in the same power line corridors in the study site during 1989-1992. Despite a lack of consecutive long-term data from my study site, I

believe a population of prairie warblers has been present in these power line corridors for at least 20 years. The demographic processes I describe are powerful tools for trying to understand population movements of early-successional species in a shifting mosaic landscape, yet they have exceptions in habitats such as persistent power line corridors where populations may not go extinct over time (Niering et al. 1986). In relation to 'fugitive species,' shrubland bird species should not be considered 'fugitive' if the majority of the species exists as persistent populations in habitats like power lines corridors.

Management Implications

Management activities creating new shrubland habitat are justified because SY shrubland birds are able to pair and produce young in newly created habitat, which subsequently may bolster the population growth rate. Management in existing shrubland habitat should also continue, as birds appear to be able to disperse to adjacent habitat and breed successfully if their territories are destroyed. Moreover, continuing management in existing shrubland habitat maintains the vegetation structure and stops forest maturation into unsuitable habitat. Creating new shrubland habitat close to existing nearby habitat may be beneficial, as my study and other research has found that juvenile or adult migratory birds can be dispersal limited (Dunning et al. 1995, Hames et al. 2001, Brotons et al. 2005). Managers should reflect not merely on patch connectivity or size, but also on temporal relationships such as how future suitable habitat could support nearby populations when existing shrubland habitat matures or is disturbed by future management activities (Donner et al. 2010). Despite a plethora of studies on the effects of isolation and forest fragmentation on mature forest bird communities (e.g. McGarigal and McComb 1995, Belisle et al. 2001),

more study is needed to address if connectivity of shrubland habitat would help boost shrubland bird populations.

Table 1.1. Vegetation characteristics in prairie warbler territories in different years since treatment in treated pitch pine habitat in the MPWMA between 2009-2011 (n=61). YST – years since treatment. P-value is the adjusted p-value using the Bonferroni-Holm method. Significant differences are indicated in bold. Means and (standard errors) are presented.

	3	4	5	6	7	8	F	Adj. p
Overstory Height (m)	**17.34 (1.25)**	**13.53 (0.95)**	**10.99 (1.79)**	**11.84 (1.3)**	**11.06 (1.05)**	**11.18 (1.04)**	**13.45**	**0.011**
Canopy Cover (%)	**14.94 (2.52)**	**19.77 (1.98)**	**11.67 (1.05)**	**22.14 (2.4)**	**25.83 (4.36)**	**32 (7.18)**	**11.76**	**0.02**
Understory Height (cm)	**64.44 (4.19)**	**83.71 (6.64)**	**107.07 (3.59)**	**88.34 (11.27)**	**109.76 (9.76)**	**136.78 (7.42)**	**34.4**	**<0.001**
Structure 0-0.5 m	4.26 (0.44)	3.29 (0.24)	3.78 (0.23)	3.38 (0.3)	3.58 (0.53)	2.95 (0.53)	3.04	0.778
Structure 0.5-1 m	1.54 (0.23)	1.64 (0.23)	1.9 (0.32)	1.28 (0.45)	1.66 (0.32)	1.16 (0.16)	0.02	1
Structure 1-1.5 m	0.47 (0.11)	0.65 (0.09)	0.98 (0.08)	0.86 (0.31)	0.68 (0.17)	1 (0.2)	6.7	0.182

Structure 1.5-2 m	**0.23 (0.06)**	**0.28 (0.04)**	**0.56 (0.13)**	**0.61 (0.18)**	**0.68 (0.15)**	**1.02 (0.34)**	**27.06**	**<0.001**
Structure 2-2.5 m	**0.06 (0.04)**	**0.08 (0.02)**	**0.2 (0.07)**	**0.24 (0.07)**	**0.22 (0.1)**	**0.43 (0.14)**	**27.06**	**<0.001**
Structure 2.5-3 m	0.07 (0.05)	0.06 (0.02)	0.08 (0.02)	0.11 (0.05)	0.08 (0.06)	0.25 (0.07)	9.21	0.057
Ground (%)	19.05 (2.92)	14.06 (2.71)	5 (2.24)	16.43 (4.72)	8.33 (3.33)	13 (4.9)	2.81	0.778
Blueberry/Dewberry (%)	10 (1.98)	13.44 (3.12)	12.5 (3.82)	18.57 (4.19)	17.5 (4.61)	18 (4.36)	5.44	0.301
Conifer (%)	6.9 (1.48)	4.69 (1.68)	6.67 (1.67)	3.57 (1.43)	1.67 (1.05)	3 (2)	3.91	0.527
Forb/Fern (%)	6.43 (1.34)	4.06 (1.39)	4.17 (1.54)	7.14 (4.06)	5 (2.24)	0 (0)	2.97	0.778
Graminoid (%)	**14.29 (1.59)**	**7.81 (2.62)**	**4.17 (2.01)**	**9.29 (2.3)**	**4.17 (0.83)**	**3 (2)**	**11.75**	**0.02**
Other woody (%)	**21.9**	**21.56**	**37.5**	**28.57**	**42.5**	**40 (4.74)**	**18.16**	**0.001**

	(2.33)	**(2.53)**	**(5.74)**	**(4.84)**	**(5.88)**			
Scrub Oak (%)	21.43 (3.24)	34.06 (5.87)	30 (6.71)	16.43 (2.83)	19.17 (4.17)	23 (4.06)	0.05	1
Spiraea sp. (%)	0.24 (0.24)	0 (0)	0 (0)	0 (0)	1.67 (1.67)	0 (0)	0.58	1
Nest Substrate (%)	47.86 (3.44)	56.25 (5.76)	72.5 (6.29)	47.86 (5.86)	62.5 (6.16)	68 (5.39)	4.96	0.357
Frost Intolerant Species (%)	33.1 (3.13)	44.69 (5.87)	47.5 (4.96)	32.14 (4.21)	45 (2.89)	55 (5.7)	4.87	0.357
Frost Tolerant Species (%)	16.67 (1.93)	15.62 (2.45)	25.83 (6.76)	16.43 (3.73)	20 (6.06)	13 (3)	0.01	1

Table 1.2. Vegetation characteristics in prairie warbler territories in four habitat types in the MPWMA (n=91), during 2009-2010. PL – power line corridors, TPP – treated pitch pine. Adj. p – is the adjusted p-value using the Bonferroni-Holm method. Means and (standard errors) are presented. Note prairie warbler territories in power line corridors extended into the forest edge, thus increasing canopy cover percentages in power line corridor habitat.

	PL	TPP	Treated SO	Untreated SO	F	Adj. p
Overstory Height (m)	12.77 (1.17)	14.41 (0.71)	8.44 (0.78)	7.72 (3.28)	9.31	<0.001
Canopy Cover (%)	18.13 (2.87)	18.14 (1.41)	7.19 (1.2)	20 (10)	5.29	0.009
Understory Height (m)	78.05 (3.24)	81.87 (3.64)	139.46 (5.51)	187.97 (17.72)	21.21	<0.001
Structure 0-0.5 m	4.15 (0.2)	3.76 (0.21)	3.51 (0.27)	4.15 (0.7)	1.28	0.285
Structure 0.5-1 m	1.79 (0.2)	1.53 (0.13)	2.63 (0.24)	1.88 (0.02)	4.97	0.009
Structure 1-1.5 m	0.64 (0.1)	0.63 (0.06)	1.98 (0.19)	2.12 (0.68)	13.79	<0.001
Structure 1.5-2 m	0.35 (0.1)	0.41 (0.06)	1.15 (0.17)	0.82 (0.12)	8.6	<0.001
Structure 2-2.5 m	0.19 (0.07)	0.13 (0.03)	0.41 (0.07)	0.88 (0.03)	8.78	<0.001

Structure 2.5-3 m	0.36 (0.12)	0.09 (0.03)	0.07 (0.03)	0.48 (0.32)	5.86	0.005
Ground (%)	17.27 (2.41)	15.29 (1.67)	0.62 (0.43)	0 (0)	19.13	<0.001
Blueberry/Dewberry (%)	17.95 (1.88)	13.92 (1.5)	2.5 (0.91)	2.5 (2.5)	12.28	<0.001
Conifer (%)	11.59 (1.87)	5.1 (0.86)	0.62 (0.43)	0 (0)	11.48	<0.001
Forb/Fern (%)	6.59 (1.29)	5.29 (0.93)	2.81 (1.51)	0 (0)	2.4	0.146
Graminoid (%)	15.45 (1.67)	9.51 (1.16)	0.62 (0.62)	0 (0)	18.53	<0.001
Other woody (%)	14.09 (3.03)	26.86 (1.82)	8.12 (2.09)	10 (0)	16.72	<0.001
Scrub Oak (%)	6.14 (0.98)	23.82 (2.29)	84.69 (2.56)	87.5 (2.5)	60.36	<0.001
Spiraea sp. (%)	11.14 (2.05)	0.2 (0.2)	0 (0)	0 (0)	43.15	<0.001
Nest Substrate (%)	27.95 (2.86)	49.12 (2.4)	86.88 (2.95)	82.5 (7.5)	31.25	<0.001
Frost Intolerant Species (%)	8.18 (1.21)	38.43 (2.24)	85.94 (2.38)	87.5 (2.5)	90.69	<0.001
Frost Tolerant Species (%)	23.64 (2.72)	12.65 (1.42)	6.88 (1.76)	10 (0)	9.89	<0.001

Table 1.3. Prairie warbler seasonal fecundity among habitats, years, years since treatment (YST) of treated pitch pine, and male age classes in 2009-2011. Successful is deemed as a territory that produced fledglings. Mean and (SE) presented for the number of fledglings produced per territory. For territories in which we only located fledglings outside of a nest, we recorded these territories as producing the mean number of young produced per successful territory in that given year.

Year	Habitat	Unsuccessful	Successful	% Successful	No. Fledglings
2009	PL	3	12	80	2.47 (0.35)
	SO	5	7	58	1.67 (0.45)
	TPP	14	20	59	1.85 (0.29)
2010	PL	5	9	64	1.79 (0.42)
	SO	2	7	78	2.67 (0.53)
	TPP	12	25	68	2.12 (0.28)
2011	TPP	19	15	44	1.55 (0.31)
	TPP YST				
	3	10	13	57	1.78 (0.36)
	4	9	17	65	2.35 (0.35)
	5	12	13	52	1.46 (0.33)
	6	7	6	46	1.55 (0.51)
	7	2	4	67	2.17 (0.70)

8	5	4	44	1.58 (0.63)
Male Age Class				
ASY	33	57	63	1.94 (0.17)
SY	14	16	53	1.68 (0.33)

Table 1.4. Return rates and site fidelity of male prairie warblers by year since treatment in treated pitch pine, among bird ages, and among habitat types during 2008-2011. Sample sizes are of all banded birds, although site fidelity sample sizes consist of only returning birds, not including disturbed habitat.

	Sample Size	Return Rate (%)	Site Fidelity (%)
YST			
2	5	80	25
3	19	63	58
4	31	65	80
5	10	80	75
6	4	50	50
7	5	100	100
Bird Age			
ASY	76	76	81
SY	33	67	55
Habitat Type			
PL	15	80	83
SO	18	89	75
TPP	76	68	71

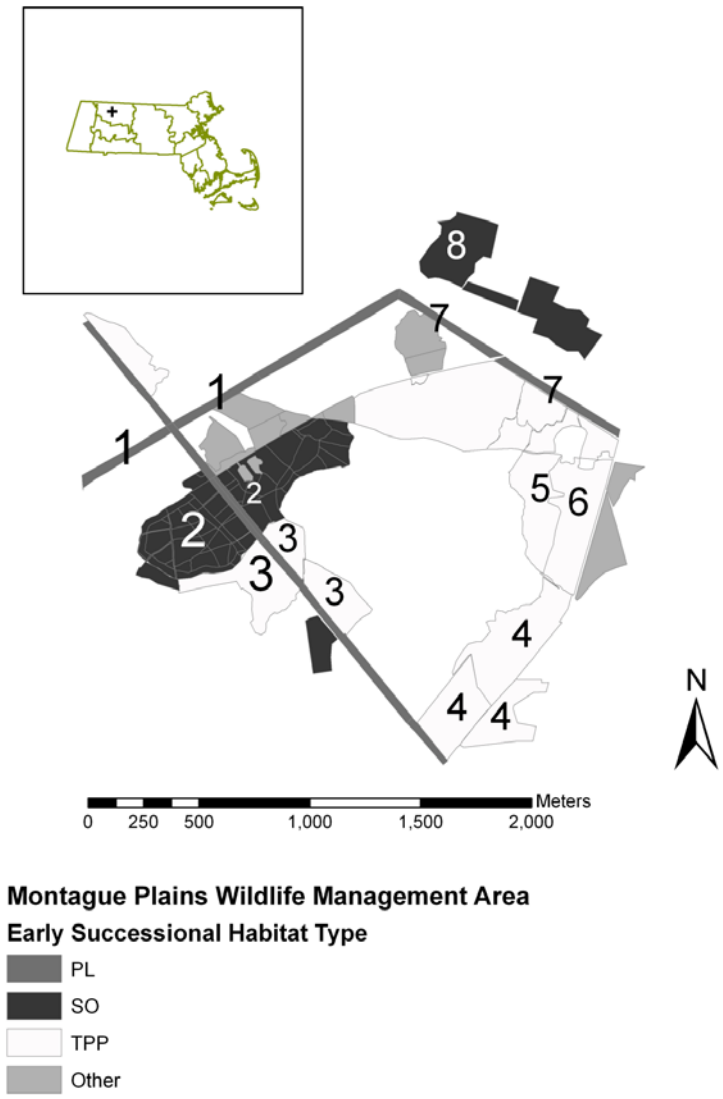


Figure 1.1. Map of the MPWMA, located in Montague, MA. PL –power line corridors, SO – scrub oak, TPP –treated pitch pine, Other- other disturbed early-successional habitat. Numbers indicate plots used in the study. Plot 2 consisted of treated scrub oak, while plot 8 was untreated scrub oak. Unmarked, white sections consist of mostly pitch pine and mixed pine and deciduous oak forest.

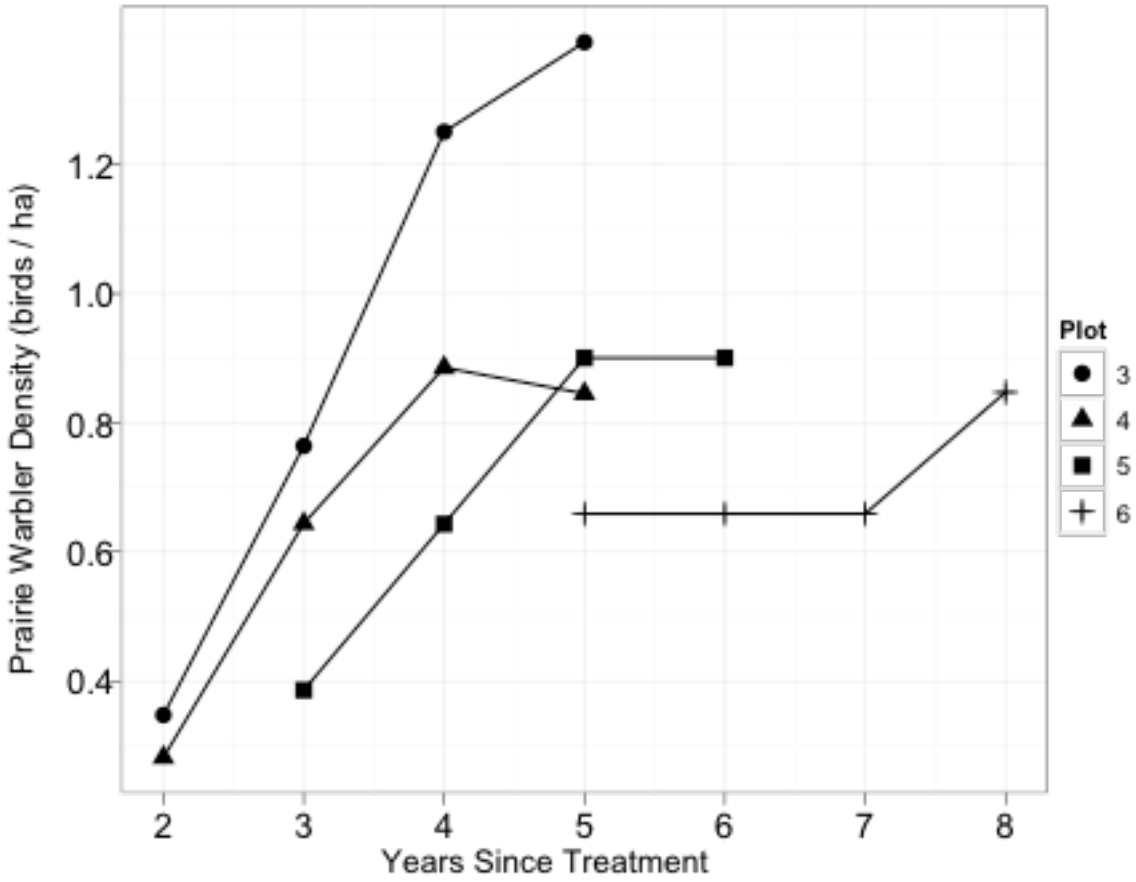


Figure 1.2. Prairie warbler density in newly created and maturing treated pitch pine in the MPWMA by years since treatment. Shapes represent 4 different plots.

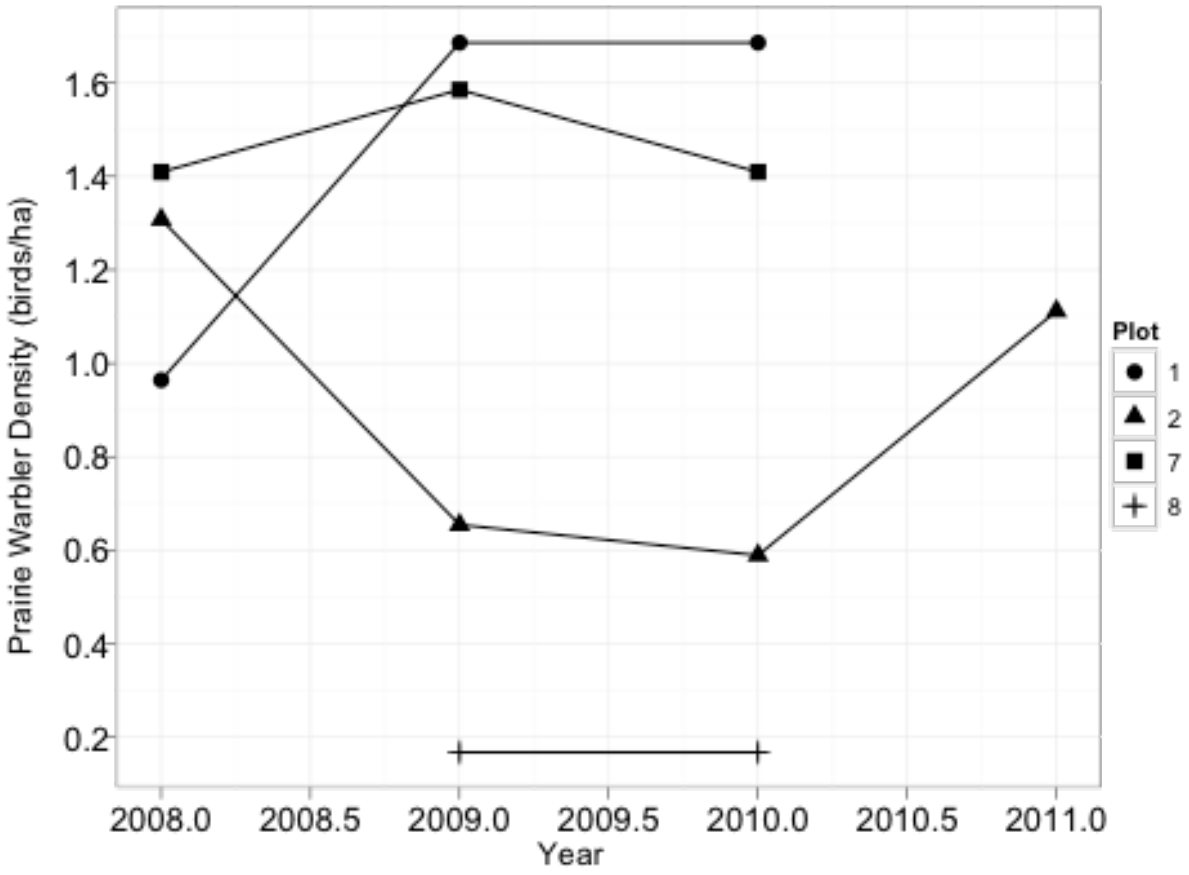


Figure 1.3. Prairie warbler density in power line corridor and scrub oak plots in the MPWMA between 2008-2011. Shapes represent 4 different plots.

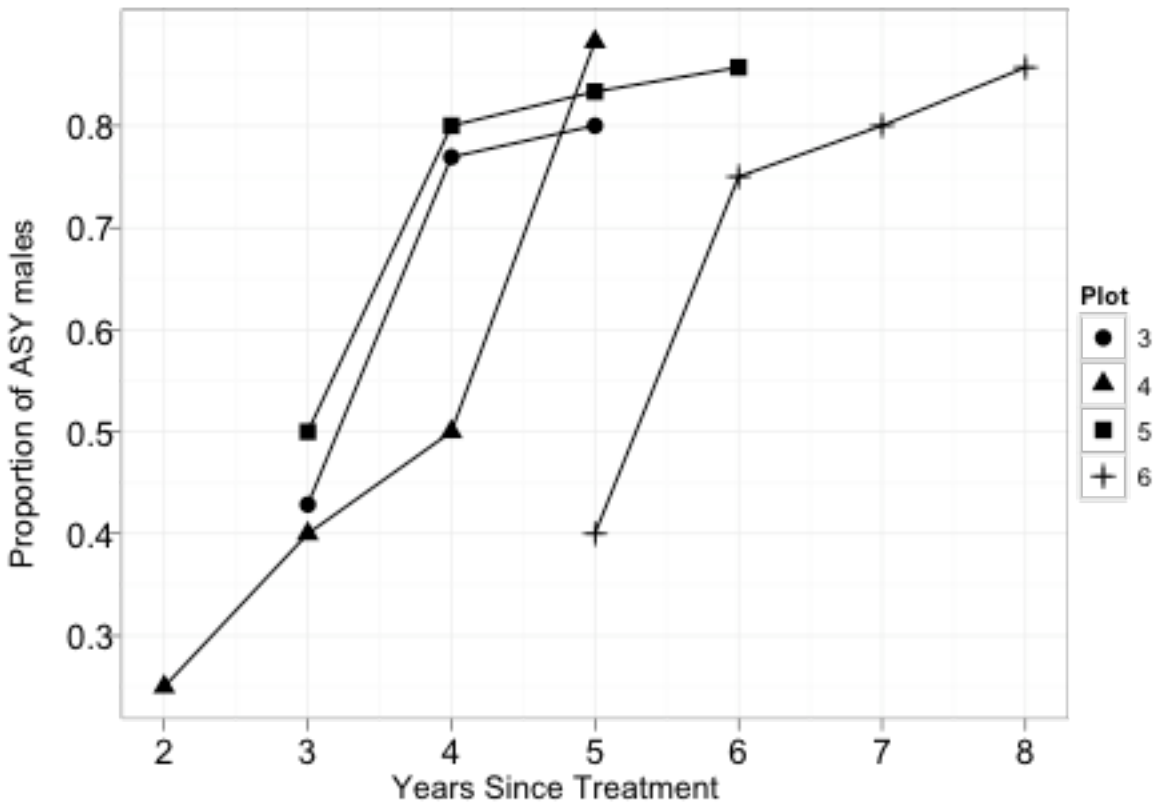


Figure 1.4. Proportion of ASY prairie warbler males in treated pitch pine by years since treatment. Shapes represent 4 different plots.

CHAPTER 2

PLANT PHENOLOGY AND OTHER FACTORS AFFECTING NEST-SITE SELECTION AND NEST SURVIVAL FOR PRAIRIE WARBLERS IN A PITCH PINE-SCRUB OAK BARREN

Introduction

Many studies have examined the microhabitat features associated with avian nest-site selection (e.g. Braden 1999, Aguilar et al. 2008, Rangel-Salazar et al. 2008), and it is generally assumed that nest-site selection is adaptive in that certain nest-site features increase reproductive output (Martin 1998). As passerine reproductive success is determined largely by nest survival (Ricklefs 1969, Thompson 2007), nest success directly affects a bird's fitness. In theory, birds that nest in more productive locations should pass their genotypes forward to subsequent generations, and their offspring would be predisposed to nest in locations that confer greater nesting success (Jaenike and Holt 1991).

Studies of the relationship between nest-site selection and nest success indicate there are effects at different temporal and spatial scales (Dinsmore et al. 2002, Royle and Dorazio 2008). At the nest-site scale, certain nest substrates may lead to higher nest success, as well as concealment, nest height, vegetation adjacent to the nest, or other factors (Martin 1998, Rangel-Salazar et. al. 2008). For instance, Nolan (1978) found more concealed nests to have higher nest survival for prairie warblers (*Setophaga discolor*). Effects of nest site factors may be overwhelmed by overall patch or habitat scale factors (Thompson 2007), such as distances to road and edge effects (Woodward et al. 2001, Schlossberg and King 2008, King et al. 2009a), and habitat types and vegetation (Nalwanga et al. 2004, Kus et al. 2008). Studies have found increased predator abundances near edges,

roads, or in certain habitats, and this can lead to decreased nest success (Woodward et al. 2001, Chalfoun et al. 2002, Fink et al. 2006, King et al. 2009a). Moreover, temporal variation such as nesting date (yearly and seasonal differences) (Grant et al. 2005, Bulluck and Buehler 2008), age of the nest (Nolan 1978, Dinsmore et al. 2002), and weather (Conway and Martin 2000, Dinsmore et al. 2002, Morrison and Bolger 2002) can be as important for nest survival rates. Temporal variation in nest survival may be driven by changes in predator abundances or behavior (Schmidt et al. 2008), as well as temporal changes in nest visibility or conspicuousness (Schmidt 1999).

Although some studies have found birds do select nest-sites that have higher nest survival (e.g. Martin and Roper 1988, Schmidt and Ostfield 2003), other studies have found selected nest sites do not lead to increased nest survival (Braden 1999, Davis 2005, Bulluck and Buehler 2008), and selected nest sites can even have low survival, thus forming an 'ecological trap' (Misenhelter and Rotenberry 2000). Birds may select habitat or nest sites that historically provided high fitness, but they may no longer have high fitness due to changes in increased urbanization and different predator assemblages found today (Misenhelter and Rotenberry 2000). In some cases the diversity of predators could be so high and predator search strategies so varied that birds may not be able to find or select for nest sites that conceal their nests from this dynamic array of predators (Filliater et al. 1994, Davis 2005).

An alternative explanation that could explain the variability in results of studies attempting to relate nest-sites to nest success is the idea that birds also select nests based on availability of preferred nest sites (Martin 1998) or favorable microclimates (Gotmark et al. 1995, Wiebe 2001), however relatively few studies have looked at nest-site selection, nest survival and their interactions with ambient temperature and plant leafing phenology.

In some habitat types or years, vegetation may leaf out fully before nesting begins and birds seeking to conceal their nests in dense vegetation are not constricted by plant leafing phenology (Martin 1993). Conversely, in certain systems or in colder years, vegetation may be killed by late frosts or leaf out later in the season, and this could dramatically affect avian nest-site selection and nest survival. There have been studies that have noted this latter occurrence (Nolan 1978, Moore 1980, Jarvinen 1993, Martin 1993, Martin 2007), but few studies if any have examined the effects of plant leafing phenology quantitatively in a nest-site selection or nest survival model. With global warming's direct and indirect effects on plant leafing phenology and bird reproductive success (Jarvinen 1993, Both et al. 2006, Martin 2007), studying the dynamics of these plant and avian interactions is crucial to understanding future impacts of climate change and informing management decisions.

Moreover, as nest survival is an important aspect of reproductive success, understanding factors that can affect nest success for shrubland birds is essential for management of these species (Thompson 2007). Early successional habitat is often actively managed to increase abundances of shrubland birds that specialize in this habitat type (Thompson and DeGraaf 2001, DeGraaf and Yamasaki 2003). With informed research on nest-site selection and survival, managers can further alter the amount of a given habitat and vegetation characteristics to maximize fitness for species of conservation concern (Bulluck and Buehler 2008, Kus et al. 2008).

The prairie warbler is a Neotropical migratory passerine that requires early-successional habitat and whose global population is declining. Prairie warblers specialize in xeric, shrubland habitats, and are particularly abundant in intensively managed pitch pine-scrub oak barrens and power line corridors (Morimoto and Wasserman 1991, Confer and Pascoe 2003, Gifford et al. 2010, King et al. 2011). Nevertheless, prairie warblers have

experienced dramatic range-wide declines in the past few decades (Sauer et al. 2007, Schlossberg and King 2007), and are listed as a species of conservation concern by Partners in Flight. Some information exists for prairie warblers on nest-site selection and survival: Nolan (1978) conducted a long-term study on prairie warblers in Indiana, and other recent studies have also examined prairie warbler nest-site selection and/or nest survival (Woodward et al. 2001, Fink et al. 2006, Shake 2009, Slay 2010, Schlossberg et al. 2011).

Despite this previous research, my study provides new insight into prairie warbler ecology and answers a variation of an age-old evolutionary question: Are birds adapted to select successful nest sites and how this is influenced by climate and plant interactions? To answer this question, I examined selected nest sites compared with available sites within territories, and I determined which specific spatial and temporal variables were affecting nest success for prairie warblers in an intensively managed pitch pine-scrub oak (PPSO) barren. Moreover, I examined nest-site selection and success as a function of the leaf lengths of dominant nest substrates over the course of the breeding season, to determine if there were leafing phenological constraints on nest-site selection and nest success. I present the results in the context of climate change and expect to assist managers in providing productive habitat for a declining shrubland bird.

Methods

Study Site

The study took place in the Montague Plains Wildlife Management Area (MPWMA), an approximately 607 ha, actively managed reserve located in Franklin County, Massachusetts (N 42° 34', W 72° 31'). The MPWMA consists of a matrix of thinned and

unthinned pitch pine (*Pinus rigida*) stands and scrub oak (*Quercus ilicifolia*) stands, most of which had been managed by mowing and prescribed fire, power line corridors, and an unmanaged section of upland oak-deciduous forest (see Chapter 1, Figure 1.1). The MPWMA, like most PPSO barrens, is located on nutrient-poor xeric soils, where plant communities are highly flammable and community retention is dependant on frequent fires (Motzkin et al. 1999). Due to the well-drained sandy soils, PPSO barrens tend to have extreme climatic fluctuations, in which killing frosts can occur in any month of the year (Motzkin et al. 2002). Within the MPWMA, wildfires occurred frequently in the early 20th century, with two fires burning parts of the nearby village of Lake Pleasant (Clark and Patterson 2003). In 2000, the Massachusetts Division of Fisheries and Wildlife started a program of habitat restoration and fuels reduction to reduce fuel loads and wildfire risk.

As a result of these management practices, habitat at the MPWMA was comprised of a mosaic of vegetation types and age classes. Scrub oak stands in the northern section of the study area were last burned in a wildfire in 1986 and I delineated this plot as untreated scrub oak. The scrub oak stands on the western side of the study site consisted of a mosaic of treatment plots. Some initial treatments were conducted in these treatment plots in 2000, while in other plots initial treatment occurred in later years (DFW Staff 2008). Most plots were mowed and/or burned twice between 2000-2005, while some treatment plots were treated just once since 2000. During the study, some treatment plots were then treated again primarily by large scale mowing (and some high-intensity burning as well), thus dramatically altering the habitat. Active cutting and burning of pitch pine stands occurred since 2004, in which 70% of the basal area of overstory pitch pine was removed (Clark and Patterson 2003). There was also some post-harvest burning and mowing treatments of treated pitch pine (DFW Staff 2008). At present approximately 50 % of the closed canopy pitch pine forests have been harvested. Scrub oak stands had a relatively

open overstory, and were dominated by scrub oak and low-bush blueberry (*Vaccinium angustifolium*) (Motzkin et al. 1996, King et al. 2011). Treated pitch-pine stands had a sparse pitch pine overstory, with an understory composed of scrub oak, low-bush blueberry, Pennsylvania sedge (*Carex pensylvanica*), ferns and forbs, and a variety of tree saplings. Power line corridors were managed by Northeast Utilities primarily by broadcast or selective herbicide applications, and this effectively maintained a persistent early-successional habitat that was dominated by mosaics of *Spiraea* species, regenerating pitch pine, and other low maturing shrubs, ferns, grasses, and forbs (VMP 2004-2009).

Sampling

Nests were found by observing parent behavior and conducting systematic searches (Martin and Geupel 1993). Nests were marked with flagging placed 10-15 m from the nest and monitored at intervals of 2-4 days until the nestlings fledged or the contents of the nest were gone (Martin and Geupel 1993, Weidinger 2008).

To compare vegetation at nest locations and nest patches versus random sites, I used point-intercept vegetation surveys (King et al. 2011). The nest location was defined at the nest itself, where we recorded nest height, nest substrate, and the vegetation structure at the north side of the nest. The nest patch was defined as a 5-m radius plot established with the nest located in the center of each plot (Braden 1999). Within the nest patch, 20 random points were selected, in which overstory substrate and height, understory substrate and height, and vegetation structure were recorded at each point. Overstory and understory levels were defined at greater than or less than 3-m in height respectively. At both the nest location and nest patch, vegetation structure was measured using a density

pole, in which we recorded the number of times vegetation contacted a 3-m pole at 0.5-m intervals.

To compare nest placement within a territory with other possible locations available within a territory, I mapped male territories within study plots (described in Chapter 1). Males were captured and color banded (72% of the population). Unbanded bird territories were determined by the consistent presence of a bird in a given area and the presence of neighboring color-banded males. In 2009 and 2010, territories were mapped extensively throughout the breeding season for each territorial male, using GPS points, treatment maps, and field markers. Researchers followed singing males and took approximately 5-10 GPS points until the bird completed a circle around his territory or until the bird was lost. On a given sampling day when a male moved his singing location, a subsequent GPS point was taken only when the male moved at least 5 m from his previous location. GPS points were only taken when the GPS accuracy was equal to or less than 5 m. GPS points were taken throughout the day (5:30-15:00), and territories were visited at different times of the day during the season to minimize bias (Houlihan 2000). Point-intercept vegetation surveys were also completed within a given territory to compare nest location and nest patch vegetation with available vegetation (Jones 2001). Random points within a territory were determined by creating 20 equally spaced locations along a transect spanning the length of a given male's territory. From these equally spaced locations, researchers selected a random direction perpendicular to the transect and paced out a random distance (using a random numbers table) between 0 and the width of a given territory. Researchers then conducted the vegetation point surveys at these random points.

I was also interested in including other nest site variables found in past studies to affect nest-site selection or nest success (Nolan 1978, Braden 1999, Bulluck and Buehler

2008). I recorded nest visibility, nest height, height and species of the nest vegetation, nest placement (fork, combined stems, or horizontal branch), the distance to the nearest road or fire break, the distance to the nearest tree (defined as woody-stemmed vegetation higher than 6 m), and the distance to the lateral edge of foliage (edge was defined as an visible opening at least 1-m squared). Most vegetation surveys were completed at the end of the breeding season, however visibility for all nests in 2010-2011 and most nests in 2009 was completed right after a given nest fledged or failed. Nest visibility was determined by averaging the percentages of the nest visible from 1-m away at nest height in the four cardinal directions and from 1-m above the nest (Martin and Roper 1988).

To determine plant leafing phenology in my study site and its effects on nest-site selection and success, we measured leaf lengths of highly used nest vegetation species in 2009-2011. At 8 representative points in each habitat type, leaf lengths of different plant species were measured weekly early in the season. In 2009 we measured leaf lengths weekly from May 4th-June 17th and then once at the end of the season on July 27-28. In 2010, we measured leaf lengths weekly from May 4-June 17, then again on June 30-July 1st, and lastly on July 28-30. In 2011, we measured leaf lengths weekly from May 2-June 16, and then again on June 28-29 and lastly on July 20-21. In 2009 we only measured *spiraea* and scrub oak plants, while in 2010 and 2011 we measured 8 or 9 species of the most used vegetation for prairie warbler nests. Phenology points were located >100 m from each other, spaced throughout the study site at points surveyed previously or concurrently for vegetation, birds, and bees (Motzkin et al. 1996, King et al. 2011). In 2010 and 2011, one separate stem was surveyed for each of the vegetation species that we could locate at or relatively near each survey point. From each of these stems of different plant species, the largest 5 leaves were measured weekly (Motzkin et al. 2002). In 2009, 5 leaves on 3 separate stems (per species) per point were measured. I found leaf length variation among

stems at a given point was not significant, and for the 2009 data I averaged leaf lengths across these 3 stems per point. In 2011 I did not survey points in untreated scrub oak habitat, and thus had 4 less phenology points in scrub oak habitat. Most points and stems were surveyed in consecutive years, however vegetation at some points was mowed (n=3), or the stem died due to herbicide applications or other reasons, and thus new stems and/or point locations were selected the following year.

Statistical Analysis

Continuous measurements (e.g. vegetation height) from the 20 data points from each point-intercept vegetation survey were averaged per nest patch or per territory. For categorical variables (substrate type), I took the proportion of the number of times each substrate was recorded divided by the 20 point surveys tallied for every nest patch or nest territory. I used paired t-tests to compare vegetation height and structure between a given nest or nest patch and the corresponding territory. Although we located re-nests for many territories, I randomly selected only one nest per territory to be included in this analysis. Since some variables were not normal, I log-transformed the data before the analysis to improve normality.

I investigated nest substrate selection by examining available vegetation in each territory with the selected nest substrates. I calculated the available vegetation species percentage means and standard errors among all territories by habitat type, and visually compared this with the number of nests located in each vegetation species by habitat type. I did not conduct any formal statistical analyses because selected nest substrates changed over the course of the season, so determining selected versus available was difficult to analyze with varying selection over time.

I used GPS points taken of singing males and conducted 95 % Minimum Convex Polygons (MCP's) to establish territory boundaries. I chose to use MCP's over fixed-kernel estimators because I found territory sizes by kernels appeared to be biased high and prairie warbler males tended to form territory boundaries from discrete singing locations (e.g., tall trees). I believe prairie warbler territories thus tend to be more of a polygon in shape compared with clustered circular areas of use obtained from 95 % fixed-kernel estimators (Nolan 1978, Anich et al. 2009). Since I found territory size to be correlated with the number of GPS points taken per territory, I only included territories in my analysis for birds in which I had a minimum of 28 GPS points. Territory size was not significantly correlated with the number of GPS points for these selected territories, and past studies using bootstrap analyses have found territory sizes computed with 25-30 GPS points to be comparable to territory sizes computed with more GPS points (Anich et al. 2009). The territories analyzed had an average number of 41 GPS points, with a standard deviation of 11 points.

We took GPS points throughout the 2009 and 2010 seasons, however most points were recorded in May and early June. I discarded points taken early in the season if a bird moved his territory to a new location later in the season. I also discarded points after a bird fledged young, as males can move their fledglings outside of their territory. On average, we visited territories and took GPS points for a given bird approximately 9 times in a season.

I sought to determine if birds were selecting nest locations within their territory relatively farther from forest edges or from roads/fire breaks than by chance. I computed distance to forest edge for nests using the "nncross" function in the "spatstat" package in R, taking the distance of the GPS point of a given nest to the nearest forest edge. This was also done to obtain nest distances to roads/fire breaks when nests were too far from roads/fire

breaks to accurately assess in the field. Using the 95 % MCP polygons of territories created from GPS points, I sampled 50 random points within a given territory and analyzed the distance to road/fire break and the distance to the forest edge for each sample point. I then took the average of these 50 distances of random points, and compared this mean sample distance to the distance to road/fire break or forest edge from a nest found within a given territory. Since the random samples and the nest were paired within a given territory, I conducted paired non-parametric Wilcox tests using samples from suitable territories in which I found a nest and obtained enough GPS points. I used non-parametric analyses because the data was non-normal. I conducted separate tests for distance to forest edges, and distance to roads/fire breaks. In a number of territories, the first nest failed and a second or third nest was attempted. Since each nest was compared with random points in one territory, to avoid pseudo-replication I randomly chose either the first or a subsequent (second or third) nest in my analysis.

I was also interested in nest-site selection and leafing phenological effects. I first plotted leaf length as a function of day of season. I averaged leaf lengths by stem per phenology point. In 2009, leaf out of scrub oak was especially delayed due to late frosts. As Motzkin et al. (2002) found habitat type could affect daily temperature and the timing of scrub oak leaf out, I also presented scrub oak leaf lengths over time in different habitat types for 2009.

I then created a simple as well as a more complex index of leaf out of the dominant nest vegetation. This was done to better understand how the process of leafing phenology ecologically affects nesting birds and their predators; whether nest selection and survival is more affected by a gradual change in leaf length (represented by the complex index), or instead by a sudden change in concealment provided by leaf growth (simple index). The

simple phenological leaf out was the approximate date when the leaves of dominant nest vegetation in each habitat visually appeared to cover the plants. This corresponded empirically to when the leaves were half their full size. S*piraea* was the most frequently used nest substrate in power line corridors and scrub oak in the scrub oak barrens and treated pitch pine. The simple index was assigned a value of as 0 before leaf out and 1 after leaf out. I also developed a complex index for leaf out based on predicted values of daily leaf lengths from generalized additive models (GAM). Leaf lengths measurements taken weekly were averaged per stem. I then conducted a GAM for each plant species each year, with average leaf length as the dependent variable and day of year as the independent variable. This allowed me to obtain accurate curves of daily leaf length that fit the weekly leaf length data. I then predicted daily leaf lengths from these GAMs for each species each year. To create the complex index, I still used the dominant nest vegetation in each habitat, as *spiraea* in power line corridors and scrub oak in the scrub oak barrens and treated pitch pine. Since scrub oak leaves are larger than spiraea leaves, to obtain the complex leaf out index I standardized leaf lengths per species per year, standardizing by the maximum leaf length (averaged per stem). In 2009 there was a gap in the collection of leaf length data between mid-June to the end of July, and the scrub oak predicted values from 2009 are not as accurate as in 2010 and 2011. Still, I believe these GAM curves are fairly reflective of leaf length growth during the season and appeared to better fit the data than models determined by linear, quadratic, cubic or logistic relationships.

I tested if selection of frost tolerant species for nesting was associated with nest initiation date by grouping nest substrate species into those that leafed out earlier and were more tolerant of late spring frosts (all species except oaks), versus oak species that leafed out later and whose leaves were frost intolerant, or died completely, with late frosts (Lechowicz 1984, Lechowicz 1995, Motzkin et al. 2002). I conducted a logistic regression,

with my dependant variable as frost tolerant nest substrate, and the independent variable as nest initiation date (first egg laid). I also included a habitat covariate because of previous knowledge of significantly different vegetation composition in each habitat. Since I had perfect separation in the data (only nests located in frost tolerant species in the power line habitat), I used the 'bias reduction' method to assist in parameter convergence (Firth 1993). This was done using the "brglm" function in the "brglm" package in R. In addition to a habitat covariate, I included a year covariate in the model to take into account yearly variation in leaf out dates and nest-site selection. I presented the mean parameter estimates (β), standard errors, and p-values.

I also wanted to examine nest-site selection in relation to the actual leaf out of frost intolerant species to test if any observed switch in nest-site selection between frost tolerant and frost intolerant species over the course of a season was a result of leafing phenology. To do this, for every nest initiation date, I obtained the value of the simple and complex leaf index of a frost intolerant species, scrub oak, for that given nest initiation day on that given year. I then used these index values as predictor variables in two logistic regression models, with frost tolerant species as the y variable, and simple or complex leaf out index as the x variable. Since there were no nests located in frost intolerant species in the power line corridors, I dropped this habitat in this analysis and did not include a habitat covariate. When running the model with the complex leaf out index, it was also necessary to exclude nests found in 2008. For both models, I included a year covariate as well to take into account yearly variation in leafing phenology and nest-site selection.

To analyze the effects of nest-site selection and other factors on nest survival rates, I used Program MARK, through the R package "RMark", which allowed me to include time-varying covariates (Dinsmore et al. 2002). I modeled daily survival of nest (i), and y_{ij} as a

series of Bernouli trials with a probability of success for each day (j) as Φ_{ij} =Pr(Nest alive at time j | alive at time j-1). Daily survival was then modeled as logit(Φ)= $\alpha + x_{ij}\beta$, where α was the parameter for the intercept, x was a vector of covariates, and β was a vector of parameters I was interested in estimating.

I included effects on nest success at the temporal, habitat, nest-patch, and nest-location scales (Table 1). Temporal variables consisted of year, day of year, quadratic day of year, nest age, quadratic nest age, minimum, mean and maximum daily temperature, average daily precipitation, and the simple as well as the complex index of leaf out of the dominant nest vegetation. Nest age was recorded as a continuous variable from the start of laying. I recorded nest age by 1) finding the nest during the building stage and knowing the actual lay date, 2) knowing the hatch date or age of the nestlings and back estimating the lay date based on a 24 day nesting cycle (Nolan 1978), or 3) if the nest was found and failed during incubation, inserting a semi-random nest age between 4 and t days old, in which t was 15 minus the number of known active survival days of the nest (assuming a 3 day laying interval and 12 day incubation period). The latter method was done for only 9% of the nests included in the nest depredation model. A weather station located in the study site recorded daily precipitation and temperature in 2008-2010. This weather station was not deployed in 2011, so I used weather data from nearby Orange Airport (18 km from study site) for 2011.

Habitat type consisted of power line corridors, treated pitch pine, and scrub oak. However, most prairie warbler territories and almost all nests found in scrub oak were located in treated scrub oak patches. Because of this, I did not differentiate between untreated and treated scrub oak in my nest survival analyses. I did not examine the effects of mowed vs. burned treatments, as most treated scrub oak was both mowed and burned at

various times since the start of management and it was hard to differentiate treatment types. I did include a time since treatment variable, in which I calculated the years since the latest mowing or burning of the treatment plot the nest was located in.

At the nest patch and nest location scale, I was interested in determining if birds were selecting for certain attributes, and if these selected attributes were affecting nest success. I included nest location or nest patch factors that I believed could affect nest success and nest-site attributes that were selected for (Nolan 1978, Bulluck and Buehler 2008). Nest location covariates consisted of nest height, average visibility, structure between 0.5-2 m, if the nest substrate was *spiraea*, scrub oak, or frost tolerant species, distance to road/fire break, distance to tree, distance to forest edge, and distance to foliage edge. Nest patch covariates consisted of nest patch structure between 0.5-1.5 m, nest patch structure between 2.5-3 m, nest patch canopy cover, and nest patch understory height.

In my nest depredation analysis, I excluded all abandoned nests and only included active nests found with at least 1 egg (Mayfield 1975). Successful nests were classified as having fledged at least one young. I also excluded nests in which I did not have more than 1 active observation day—these were nests we found with nestlings that were 8-9 days old and on a subsequent nest check, the nestlings had fledged. I did not standardize continuous covariates as suggested by Dinsmore et al. (2002) when running nest survival models in MARK because the models are still able to numerically optimize with unscaled covariates and scaling the covariates leads to nonsensical results. If there were any missing data in the covariates, I filled missing data in with the median value for that given covariate (for most covariates, missing data accounted for 0-3% of the data). An exception to this was the structure at the nest between 0.5-2 m. In 2008, we measured structure at 1 m increments, instead of 0.5 m increments. However, I found structure between 0.5-2 m to be highly

correlated with structure between 0-2 m (r=0.93), so I ran a simple linear regression between these two structure groups, and obtained parameter estimates of the relationship. I then predicted structure between 0.5-2 m for the missing 2008 data using these parameter estimates. Although birds selected nest locations with low structure at 2.5-3 m, I did not include a covariate for this in my nest models because only 2 % of the nests had structure at this height.

To determine the best model, I used a manual forward-selection AIC process (Burnham and Anderson 2002). I started with the null model and then independently added single variables into separate models. I then compared these single-variable models with the null model using AICc values. I decided *a priori* to keep single variable models in my model selection process if they decreased the AICc value compared with the null model. Otherwise, I discarded the covariate/model from my analysis. I then continued to build more complex models by combining covariates of the previous models, and continued to add covariates into the model if the given addition of a covariate decreased the AICc value. As all of my selected covariates have been found to affect nest parasitism or nest success in past studies, I could not create models based on *a priori* combinations of variables, and rather chose to conduct this manual forward selection AIC process to produce the best fitting models. I determined the 'best' models by selecting models that were <2 ΔAICc from the top model. Significance of individual covariates within models was assessed based on whether 95 % confidence intervals of the parameter included 0.

I attempted to include an interaction term between year and the leaf out indexes (simple and complex), to take into account any variation in leaf out differences among years and the effect on nest survival. However, the simple leaf out index and year interaction did not converge in RMARK, and thus I could not run this interaction. I was able to run an

interaction term of complex leaf out index and year in the analysis, however this interaction term did not come out in any of top models, and for simplification purposes I decided to discard this interaction term before running the final analyses.

For certain covariates I did not have a complete dataset from all four years or in all habitat types. These covariates were the complex leaf out index, nest patch data (structure, canopy cover, understory height), and time since treatment. I only had a complex leaf out index variable in 2009-2011, as leaf lengths were not recorded in 2008. I thus created a subset of nests, with just nests from 2009-2011 (reduced year subset). Likewise, I only recorded nest patch data for 108 out of 265 nests (recorded for all nests in 2009 and a random sample of the nests found in 2010), and created a separate subset dataset with these nests (nest patch subset). Lastly, the time since treatment variable was only practical for nests located in scrub oak and treated pitch pine habitats. Power line corridors were treated with selective herbicide applications and I believe that this minimal disturbance management technique is inherently different than a highly intensive mowing or burning application. Therefore, I also created a subset with only nests in treated pitch pine and scrub oak habitats (habitat subset).

In addition to running an analysis with a full dataset with all the nests, because of the missing data I also ran a number of independent analyses with reduced numbers of nests (subset datasets). I did this in order to examine all covariates' affect on nest depredation and cowbird parasitism rates, despite the missing data. For subset analyses, I included all other covariates with no missing data in the analysis and model selection, however, I did not include other covariates that also had missing data, as this would further subset the useable number of nests. For instance, I ran a model selection procedure analysis with the 'reduced year subset' of nests. For this analysis, I included the complex leaf out

index, did not include nest patch covariates or time since treatment, and included all other possible covariates.

I examined cowbird parasitism rates on all active nests that had at least 1 cowbird or prairie warbler egg, including those that were later abandoned. I conducted logistic regression models to assess if certain variables explained whether a nest was parasitized or not. As in the nest depredation analyses, I used the same manual forward-selection AIC process, and compared models based on AICc values. To include covariates with missing data, I conducted separate analyses and model selection with the full dataset, the reduced year subset, the nest patch subset, and the reduced habitat subset. In these analyses I included most of the covariates as in the nest depredation analyses, however, I did not include age, temperature, or precipitation covariates. Instead of the time-varying covariate for the day of year in the nest depredation analyses, I included a covariate of the initial lay date for each nest. Since some nests were found and failed during incubation, for these nests I used a semi-random nest age when found between 4 and t days old, in which t was 15 minus the number of known active survival days of the nest, and backtracked nest age when found to the estimated initial lay date. I estimated the initial lay date for 13 % of the nests in my cowbird parasitism analysis. Although I discarded nests with these estimated lay dates when examining nest-site selection, I did not do this here because a number of parasitized nests were found and then abandoned without observing the actual lay date. A quadratic initial lay date was also included in the analysis. I also was interested in examining simple and complex leaf out phenology indexes affect on parasitism rates. As done in the nest-site selection analysis, for every nest initiation date, I obtained the value of the simple and complex leafing index for that given nest initiation day on that given year in the given habitat the nest was in (using the *spiraea* leafing index for nests in power lines, and the scrub oak leafing index for nests in scrub oak and treated pitch pine habitats).

I presented the best model(s) for each subset of the data. In the cowbird parasitism analyses, since I found only a few covariates that had lower AICc values than the null, and these covariates were correlated, I did not model average parameter estimates. Instead I presented parameter estimates and standard errors from single-covariate models. For the cowbird parasitism analyses, I determined significance of a given covariate based on a p-value of <0.05 (instead of using 95 % CI's) because I used logistic regression and this analysis in R presents p-values instead of 95% CI's. I used the program R, version 2.13 to conduct all nest-site selection and cowbird parasitism analyses (R Development Core Team 2011).

Results

Prairie warblers selected distinct nest patches and nest site locations in relation to non-nest, random locations in all habitat types. Prairie warblers appeared to seek out distinct nest substrates (Table 2.2), despite some of these plant species being relatively scarce within breeding territories (Table 2.3). Highly used nest substrates included *spiraea sp.* in power line corridors, and scrub oak and other woody plants in the other habitats. Birds built nests at heights predominantly between 0.5-1.5 m (mean = 0.80 m, StDev = 0.31 m), with low visibility (mean= 26 % visible, StDev = 18 %), at short distances to foliage edges (mean= 1.5 m, StDev = 1.5 m), and at a large range of distances to nearest trees (mean = 10.1 m, StDev = 5.9 m). Nest vegetation substrate heights were predominantly between 0.5-2 m (mean 1.39 m, StDev = 0.5 m), and the nest was most often located in the middle to top portion of the vegetation (nest height/substrate height mean = 58 %, StDev = 14 %). Nests were placed predominantly on upright forks of a single stem (72 %) or on combined stems (25 %), with few nests placed on horizontal branches. Compared with random points

in territories, birds selected a high amount of vegetation structure between 0.5-1.5 m at the nest and patch locations (Table 2.4). Also, birds selected less canopy cover in the nest patch, and less structure between 2.5-3 m at the nest location and patch, compared to non-nest points within the territory.

Leafing phenology varied by vegetation species and year, with frost intolerant oak species leafing out later in the season (Figure 2.1). This was especially prevalent in 2009, when late frosts killed scrub oak leaves in many areas of the study site in late May. In 2009, habitat type appeared to affect scrub oak leaf out dates, with untreated scrub oak habitat having later leaf out dates (Figure 2.2).

In scrub oak and treated pitch pine habitats, prairie warblers significantly selected frost tolerant species early in the nesting season, and then almost completely switched to frost-intolerant species later on (initial lay date β=-0.19, SE=0.027, $p<0.001$) (Figure 2.3). Conversely, in power line corridors birds selected frost-tolerant species throughout the breeding season (PL vs. SO habitat β=-7.20, SE=1.75, $p<0.001$, PL vs. TPP habitat β=-6.42, SE=1.68, $p<0.001$), however there were few suitable frost-intolerant nest sites in the power line corridors (Table 2.3). In this analysis with all 3 habitat types, selection of frost tolerant nest substrates was not different in 2009, the year that had the latest leaf out of frost intolerant species, compared with other years (2009 vs. 2008 β=0.001, SE=0.95, p=1; 2009 vs. 2010 β=0.43, SE=0.54, p=0.42; 2009 vs. 2011 β=-0.92, SE=0.50, p=0.06).

In scrub oak and treated pitch pine habitats, the switch in nest substrate was highly explained by both the simple and complex frost intolerant leaf out index, such that as leaf length increased, more nests were placed in frost intolerant species. (Simple Index β=-3.7, SE=0.75, $p<0.001$, Complex Index β=-10.6, SE=1.4, $p<0.001$) (Figure 2.4). Interestingly in the analysis with the complex leaf out index within scrub oak and treated pitch pine

habitats, yearly variation in 2009 did help explain nest-site selection. However, contrary to what one would expect in a year of delayed leafing phenology, 2009 had slightly fewer nests found in frost tolerant species (2009 vs. 2010 β=3.4, SE=0.7, $p<0.001$, 2009 vs. 2011 β=3.4, SE=0.7, $p<0.001$) (Figure 2.4).

I mapped 66 territories with a sufficient number of GPS points, in which mean territory size was 0.94 ha (StDev = 0.43 ha). Using 59 territories in which I also located nests, I found that birds significantly selected nest locations closer to roads and fire breaks, compared with random points within their territories (p= 0.03) (Figure 2.5). There was no significant selection of nests closer or farther away from forest edges (p=0.36).

In the study, 316 prairie warbler nests were found, of which 265 were included in my full subset nest depredation model, as 5% of nests were abandoned due to cowbird parasitism, and another 7% were abandoned for other reasons. A total of 3,444 observation days (or effective sample size (see Rotella et al. 2004)) were included in the full nest depredation model. The full nesting season was 70 days long, beginning May 17th as the earliest lay date for a nest, and ending with the last active nest day on July 25th. In the subset nest depredation analyses, reduced year subset had 244 nests (3263 observation days), reduced habitat subset had 212 nests (2,542 observation days), and the nest patch subset had 108 nests (1,600 observation days).

Of all nests, 37 % were successful in fledgling at least one prairie warbler, while 43 % of nests that were not abandoned were successful. Overall, in the constant survival (null) model with my full dataset, the daily nest survival rate was 0.958 (95 % CI: 0.951-0.964). Given a 24-day nesting interval, this leads to a refined nest survival rate due to predation of 36 % (95 % CI: 30-42 %).

Prairie warbler nest depredation was associated with multiple temporal and spatial factors (Table 2.5). In the full, reduced habitat, and reduced year subsets, the top models contained similar covariates. These top predictor variables were nest age, year, average visibility, distance to road/fire break, structure between 0.5-2 m at the nest location, and nest height (Table 2.6). In 2008 and 2011, the nest depredation rates were higher compared with 2009 and 2010 (Figure 2.6). As nests became older in age, they had higher depredation rates, and nests that were more visible had higher depredation rates. Interestingly, nests closer to a road or a fire break had lower depredation rates. Higher nests had slightly lower depredation rates in the reduced year analysis. The analysis conducted on the subset of nests that had nest patch data differed from the other analyses on all or subsets of nests, in that simple leaf out index was in all the top models, and this variable was highly significant in explaining nest depredation rates. For these nests, daily nest survival was higher when the dominant nest vegetation was leafed out. Although there were some other variables in the top models in the different subset analyses, none of these other variables were significant in their effect on nest depredation rates.

Of the 316 nests found, 16% were parasitized by cowbirds. Due to high nest depredation and abandonment rates, only 8 nests (< 3 % of nests) fledged a single cowbird young. The top models for cowbird parasitism rates included distance to forest edge and *spiraea* vegetation substrate. In all the different subset analyses (the habitat subset, reduced year subset, and nest patch subset of nests), few variables decreased the AICc value below the null model. In the full nests analysis, nests farther from forest edges were significantly more likely to be parasitized, however this was not significant in other subset analyses.

Discussion

In my study, prairie warblers selected nest sites based on certain vegetation structure and composition at the nest location and patch, spatial location within the territory, and vegetation substrate. My results are consistent other studies reporting that prairie warblers build nests between 0-2 m in height (Folsom 2008, Slay 2010, but see Nolan (1978) study which found slightly higher nest heights), and select dense vegetation close to the nest. Birds in my study selected low canopy cover in the nest patch; few other studies have noted this preferred nest-site selection for prairie warblers, but this generally coincides with these birds' preferred habitat (Nolan 1978). Also, high structure was selected at the nest location and nest patch scales, and low visibility of selected nest sites.

My results indicate that nest site features that were selected for promoted nest survival. For example, lower visibility of the nest did significantly increase nest survival. Many other studies, including studies on prairie warblers, have found birds that select nest locations with high concealment have higher nesting success (e.g. Nolan 1978, Martin and Roper 1988, Rangel-Salazar et al. 2008). On the other hand, there have been a number of other studies that have found no significant relationship of survival with selected nest sites (e.g. Filliater et al. 1994, Braden 1999, Davis 2005, Bulluck and Buehler 2008). Hypotheses for these latter non-significant findings are that predation can be random, current nest-site selection reflects historical adaptations to past predator communities, or that birds cannot adapt to a diverse suite of nest predators which varies in space and time (Filliater et al. 1994, Davis 2005, Bulluck and Buehler 2008). In contrast, my study gives support that birds are adapted to select nest sites to increase nest survival, despite an array of predators or other mechanisms that may obscure this adaptation. Interestingly, although I found high vegetation structure at and around the nest was selected for, the effect of structure at the

nest location on nest survival was only marginally significant, and structure at the nest patch was not significant. Nest predators may have been less deterred by high vegetation density and more impeded by nest concealment in my system. Determining the variables that birds are adapted to select and are biologically relevant for predators is important in making inferences about nest-site selection adaptations for survival (Bulluck and Buehler 2008).

My observation that nest sites selected by prairie warblers were associated with nest survival does not rule out the possibility that birds may be selecting microhabitats using other selection criteria. Birds may select sites with increased thermal cover, as colder nests inflict higher energy costs for incubating females and may affect nesting success (Vleck 1981, Gloutney and Clark 1997, Hooge et al. 1999, Wiebe 2001). Studies have found that birds can select nest sites that buffer nests from cold conditions (Calder 1973, Hooge et al. 1999), or oppositely select nest sites that shield nests from strong solar radiation and high temperatures (Walsburg 1981, With and Webb 1993). Conway and Martin (2000) found orange-crowned warbler (*Oreothlypis celata*) females spent less time incubating nests when ambient temperature was lower; females that incubate less and are less attentive at the nest can result in lower nest survival (Martin and Ghalambor 1999). In my study, birds appeared to primarily place nest sites in leafed out vegetation, but I did not examine nest-site selection in relation to temperature, wind speed, and solar radiation. Selection for concealed nests may also inherently lead to nests being more protected from solar radiation and strong winds than unconcealed nests, and thus the same selection pressures could be acting on birds to reduce energetic costs and increase nest survival.

I found prairie warblers selected nest sites close to large foliage edges, most often along dirt roads and fire breaks that were highly prevalent in my study area; this selection

appeared to be adaptive as nests close to roads and fire breaks had significantly lower nest depredation rates. Nolan (1978) did not mention any specific nest-site selection close to openings in his two study areas. However, consistent with my study, Slay (2010) found a prominent decrease in the density of woody stems at 3-10 m from the nest compared with 0-3 m from the nest, while a concurrent study on prairie warblers in the Albany Pine Barren also noted nest-site selection close to vegetation breaks and openings (Neil Gifford personal communication). One hypothesis for this selection would be that higher vegetation density exists along edges such as fire breaks in my study site, thereby increasing nest concealment and nest success. A simple linear regression of average visibility of nests and distance to fire break/road does show a significant relationship, although this relationship appears to be weak (r-squared value 0.02) (MA unpublished data). In scrub oak habitat, I found vegetation closer to roads and fire breaks did leaf out earlier than vegetation within 'frost pockets' of large continuous areas of scrub oak (Motzkin et al. 2002), thus birds could have been selecting nest sites close to these breaks due to this earlier leaf out. However, distance to roads of selected nests did not change as a function of leaf out, and birds selected nest sites close to roads/fire breaks even late in the breeding season (MA unpublished data).

Other studies have also found forest roads do not negatively impact nest survival (Rodewald 2002, Benson et al. 2010), indeed King and DeGraaf (2002) also noted higher nest survival for ovenbirds (*Seiurus aurocapilla*) along forest dirt roads. Although studies have found certain nest predators can increase in abundance along certain types of edges (review in Chalfoun et al. 2002), this may not be the case for forest roads (Rich et al. 1994). It is possible that snakes and other small mammal predators are avoiding or are less abundant on fire breaks and roads and foraging farther within cohesive shrub cover away from these breaks (Klug et al. 2009). Interestingly, I did not find a similar effect of distance from the nest to the closest gap in vegetation greater than 1 m squared (distance to foliage

edge) on nest survival. The foliage edge often tended to be a small opening in the vegetation compared to a large opening created by a fire break or road. This contrast in edge type may have had an effect on predator densities along the two different edge types and subsequently nest survival. Other possibilities exist for selection close to roads; in dense, shrubby habitats, females may be selecting these nest sites to increase their own survival – using openings to increase visibility of incoming predators or as an easier escape route (Gotmark et al. 1995, Burhans and Thompson 2001). Although I did not quantify this, food abundance or microclimate along these fire breaks/roads could also be related to nest-site selection and survival (Hooge et al. 1999, Conway and Martin 2000). Lastly, nests at times were placed close to territorial borders (MA personal observation), and I cannot rule out that nest-site selection along fire breaks facilitated social behaviors by allowing females to acquire more or preferred extra-pair copulations with neighboring males (Ramsey et al. 1999). Despite these other possibilities, this selection near roads and breaks appears to be adaptive in part for higher nest survival.

In past studies on shrubland birds, nests closer to forest edges tend to have higher depredation rates, but not always (King et al. 2001a, Woodward et al. 2001, King et al. 2009a, Shake 2009). In power line corridors in Massachusetts, King et al. (2009a) found shrubland bird nests had higher depredation rates closer to forest edges. Woodward et al. (2001) found a similar effect for prairie warbler nests in Missouri, however, there was no edge effect for other shrubland bird species. In a study in North Carolina shrublands, distance to mature forest edges had no effect on nest depredation, but depredation of nests closer to agricultural edges was significantly lower (Shake 2009). I did not find any relationship with nest-site selection or depredation rates with distance to forest edges. Mature forest edges may not be as detrimental to shrubland birds as agricultural edges, as

the latter can increase predator abundance due to available food supplies (Suarez et al. 1997, Dijak and Thompson 2000).

I found temporal variables of nest age and year to significantly affect nest depredation rates. Small mammals have been important nest predators in other studies conducted at northern latitudes (Thompson 2007), and yearly variation could be due to fluctuations of small mammal densities after mast years and/or community interactions with raptors (Schmidt and Ostfield 2003, Clotfelter et al. 2007, Schmidt et al. 2008). However, I do not know the relative importance of specific nest predators at my study site, and thus I cannot rule out fluctuating snake or avian predator populations (Seigel and Fitch 1985). Changes in predator space use or behavior among years can also be a factor (Schmidt and Ostfield 2003). In relation to nest age, Nolan (1978) also found older prairie warbler nests were more likely to be depredated, as nestlings become more conspicuous and parents make more feeding trips to the nest.

I found few significant effects for spatial or temporal covariates on cowbird parasitism, past studies have observed variation in cowbird parasitism more at a landscape scale (Robinson et al. 1995, Thompson et al. 2002, Folsom 2008, Schlossberg et al. 2011). I did find slightly more nests were parasitized farther away from forest edges in the full subset model. Cowbirds prefer agricultural fields and suburban areas to forage in (Thompson 1994), and as my study site has a mosaic of vegetation types including graminoid, shrubby and forest vegetation, cowbirds are most likely using areas in the study site as suitable foraging habitat. Possibly cowbirds are more centrally located within the study site, and thus parasitism is slightly higher away from forest edges. In comparison with prairie warbler nest data from the Albany Pine Bush Reserve, cowbird parasitism was much lower at my study site (~54% in Albany) (N. Gifford unpublished data). Albany Pine Bush

Reserve is surrounded by a much more urbanized landscape (Gifford et al. 2010). Another concurrent study in a much less urbanized landscape, the Ossipee Pine Barrens in New Hampshire, found no signs of cowbirds or cowbird parasitism on prairie warbler nests (n=8) (T. Maikath personal communication). Therefore, landscape factors such as urbanization and forest fragmentation are probably contributing to nest parasitism and also to nest depredation rates (Thompson 2007, Schlossberg et al. 2011), but I did not examine landscape factors due to the limiting spatial scale of this study.

My findings are consistent with past studies that have examined leafing phenology and nest-site selection. In a study site in Arizona, Martin (1993) recorded a switch in the dominant nest substrate used by MacGillivray's warblers (*Geothlypis tolmiei*) from maples to firs in years when maple leaf development was hindered by late frosts and drought. Schmidt and Whelan (1999) noted American robins (*Turdus migratorius*) predominantly selected nest sites in invasive species vegetation (*Lonicera maackii*) early in the season due to early leaf out of this species. Nolan (1978) found prairie warblers chose higher nest sites in a year when a late frost damaged leaves on smaller shrubs and saplings. In a concurrent study in the Albany Pine Bush Reserve, prairie warblers nested early in the season in leafed out scrub oak vegetation upslope from bare, frost killed scrub oak located in low-lying frost pockets (Neil Gifford personal communication). I found prairie warblers selected frost tolerant nest substrates that were leafed out early in the nesting season, in preference to available but not-leafed out oak vegetation in the scrub oak and treated pitch pine habitats.

Preference for leafed-out vegetation is most likely due to higher nest concealment provided in nest substrates that are leafed-out; and at least in some studies, higher concealment presumably results in higher nest survival (Nolan 1978, Martin 1993). Since in these previous systems studied and in my study birds selected leafed out vegetation rather

than building their nests on bare branches, it is difficult to fully determine if nest survival would be lower in bare vegetation. In an experiment using artificial nests in a temperate forest, Santos and Telleria (1991) did not find any difference in nest survival between nests placed in leafed out versus non-leafed out oak species. Nevertheless, many studies, including my study, have found more concealed nests significantly lower depredation rates (i.e. Nolan 1978, Rangel-Salazar et al. 2008), and I would thus presume that if birds did nest on bare branches, these nests would get depredated at higher rates. Other considerations are that leafed out nest sites could be selected for due to higher microclimate or food availability close to the nest site (Van Riper et al. 1993, Hooge et al. 1999, Conway and Martin 2000), but these hypotheses are not mutually exclusive from nest concealment.

In addition to selection for frost tolerant species early in the season, I found birds switched almost completely to nesting in frost intolerant substrates later in the season in certain habitats and this was highly explained by the leaf out of these frost intolerant oak species. Other studies have found birds can change nest location, including nest height, as the season progresses (Holcomb and Twiest 1968, Nolan 1978, Van Riper et al. 1993). Studies have attributed this change in nest location to birds adapting to a change in suitability and concealment of the vegetation and possibly higher nest survival at these new nest sites (Holcomb and Twiest 1968, Nolan 1978, Martin 1993, Chalfoun and Martin 2010). Therefore, one could hypothesize that prairie warblers would switch to leafed-out oak species substrates later in the season because they increase nest survival. Increased nest survival could occur if predators have a harder time searching for nests located in oak species, because 1) oaks are the dominant vegetation and thus predators have to search more sites to locate a given nest (potential prey-site hypothesis; Martin 1988), or 2) by switching substrates in mid-season, predators might lose their search image and be less accustomed to finding their nests (Martin 1987, Chalfoun and Martin 2009). Interestingly

however, I found no difference in nest depredation in frost tolerant versus frost intolerant species. The complete switch of nesting substrates in the scrub oak and treated pitch pine habitats is possibly due to other nest-site selection criteria. Nolan (1978) noted certain nest substrates were avoided in his study site because of their lack of "Y," upright forks that prairie warblers prefer to nest in. Stems of scrub oak and other oak saplings have many "Y" forks and tend to be more stable and move less in high wind conditions than grey birches and *prunus sp.* selected early in the season (MA personal observation); this could be important to avoid damage to nests during stormy conditions such as thunderstorms prevalent during the breeding season. Moreover, birds could be taking into account the stability of the nest with the full weight of a clutch of nestlings—although females sometimes placed nests along the trunk and branches of small pine saplings early in the season, if successful these nests in pines often did not hold up well and became tipped with the weight of older nestlings.

Nest placement was consistent in *spiraea* and *Rubus sp.* vegetation in power line corridors throughout the breeding season. Prairie warblers appear to prefer nesting in *spiraea* vegetation, despite nesting in *spiraea* does not significantly increase nest survival. *Spiraea* vegetation tended to conceal nests well; in addition it provided multiple forks and stems for preferred placement. Although there was some scrub oak vegetation in one of the power line corridor plots, these plants tended to be older, taller, and of a different structure than younger scrub oak found in other habitat types (MA personal observation). I found prairie warblers tended to avoid nesting in taller vegetation, this could therefore explain avoidance of these oaks in the power line corridor. Another unperceived finding is that I observed fewer frost tolerant nest substrates in 2009, a year with delayed leaf out. I believe this is more due to a sampling bias of fewer re-nests found that year (with generally more

re-nests located in frost intolerant species), rather than actual yearly variation due to leafing phenology.

I believe that there was a real effect of leafing phenology on nest survival in 2009, but not in other years. In the nest patch subset analysis, I found nest depredation rates were significantly affected by the simple leaf out index, but in other subset analyses this variable was not in the top models. The nest patch subset consisted of a majority of nests from 2009, and this year had the most pronounced delay in oak species leaf out. Although the year and leaf out interaction did not converge in the analysis, I ran a p*ost-hoc* analysis with a subset of nests from just 2009, and found similar results, with simple leafing index still significant (MA unpublished data). Furthermore, a *post-hoc* analysis of nests from just 2010 did not find any significant relationship between simple leaf index and nest survival (MA unpublished data).

I thus believe that in certain years with delayed leaf out, the presence versus absence of leaves can have an impact on nest survival. The simple leaf out index, based on roughly when leaves covered the vegetation, could be a better indicator of how predators and nests are affected by leafing phenology compared with the complex index, which measured standardized leaf length over time. Initially in the breeding season, branches were mostly bare and small buds and leaf growth did not cover most branches. Moreover, once leaves grew approximately half of their full length and covered vegetation, further growth did not appear to contribute much to further concealing branches or nests. Prairie warbler females also appeared to be cueing in on when leaves were approximately half to two-thirds their full growth, as this correlates highly to when they switched nest site substrates to frost intolerant species (Figure 2.4). Thus, this 'present versus absent' simple

leaf out index seems more biologically significant to this system and possibly for other predator/nest-prey systems, compared with the actual leaf length over time.

Explanations for this leaf out effect include the non-mutually exclusive potential-prey hypothesis and the 'total foliage hypothesis'. The potential-prey hypothesis states that predators should have more difficulty locating nests if there are more potential nesting sites, and studies have found some support for this influencing nest survival (Martin and Roper 1988, Martin 1993, Chalfoun and Martin 2009). The total foliage hypothesis proposes that increased vegetation density or nest concealment can impede predators from hearing, seeing, or smelling the nest (Martin 1993). In my study site, before the dominant vegetation was leafed out, the number of potential leafed-out nest sites was relatively low. Early in the breeding season, leafed-out frost tolerant vegetation was conspicuous, with leafed-out shrubs scattered throughout the more dominant oak vegetation. Based on the potential-prey site hypothesis, predators should find these nest sites more easily (Chalfoun and Martin 2009). After leaf out of the oak vegetation, the number of suitable nest sites greatly increased, which presumably would lead to predators having increased difficulty locating nests (Nolan 1978, Davis 2005, Chalfoun and Martin 2009). Also, nests most likely became more concealed over time, as I found nest visibility was higher for nests that had an earlier nest initiation date and a lower complex leaf out index value at the nest initiation date (MA unpublished data) (however, note that nest visibility measurements were done after a nest fledged or failed). Therefore, the potential-prey site or total foliage hypotheses appear to be suitable explanations for simple leaf out index's effect on nest survival, but why did this not occur every year? One explanation could be that in other years besides 2009, most of the first initiated nests were only active less than 1 week before the oak species leafed out. In these years, predators may not have had enough time to cue in on bird nests, a new available food resource of the season, before the dominant vegetation was leafed out.

However, in 2009, the delayed leaf out of the dominant oak vegetation was especially prolonged, and nests were active for 3-4 weeks, with peak numbers of nests active, before leaf out occurred. Early in the 2009 season, predators may have opportunistically found prairie warbler nests located in leafed out vegetation (Schmidt et al. 2001), but only in 2009 would these predators be able to use this search image to further locate and depredate more nests.

As simple leaf out was related to nest placement in frost intolerant species and habitat type, and these factors should also be considered in relation to the nest survival results. As mentioned earlier, in all nest depredation analyses there was no significant difference in nest depredation if the nest was built in frost tolerant versus frost intolerant species. Therefore, from the results it appears that regardless of what substrate the nest was initially built in, even if it was frost tolerant species, after leaf out occurred in 2009 there was better daily nest survival. Moreover, a habitat effect could have been correlated with my results. In 2009, I observed high nest survival in power line corridors. In all 4 years, the dominant vegetation, *spiraea*, in power line corridors was already leafed out before prairie warbler nesting began, thus all daily observations of nests in power line corridors received a '1' for the simple leaf out index (Appendix 1). Despite this possible habitat and leaf out interaction, when I ran an analysis on the nest patch subset excluding nests found in power line corridors, I found similar results, with simple leaf index still significant and in the top candidate models (MA unpublished data).

The potential-prey site or total foliage hypotheses seem to be best suited for my results. A different explanation for the association of nest survival with calendar date is the 'predator food availability' theory suggests that predators may switch from nests as a primary food source early in the season, to more plentiful, easily-accessible food source

later in the season, thus lowering nest depredation rates (Schmidt 1999). Another theory proposes that foraging becomes easier for nesting birds later in the season, thereby increasing the amount of time females can be vigilant at the nest and deterring active predators (Schmidt 1999). Although I cannot rule out these theories, I did find evidence for plant leaf out phenology to have an impact on nest success, and did not find a similar strong effect of time of year. Other studies have also found nesting success to be higher later in the season and also have hypothesized this higher survival was due greater vegetation density later in the season (Nolan 1978, Davis 2005). This potential explanation appears to best match with my results.

As global climates change, interactions between climate, plant leafing phenology and avian reproductive success can be affecting birds both in their core range as well as at the northern edge of their range. Climate warming is projected to increase growing season length and decrease the number of days with frost in the United States (Easterling et al. 2000, Planton et al. 2008). Throughout their range, birds may benefit from this warming as plants leaf out earlier and have longer durations of full leaf-out conditions, providing birds with suitable early-season nest sites, and possibly higher nest survival associated with early leaf-out conditions. Power line corridors in my study site, in which *spiraea* vegetation was leafed out fully during the entire breeding season, had earlier nest initiation dates and higher seasonal fecundity than other habitats in the delayed leaf out year in 2009 (MA unpublished data). On the other hand, variation in temperature can change peak biomass of prey caterpillars, mismatch food abundance and fledgling times, and can correspondingly reduce productivity (Both et al. 2006, Visser et al. 2006). Also, climate change may have other direct or indirect detrimental effects on productivity because of altered plant communities or predator abundances (Martin 2007), or a higher likelihood of extreme weather events, such as severe storms (Kunkel et al. 1999, Easterling et al. 2000, Planton et

al. 2008). Past studies have found severe storms can damage nests and significantly lower breeding productivity (Mahony et al. 2006). In 2009, a severe hailstorm in Albany, NY, caused failure for about 66 % of active prairie warbler nests (n=6) (Neil Gifford unpublished data), and I also found a small proportion of nests failed due to severe thunderstorms in the MPWMA.

As climates warm, the geographic ranges of many bird species are moving northward (Hitch and Leberg 2007), but these species can be restricted at the edge of their ranges by climate-biotic interactions (Mahony et al. 2006, Collister and Wilson 2007). In a northern population of pied flycatchers (*Ficedula hypoleuca*), Jarvinen (1993) found leafing phenology and climate to affect laying dates and clutch sizes, and reproduction success was limited by cold weather. Collister and Wilson (2007) found weather directly affected nest survival in a population of loggerhead shrikes (*Lanius ludovicianus*) at the northern edge of their range. In Massachusetts, prairie warblers are at the northern edge of their range and were not present before the 1870's (Nolan 1978). In the northern edges of their range, birds have shorter breeding seasons and fewer chances to re-nest after nest failure, these populations could be more negatively affected by nest losses early in the season due to delayed leaf-out. The direct and indirect effects of climate change on the complex interactions of plants and wildlife deserves more study to fully determine how birds' reproduction and populations will be impacted in the future.

Management Implications

Based on my findings, I propose that managers consider plant, climate, and wildlife interactions when managing habitat for avian species. In managed pitch pine-scrub oak barrens and other shrubland habitat, nesting shrubland birds would benefit by maintaining

frost tolerant species in the understory in which they can nest in during years with delayed leafing phenology. Although forest managers prefer to cut down fast-growing hardwood saplings like grey birches, red maples, and *prunus* species that can out-compete scrub oaks in a pitch-pine scrub oak barren (Patterson personal communication), retaining some of this vegetation diversity would be useful for shrub-nesting birds and other wildlife (Wagner et al. 2003). If these fast-growing species must be cut-down, retention of other early-leafing, low-lying shrubs such as *spiraea*, high-bush blueberry, and mountain laurel, or small pine saplings, should be considered.

Other considerations for increasing productive prairie warbler nesting habitat are creating a dense vegetation understory with low canopy cover, including vegetation breaks, and consisting of relatively young growth. The inclusion of roads and fire breaks within the vegetation can prevent large-scale wildfires (Clark and Patterson 2003) and I found may even benefit birds' reproductive success. Like other studies, I did not find much evidence for consistent effects of habitat or time since treatment on nest survival (Chandler et al. 2009a, King et al. 2009b). This is promising for the creation and maintenance of different habitat types and treatment times to promote more natural and heterogeneous shrubland habitat. Nevertheless, I found surprisingly few prairie warbler territories and nests located in untreated, older scrub oak vegetation. Moreover, I found leaf out can be delayed in large patches of untreated scrub oak compared to treated scrub oak and treated pitch pine habitats. Therefore, treating scrub oak patches with prescribed burning or mowing would be beneficial to prairie warblers as well as for other wildlife species (Wagner et al. 2003).

Table 2.1. Covariates and their notation used in the nest survival and cowbird parasitism analyses. Note not all covariates were examined, depending on the subset of the nest data.

Covariate Type	Covariate	Notation
Temporal Variation		
	Year	$S_{(Year)}$
	Age	$S_{(Age)}$
	Quadratic Age	$S_{(Age2)}$
	Day	$S_{(Day)}$
	Quadratic Day	$S_{(Day2)}$
Weather/Leafing Phenology		
	Daily Precipitation	$S_{(precip)}$
	Minimum Daily Temperature	$S_{(Mintemp)}$
	Mean Daily Temperature	$S_{(Meantemp)}$
	Maximum Daily Temperature	$S_{(Maxtemp)}$
	Simple Leaf Out Index	$S_{(SimpleLO)}$
	Complex Leaf Out Index	$S_{(ComplexLO)}$
Habitat		

	Habitat Type	$S_{(Hab)}$
	Time Since Treatment	$S_{(TST)}$
Nest Location		
	Nest Height	$S_{(Nheight)}$
	Average Visibility	$S_{(Vis)}$
	Structure between 0.5-2 m	$S_{(Str0.5-2)}$
	Spiraea Nest Substrate	$S_{(Spiraea)}$
	Scrub Oak Nest Substrate	$S_{(SO)}$
	Frost Tolerant Nest Substrate	$S_{(FrostTol)}$
	Distance to Road	$S_{(DistRd/FB)}$
	Distance to Tree	$S_{(DistTree)}$
	Distance to Foliage Edge	$S_{(DistFolEdge)}$
	Distance to Forest Edge	$S_{(DistForestEdge)}$
Nest Patch		
	Nest Patch Structure bet. 0.5-1.5 m	$S_{(NPStr0.5-1.5)}$
	Nest Patch Structure bet. 2.5-3 m	$S_{(NPStr2.5-3)}$
	Nest Patch Canopy Cover	$S_{(NPCanopycover)}$
	Nest Patch Understory Hieght	$S_{(NPUnderHght)}$

Table 2.2. Number of nest substrates by plant species and habitat type for prairie warbler nests found in 2008-2011.

Nest Vegetation Species	Frost Tolerance	Power Line Corridors	Scrub Oak	Treated Pitch Pine

Scrub Oak (*Quercus ilicifolia*)	Intolerant	0	27	58
Black/Red/Scarlet Oak (*Quercus sp.)*	Intolerant	0	0	25
Dwarf Chestnut Oak (*Quercus prinoides)*	Intolerant	0	3	3
White Oak (*Quercus alba)*	Intolerant	0	0	1
Spiraea sp.	Tolerant	53	0	7
Red Maple (*Acer rubrum)*	Tolerant	0	9	26
Rubus sp.	Tolerant	9	0	8
Sweet Fern (*Comptonia peregrina*)	Tolerant	0	0	16
Grey Birch (*Betula populifolia*)	Tolerant	0	2	13
Prunus sp.	Tolerant	0	7	5
Highbush Blueberry (*Vaccinium corymbosum*)	Tolerant	1	0	8
Pitch Pine (*Pinus rigida*)	Tolerant	0	1	8
Quaking Aspen (*Populus tremuloides*)	Tolerant	0	1	7
Rounded Serviceberry (*Amelanchier* sp.)	Tolerant	0	3	2
Mountain Laurel (*Kalmia latifolia*)	Tolerant	0	0	4
Silky Dogwood (*Cornus amomum*)	Tolerant	2	0	0
Hazelnut *(Corylus* sp.)	Tolerant	0	1	0
Red Osier (*Cornus stolonifera*)	Tolerant	0	0	1

Table 2.3. Estimated percentage amounts of the most used nest substrates in prairie warbler territories (n=103), in relation to amounts of all vegetation and ground cover in the territories. Means and (SE) presented.

	Power Line Corridors	Scrub Oak	Treated Pitch Pine
Rubus sp.	4.8 (1.5)	0 (0)	0.3 (0.2)
Grey Birch	1.3 (0.5)	1.9 (0.8)	5.2 (0.9)
Live SO	4.6 (0.7)	79.2 (3.5)	23.1 (2)
Live *Spiraea*	11 (1.8)	0 (0)	0.2 (0.2)
Oak Species	2.1 (0.7)	1.1 (0.8)	15.8 (1.4)
Prunus sp.	0.4 (0.3)	0.8 (0.5)	1.4 (0.3)
Red Maple	0.4 (0.3)	3.3 (1)	1.9 (0.5)
Rounded Serviceberry	0 (0)	0 (0)	0.1 (0.1)
Sweet Fern	3.3 (1)	0 (0)	1.4 (0.3)
Pines (White and Pitch Pine)	10.4 (1.6)	0.3 (0.3)	4.6 (0.7)
Quaking Aspen	0 (0)	0 (0)	1.7 (0.6)
High Bush Blueberry	0.8 (0.5)	0 (0)	0.3 (0.2)

Table 2.4. Vegetation characteristics between the nest location, nest patch, and random points within a territory in 2009-2011. These data only include nests (n=107) and nest patches (n=93) that were analyzed with data from territories. Means and (standard errors) presented. * denotes p-value<0.001, ** p<0.01, and * p<0.05.**

	Nest Location	Nest Patch	Random Points	Location vs. Random	Patch vs. Random
Overstory Height (m)	NA	12.41 (1.12)	13.09 (0.55)		
Canopy Cover (%)	NA	0.07 (0.02)	0.16 (0.01)		***
Understory Height (m)	NA	91.97 (3.29)	88.77 (3.31)		
Structure 0-0.5 m	3.48 (0.32)	3.77 (0.14)	3.86 (0.14)	***	
Structure 0.5-1 m	5.63 (0.37)	2.52 (0.13)	1.78 (0.1)	***	***
Structure 1-1.5 m	2.88 (0.33)	1.07 (0.1)	0.81 (0.07)	***	**
Structure 1.5-2 m	0.94 (0.18)	0.39 (0.06)	0.45 (0.05)	***	*
Structure 2-2.5 m	0.26 (0.10)	0.13 (0.02)	0.16 (0.02)	***	*
Structure 2.5-3 m	0.03 (0.02)	0.03 (0.01)	0.13 (0.03)	***	***

Table 2.5. Model selection results for the top models from nest depredation and nest parasitism analyses. Presented models are within 2 AICc from the best model. Models with less support than the null model were omitted. Covariate notation is described in table 2.1.

Analysis Type	Model	Number of Parameters	AICc	Δ AICc	Weight
Cowbird Parasitism Full					
	$S_{(DistForestEdge)}$	2	269.28	0	0.42
	$S_{(DistForestEdge + Spiraea)}$	3	269.91	0.63	0.307
	$S_{(Spiraea)}$	2	270.14	0.866	0.273
Cowbird Parasitism Reduced Year					
	$S_{(Spiraea)}$	2	242.82	0	0.503
	$S_{(Null)}$	1	242.84	0.021	0.497
Cowbird Parasitism Reduced Habitat					
	$S_{(DistForestEdge + Spiraea)}$	3	219.3694	0	0.433

$S_{(DistForestEdge)}$	2	219.7397	0.37	0.36
$S_{(Spiraea)}$	2	220.8434	1.474	0.207

Cowbird Parasitism Nest Patch

$S_{(Vis + DistRd/FB)}$	3	115.72	0	0.426
$S_{(DistRd/FB)}$	2	117.34	1.518	0.199
$S_{(Vis)}$	2	117.5572	1.637	0.188
$S_{(Null)}$	1	117.5702	1.65	0.187

Nest Depredation Full

$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB)}$	9	909.2885	0	0.1123
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + FrostTol + DistRd/FB)}$	10	909.741	0.4525769	0.0896
$S_{(Year + Age + Nheight + Vis + DistRd/FB)}$	8	909.9968	0.7083544	0.0788
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + Spiraea + DistRd/FB)}$	10	910.3847	1.0962069	0.0649

$S_{(Year + Age + Vis + Str0.5\text{-}2 + DistRd/FB)}$	8	910.7118	1.4233744	0.0551
$S_{(Year + Age + Vis + DistRd/FB)}$	7	910.7794	1.490979	0.0533
$S_{(Year + Age + Nheight + Vis + Spiraea + DistRd/FB)}$	9	910.8147	1.52626	0.0524
$S_{(Year + Age + Vis + Spiraea + DistRd/FB)}$	8	910.946	1.6574844	0.0490
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB + DistForestEdge)}$	10	911.0368	1.7483669	0.0469
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + SO + DistRd/FB)}$	10	911.2359	1.9474369	0.0424
$S_{(Year + Age + Day + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB)}$	10	911.2512	1.9627169	0.0421
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB + DistTree)}$	10	911.2597	1.9712569	0.0419

Nest Depredation Reduced Year

$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB)}$	8	834.1127	0	0.12087
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + FrostTol + DistRd/FB)}$	9	834.6049	0.4921303	0.09450
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + Spiraea + DistRd/FB)}$	9	834.8104	0.6976503	0.08527
$S_{(Year + Age + Nheight + Vis + DistRd/FB)}$	7	835.0195	0.9067354	0.07681

$S_{(Year + Age + Nheight + Vis + Spiraea + DistRd/FB)}$	8	835.4393	1.32656	0.06226
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB + DistForestEdge)}$	9	835.9493	1.8365903	0.04825
$S_{(Year + Age + Nheight + Vis + Str0.5\text{-}2 + SO + DistRd/FB)}$	9	836.0587	1.9459703	0.04568
$S_{(Year + Age + Vis + Str0.5\text{-}2 + DistRd/FB)}$	7	836.0637	1.9509354	0.04557
$S_{(Year + Age + Vis + Spiraea + DistRd/FB)}$	7	836.0699	1.9571754	0.04543
$S_{(Year + Age + Day + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB)}$	9	836.0819	1.9691803	0.04515

Nest Depredation Reduced Habitat

$S_{(Year + Nheight + Vis + Str0.5\text{-}2 + DistRd/FB)}$	8	739.6067	0	0.17155
$S_{(Year + Nheight + Vis + DistRd/FB)}$	7	739.9977	0.3910293	0.14109
$S_{(Year + Vis + DistRd/FB)}$	6	740.2472	0.6405265	0.12454
$S_{(Year + Vis + Str0.5\text{-}2 + DistRd/FB)}$	7	740.3453	0.7386593	0.11858
$S_{(Year + Nheight + Vis + Str0.5\text{-}2)}$	7	740.4336	0.8268993	0.11346

$S_{(Year + Nheight + Vis)}$	6	740.8881	1.2814165	0.09039
$S_{(Year + Vis)}$	5	741.5771	1.9704397	0.06405

Nest Depredation Nest Patch

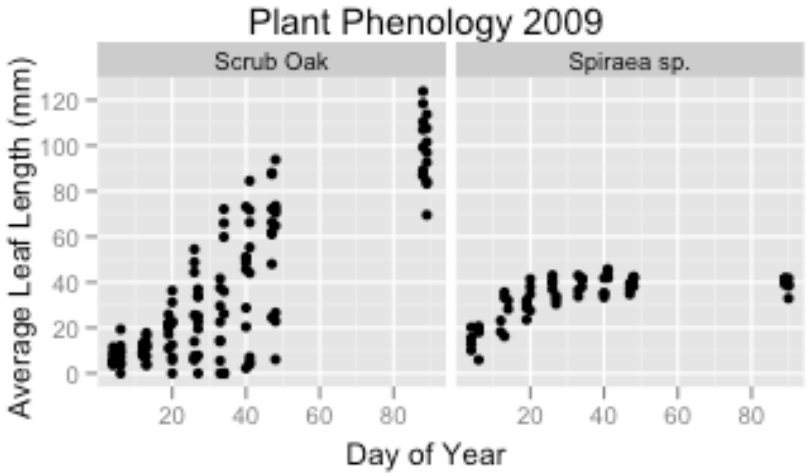
$S_{(Age + SimpleLO + Str0.5\text{-}2 + DistRd/FB)}$	5	325.8065	0	0.0811
$S_{(Year + Age + SimpleLO + Str0.5\text{-}2 + DistRd/FB)}$	6	326.0626	0.2561295	0.0713
$S_{(Year + Age + SimpleLO + DistRd/FB)}$	5	326.0737	0.2672	0.0709
$S_{(Age + SimpleLO + Nheight + DistRd/FB)}$	5	326.3426	0.53614	0.0620
$S_{(Age + SimpleLO + Vis + DistRd/FB)}$	5	326.9	1.09359	0.0469
$S_{(Age + SimpleLO + DistRd/FB + NPStr0.5\text{-}1.5)}$	5	326.9129	1.10647	0.0466
$S_{(Year + Age + SimpleLO + Nheight + DistRd/FB)}$	6	326.9809	1.1744795	0.0451
$S_{(Year + Age + SimpleLO + ComplexLO + Str0.5\text{-}2 + DistRd/FB)}$	7	327.039	1.2325006	0.0438
$S_{(Year + Age + SimpleLO + Nheight + Str0.5\text{-}2 + DistRd/FB)}$	7	327.0575	1.2510606	0.0434
$S_{(Year + Age + SimpleLO + Vis + DistRd/FB)}$	6	327.0741	1.2676195	0.0430

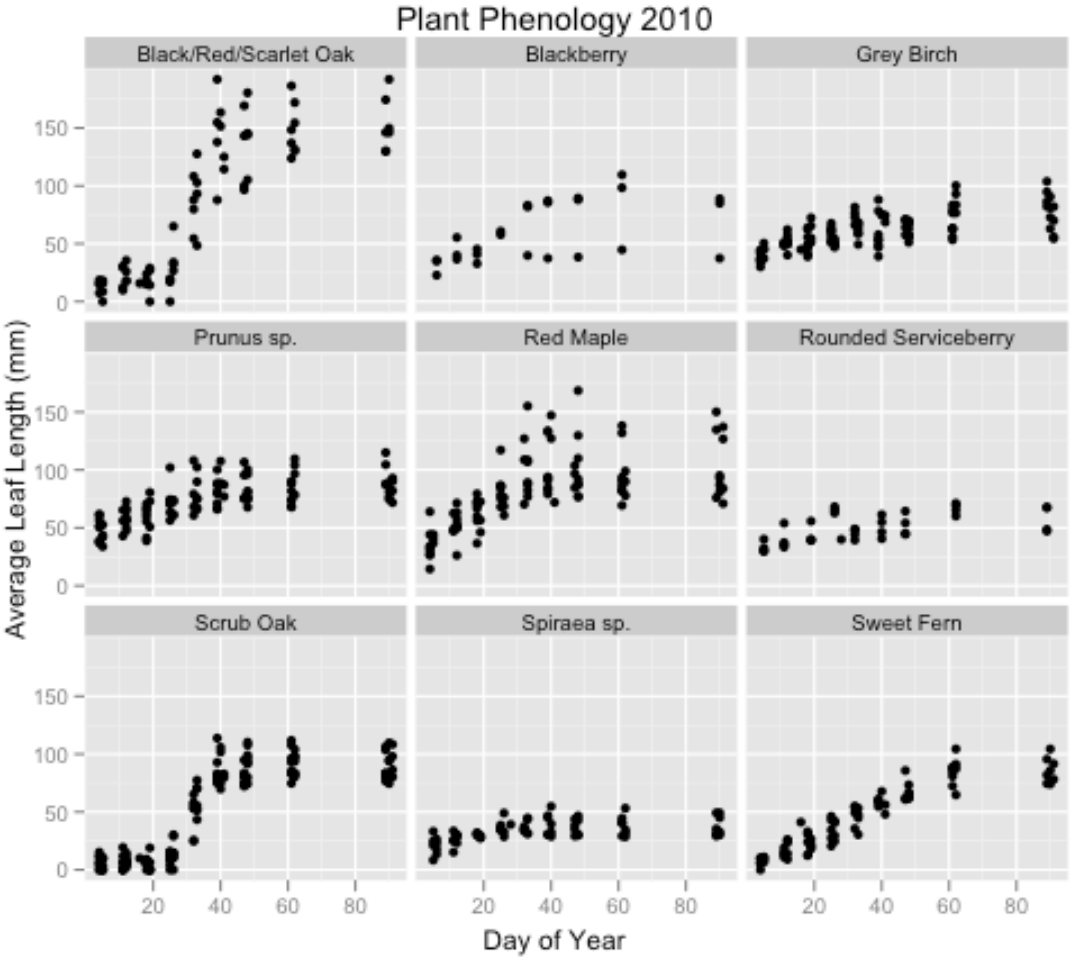
$S_{(Year + Age + SimpleLO + Spiraea + DistRd/FB)}$	6	327.2128	1.4063895	0.0401
$S_{(Year + Age + SimpleLO + DistRd/FB + NPStr0.5\text{-}1.5)}$	6	327.2757	1.4692595	0.0389
$S_{(Year + Age + SimpleLO + Vis + Str0.5\text{-}2 + DistRd/FB)}$	7	327.3817	1.5752706	0.0369
$S_{(Year + Age + SimpleLO + Str0.5\text{-}2 + Spiraea + DistRd/FB)}$	7	327.7803	1.9738406	0.0302
$S_{(Year + Age + SimpleLO + Str0.5\text{-}2 + DistRd/FB + NPStr0.5\text{-}1.5)}$	7	327.7836	1.9771006	0.0302

Table 2.6. Parameter estimates from the best model of each subset analysis. Means and (SE) presented, significant parameters are in bold. CBP – cowbird parasitism analysis, ND – nest depredation analysis, RYear – reduced year, Rhabitat- reduced habitat, NPatch – nest patch.

Parameter	CBP Full	CBP RYear	CBP Rhabitat	CBP NPatch
$S_{(Year08vs.09)}$				
$S_{(Year08vs.10)}$				
$S_{(Year08vs.11)}$				
$S_{(Year09vs.10)}$				
$S_{(Year09vs.11)}$				
$S_{(Age)}$				
$S_{(SimpleLO)}$				
$S_{(Nheight)}$				
$S_{(Vis)}$				-0.02 (0.015)
$S_{(Str0.5-2)}$				
$S_{(Spiraea)}$	-0.85 (0.50)	-0.67 (0.50)	-15.02 (906.94)	
$S_{(DistRd/FB)}$				0.0063 (0.0041)
$S_{(DistForestEdge)}$	**0.0057 (0.0027)**		0.0060 (0.0031)	

Parameter	ND Full	ND RYear	ND RHabitat	ND Npatch
$S_{(Year08vs.09)}$	**0.86 (0.31)**		0.65 (0.34)	
$S_{(Year08vs.10)}$	**1.09 (0.33)**		**0.99 (0.36)**	
$S_{(Year08vs.11)}$	0.47 (0.30)		0.36 (0.33)	
$S_{(Year09vs.10)}$		0.22 (0.26)		
$S_{(Year09vs.11)}$		-0.39 (0.21)		
$S_{(Age)}$	**-0.044 (0.014)**	**-0.039 (0.014)**		**-0.12 (0.027)**
$S_{(SimpleLO)}$				**1.45 (0.34)**
$S_{(Nheight)}$	-0.0053 (0.0028)	**-0.0059 (0.0029)**	-0.0048 (0.0028)	
$S_{(Vis)}$	**-0.014 (0.0049)**	**-0.014 (0.0051)**	**-0.011 (0.0052)**	
$S_{(Str0.5-2)}$	0.020 (0.013)	0.021 (0.014)	0.02 (0.014)	0.051 (0.035)
$S_{(Spiraea)}$				
$S_{(DistRd/FB)}$	**-0.0042 (0.0015)**	-0.0032 (0.0017)	-0.0029 (0.0016)	**-0.0060 (0.0026)**
$S_{(DistForestEdge)}$				


Plant Phenology 2009
Scrub Oak
Spiraea sp.
Average Leaf Length (mm)
0
20
40
60
80
100
120
20
40
60
80
Day of Year


Plant Phenology 2010
Black/Red/Scarlet Oak
Blackberry
Grey Birch
Prunus sp.
Red Maple
Rounded Serviceberry
Scrub Oak
Spiraea sp.
Sweet Fern
Average Leaf Length (mm)
0
50
100
150
20
40
60
80
Day of Year

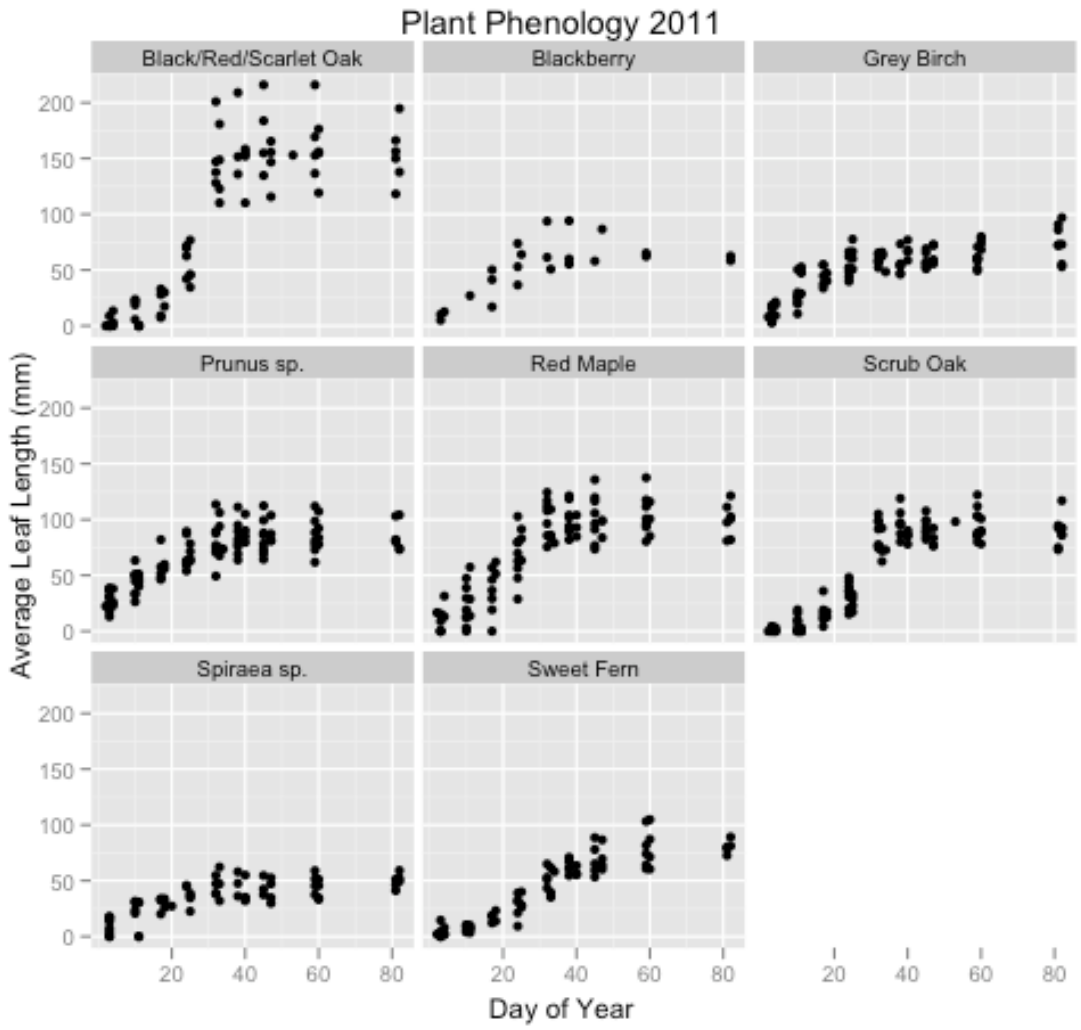


Figure 2.1. Leaf length (mm) averaged per stem by year, day, and vegetation species in 2009-2011. Frost-intolerant species (oak sp.) often did not fully leaf out until June (Motzkin et al. 2002). This pattern was especially pronounced in 2009, oak species did not reach maximum leaf lengths until after mid-June. Day of year starts (1) at May 1st.

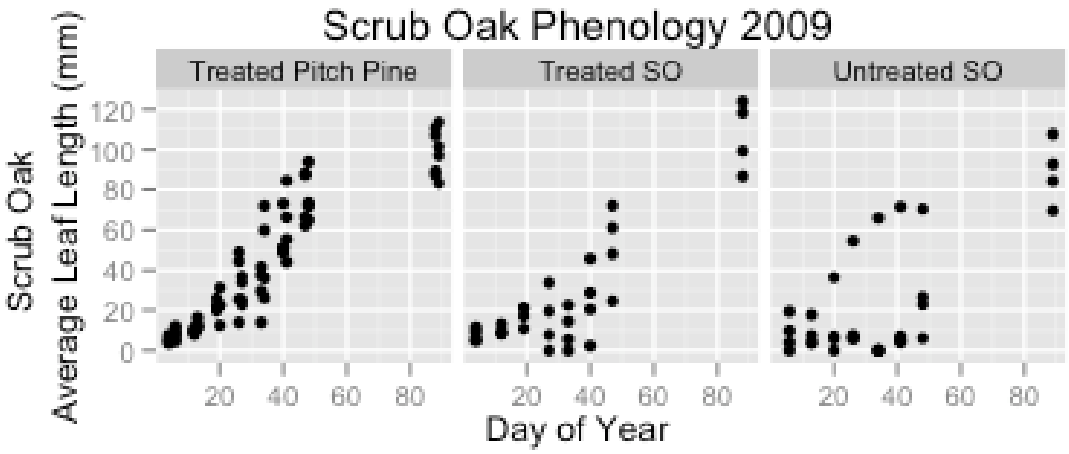


Figure 2.2. Leaf length (mm) of scrub oak averaged per sampling point by day and habitat type in 2009. SO-scrub oak.

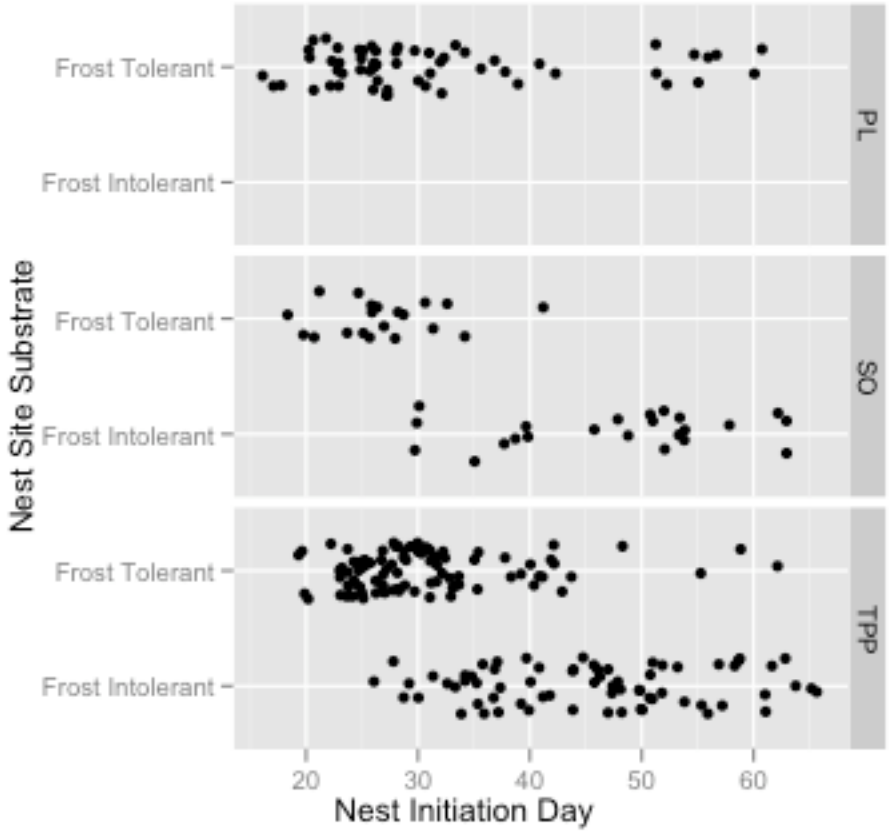
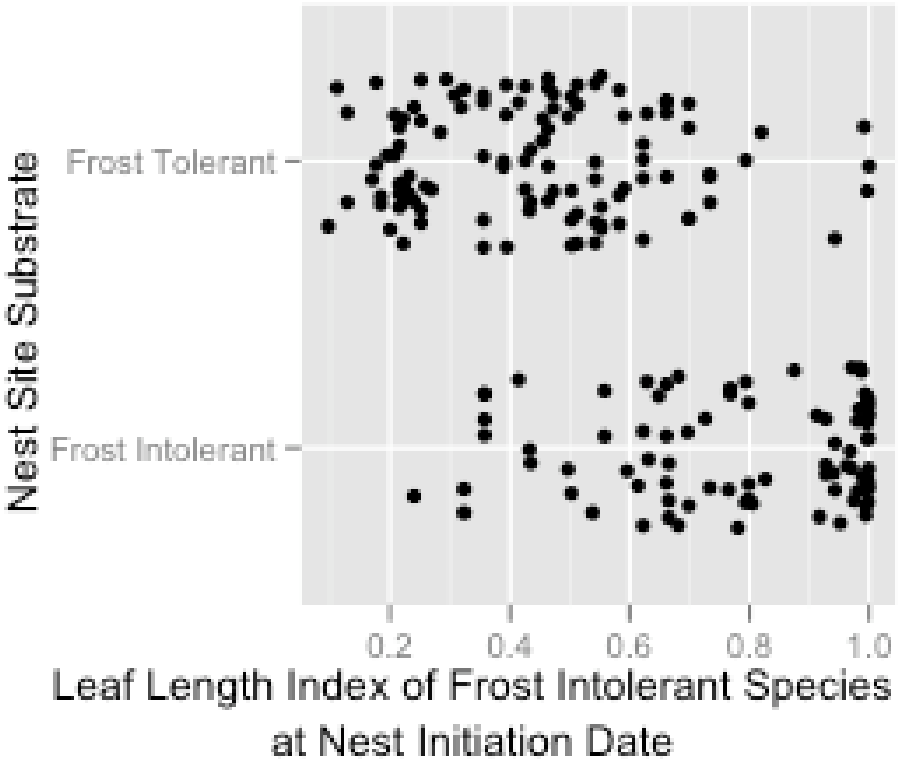


Figure 2.3. Nest-site selection of frost tolerant versus frost intolerant species over time in three habitat types during 2008-2011. TPP – treated pitch pine, PL – power lines, SO – scrub oak. Data points (n=266) are scattered to enhance visibility of the number of nests for each nest initiation day. Nest initiation day starts (1) at May 1.


Nest Site Substrate
Frost Tolerant
Frost Intolerant
0.2
0.4
0.6
0.8
1.0
Leaf Length Index of Frost Intolerant Species
at Nest Initiation Date

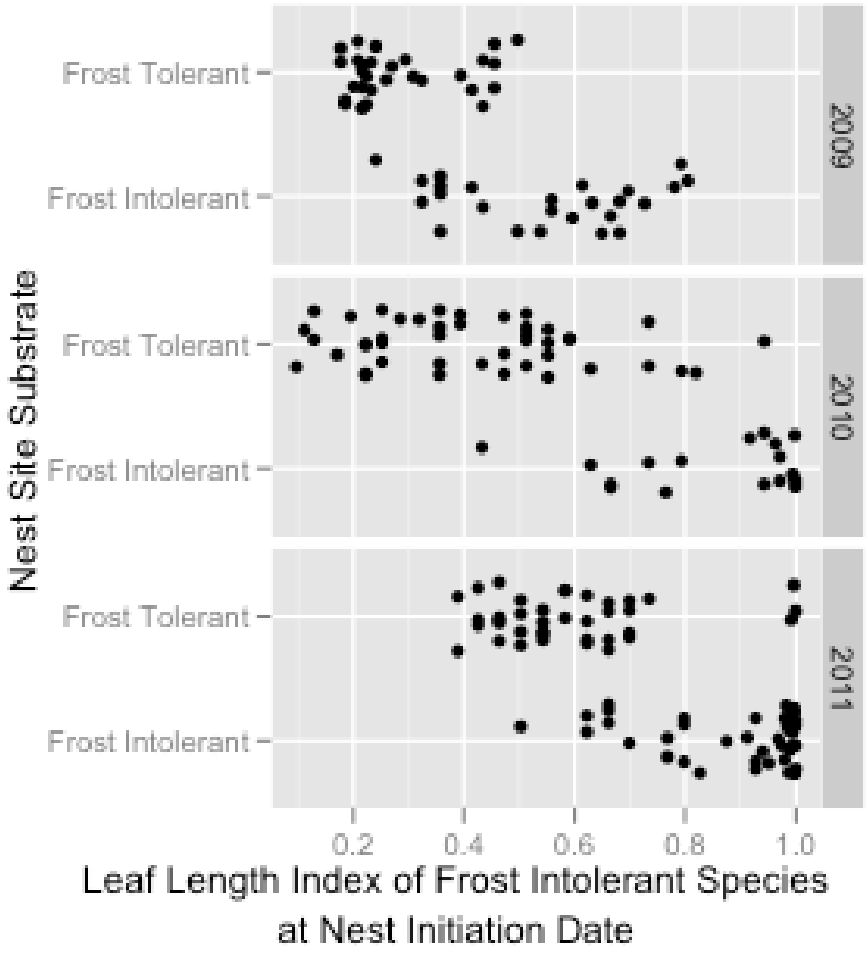


Figure 2.4. Nest-site selection of frost tolerant versus frost intolerant substrate in relation to the complex leaf length index of a frost intolerant species (scrub oak) at the nest initiation date. Nests from power line corridors and 2008 are omitted. The first figure combines all years, while the second partitions nests by year. Data points (n=195) are scattered to enhance visibility.

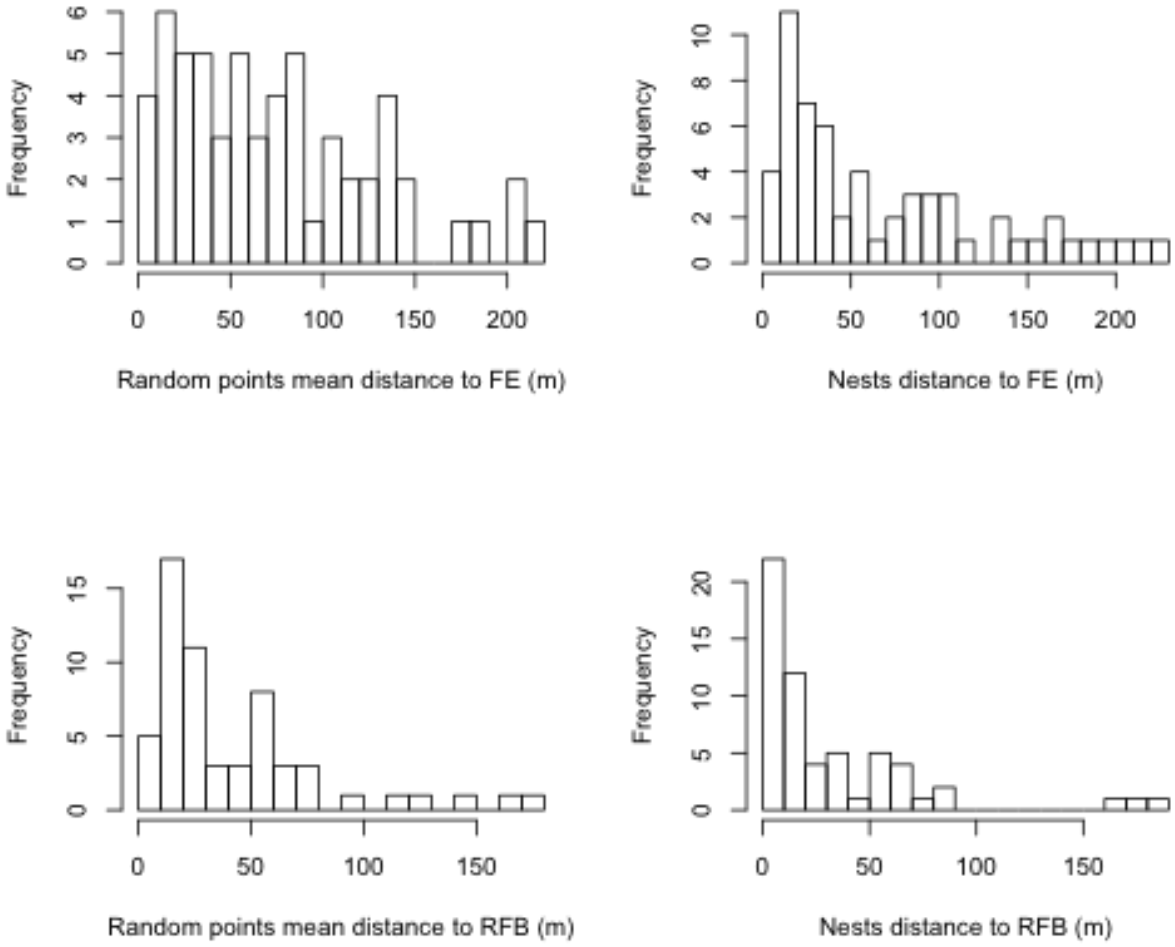
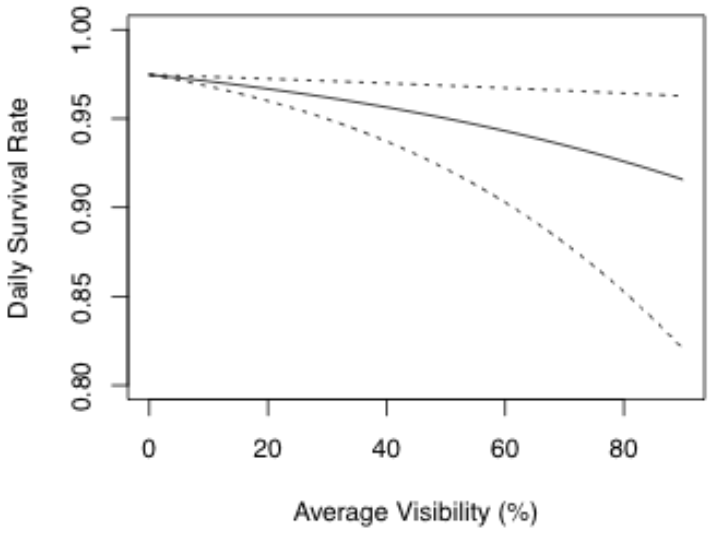
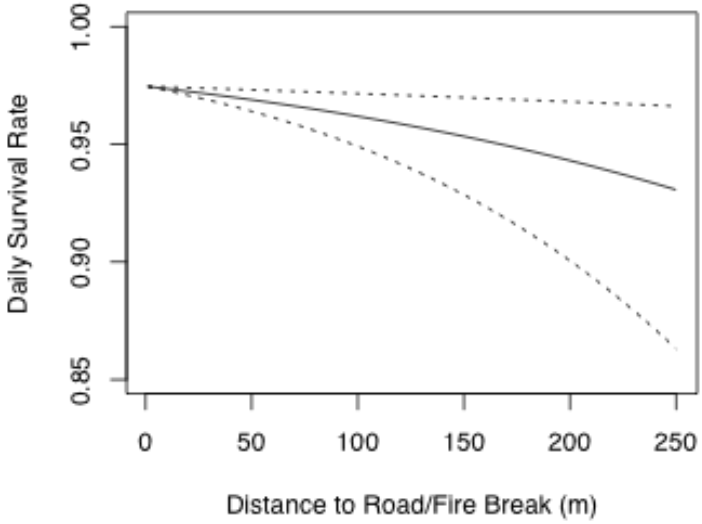
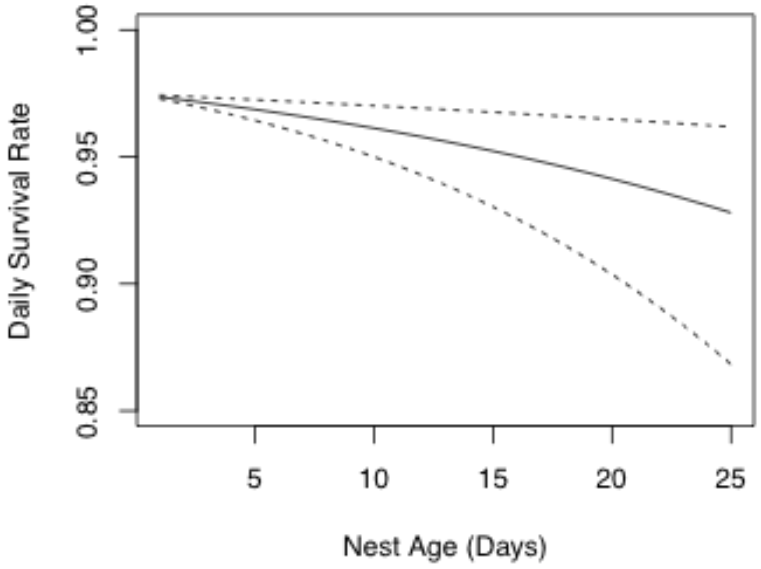
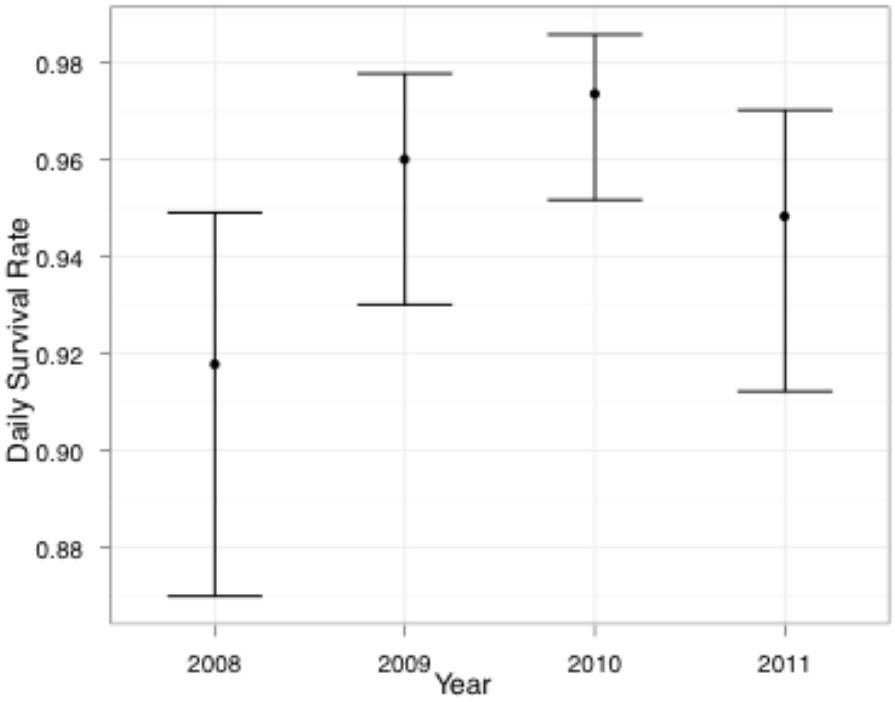


Figure 2.5. Distances to roads/fire breaks (RFB) and forest edges (FE) of nests found between 2009-2010, compared with mean distances of random points within territories to RFB and FE.


Daily Survival Rate
1.00
0.95
0.90
0.85
0.80
0
20
40
60
80
Average Visibility (%)


Daily Survival Rate
1.00
0.95
0.90
0.85
0
50
100
150
200
250
Distance to Road/Fire Break (m)


Daily Survival Rate
1.00
0.95
0.90
0.85
5
10
15
20
25
Nest Age (Days)


0.98
0.96
0.94
0.92
0.90
0.88
Daily Survival Rate
2008
2009
2010
2011
Year

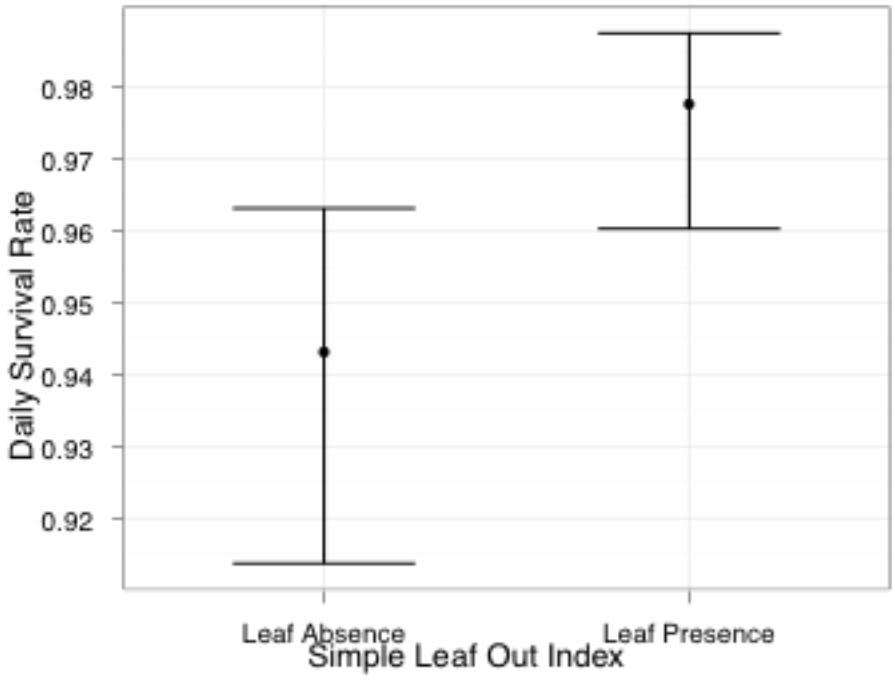
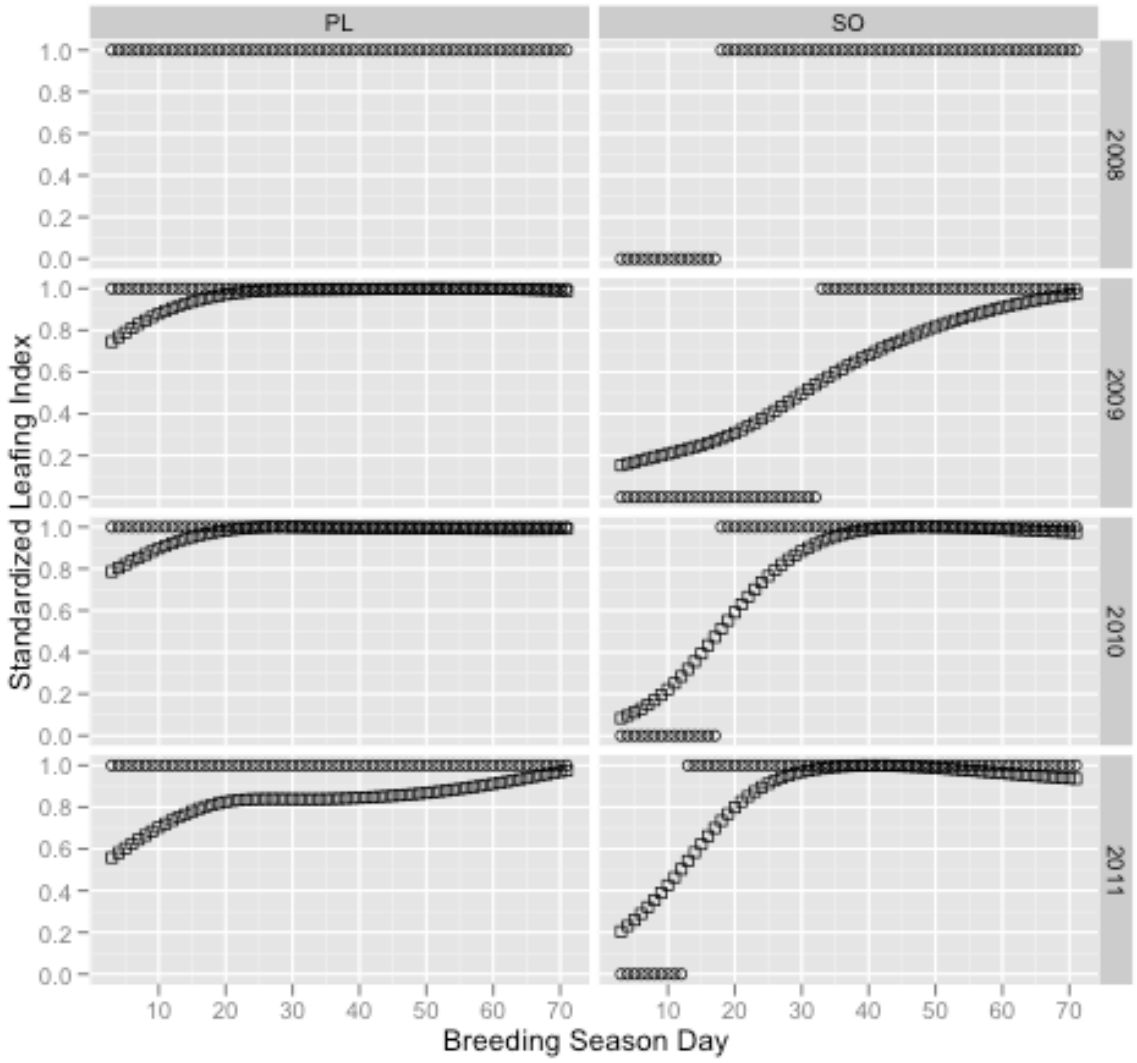

0.98
0.97
0.96
0.95
0.94
0.93
0.92
Daily Survival Rate
Leaf Absence
Leaf Presence
Simple Leaf Out Index

Figure 2.6. Prairie warbler nest daily survival rates (DSR) relationships with significant covariates. Average visibility, distance to road/fire break, and nest age are plotted with DSR predicted values using the parameter estimates from the top model in the full nest depredation analysis. For these 3 covariates, this prediction was done by taking the intercept parameter and the given individual covariate parameter from the top model, and excluding all other variables. For year, I used parameter estimates from the single covariate 'Year' model, using the full dataset. This was done because in the top model, the DSR estimates for individual years were biased high due to the effect of other covariates in the model. The simple leaf out index graph used parameter estimates from the single covariate 'SimpleLeaf' model, from the nest patch subset analysis. Solid lines or points are the mean DSR, dotted lines or error bars are 95 % confidence intervals.

APPENDIX

PHENOLOGY INDEXES

Simple and complex leafing phenology indexes by year and habitat type, PL=power line corridor (based on *spiraea)*, SO = scrub oak and treated pitch pine habitats (based on scrub oak). Circles represent the simple leaf out index, squares the complex leaf out index. The complex leaf out is predicted values based on GAMs of the dominant nest substrate leaf length data. Breeding season day starts (1) at May 17th, the first nest initiation date for prairie warblers found in the study area.


PL
SO
2008
2009
2010
2011
Standardized Leafing Index
Breeding Season Day
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
50
60
70

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