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Habitat Characteristics Affecting Site Occupation in Wintering Henslow's Sparrows at Mississippi Sandhill Crane National Wildlife Refuge

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Habitat Characteristics Affecting Site Occupation in Wintering Henslow's Sparrows at
Mississippi Sandhill Crane National Wildlife Refuge

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
In partial fulfillment of the
Requirements for the degree of

Master of Science
In Biological Sciences

By

Mary E. Nicholson

B.S Loyola University New Orleans, 2009

December 2011

Dedication

I would like to dedicate this thesis to my grandparents: Harold and Mary Schultz and W.L. and Sandra Nicholson. Without the love and support they have provided me, I would not be the person I am today. They have always valued my education, and for that I thank them.

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Abstract

Henslow's sparrow (*Ammodramus henslowii*) winters in recently burned sites in pine savannas of the Southeastern United States. Previous studies have suggested that factors such as seed abundance and litter depth are important to wintering Henslow's sparrows. My study asked how habitat variables including vegetation structure, seed abundance, and arthropod abundance predict Henslow's sparrow site occupancy at Mississippi Sandhill Crane National Wildlife Refuge. In this study, Henslow's sparrow more often occupied sites burned one growing season earlier than sites burned two growing seasons earlier, and did not occupy sites burned three or more growing seasons earlier. Data indicated that mass of graminoid seeds borne on stalks in November and minimum total seed mass were higher in occupied sites vs. unoccupied sites while litter density was lower. This suggests that Henslow's sparrow selects habitats that maximize foraging efficiency and probability of survival based on information about litter density and seed availability.

Keywords: Henslow's sparrow, *Ammodramus*, seeds, arthropods, litter, vegetation

INTRODUCTION

Migratory Bird Population Declines

Migratory birds face a variety of pressures on both their breeding and wintering grounds, as well as during spring and fall migration (Kirby et al. 2008). Over the last half-century populations of many migratory bird species have been in decline, with 8% of migrants in the Americas either threatened or near-threatened (Kirby et al. 2008). Declines are not limited to species making risky, long distance migrations; 42% of short-distance Nearctic migrants show significant declines (Sauer et al. 2011). In order to reverse these trends, it is important to improve our understanding of factors that interact to limit populations in different parts of their migratory range (Rappole and McDonald 1994, Kirby et al. 2008).

Habitat loss on the breeding grounds has long been recognized as a major pressure for migratory birds. Many migratory species occupy breeding grounds in the grasslands of the Midwestern US, which have become highly fragmented and have undergone vast decreases in area since the time of European settlement, with decreases as high as 80% for mixed-grass and 99.9% for tallgrass prairies (Johnson 2000). Breeding grassland bird communities are area sensitive, and some species require habitats much larger than their individual home ranges to maintain viable populations. This makes them vulnerable to habitat fragmentation (Herkert 1994). Fragmentation may cause deleterious edge effects, with increased predation, competition, and invasion of unsuitable woody vegetation that may negatively influence populations of some grassland bird species (Johnson 2000, Herkert et al. 2003).

While pressures on the breeding ground are important to migratory bird populations, some researchers have suggested that conditions on the wintering ground are of equal or

greater importance to population decline of Nearctic migrants (Rappole and McDonald 1994, Rappole et al. 2003). Habitat availability and quality on the wintering grounds can have a carry-over effect on the condition and survival of individuals that affects their success on the breeding grounds (Norris et al. 2004, Norris 2005). Recent studies have found that habitat loss and fragmentation of wintering grounds may be responsible for population declines of Nearctic-Neotropical migrants (Keller and Yahner 2006, Rappole et al. 2003). Other studies have focused on the importance of food availability among habitats on the distribution of wintering migrants (Johnson and Sherry 2001, Pulliam and Dunning 1987). These studies suggest that devoting more attention to factors limiting migratory bird populations on wintering grounds is necessary for effective conservation planning.

Biology and Conservation of Henslow's sparrow

Henslow's sparrow (*Ammodramus henslowii*) is small, short-distance migrant of North America's grasslands (Hyde 1939). Since the beginning of the second half of the 20th century, Henslow's Sparrows have experienced a sharp decrease in their breeding population, with an average estimated population decline of 8.1% per year from 1966 through 2007 (Sauer et al. 2008). Due to its declining population, Henslow's Sparrow has been listed nationally as a "Bird of Conservation Concern" by U.S. Fish and Wildlife Service (2008), and receives special legal status in 22 U.S. states, including the designation of species of management concern in Mississippi (Burhans 2002). Henslow's Sparrow has also been listed as endangered in Canada since 1993 (COSEWIC 2004).

Henslow's Sparrow depends on fire-mediated grassland habitats on both its breeding and wintering grounds. Large patches of prairies and other grassland habitats with dense

standing dead vegetation and a thick litter layer that has been burned, mowed, or grazed within the last 2 to 4 years (Zimmerman 1988, Herkert et al. 2002, Herkert 2003) provide habitat for Henslow's sparrow on the breeding grounds, which range throughout the Mid-Western plains, Northeastern US, and Southern Ontario (Hyde 1939, Burhans 2002, Herkert et al. 2002). Habitat loss on the breeding ground, stemming from a variety of anthropogenic causes, has contributed to declines in Henslow's Sparrows populations for several decades (Herkert et al. 2002).

Recent management efforts on the bird's breeding grounds, such as the Conservation Reserve Program (CRP), have managed to help reduce the rate of decline (Herkert 2007, Herkert et al. 2002). The CRP increases grassland area by providing landowners with incentives to plant areas of cropland with grassland vegetation (Johnson and Schwartz 1993). This reversion of cropland to prairie has been beneficial for numerous grassland birds, since croplands do not provide suitable habitat for many grassland species (Johnson and Schwartz 1993, Johnson 2000). In Herkert's (2007) analysis of Breeding Bird Survey (BBS) trends for Henslow's sparrow, whether a population increased or decreased was significantly related to the proportion of CRP lands found among BBS routes, with CRP lands more likely to produce increasing population counts over time. According to the 2009 BBS, the population trend for Henslow's sparrow has slowed to a long-term yearly decline of 0.9% (Sauer et al. 2011).

The longleaf pine ecosystems of the Southeastern U.S., which range from eastern Texas through Florida and along the East Coast as far north as North Carolina, serve as wintering grounds for Henslow's Sparrow (Hyde 1939, Herkert et al. 2002). Longleaf pine ecosystems are complex, fire-mediated systems, and have some of the highest floristic diversity outside the

tropics (Outcalt and Sheffield 1996). Here, low-intensity, high frequency fires favor herbaceous vegetation and maintain the open understory of pine savannas without damaging the overstory of longleaf pine (Van Lear and Harlow 2002). In the time since European settlement, timber harvest and conversion of land for other human uses such as agriculture, combined with fire suppression, consumption of seedlings by hogs, and irregular seed production has reduced longleaf pine ecosystems of the Southeast U.S. to approximately 3% of the original 60 million acres they once dominated. (Frost 2006, Outcalt 2000, Outcalt and Sheffield 1996). Three-quarters of the remaining longleaf pine habitat is distributed in fragments of less than 100 acres (Outcalt and Sheffield 1996). These reductions in longleaf pine ecosystems have decreased winter habitat available for Henslow's Sparrow, which may have also negatively influenced their populations (Herkert et al. 2002).

Fire suppression over the past century has had major effects on the longleaf pine system (Johnson and Hale 2002). In longleaf pine ecosystems, long-term fire suppression leads to the accumulation of dense woody understories and a gradual conversion to forest in areas that were previously open savanna habitat (Outcalt and Sheffield 1996, Gilliam and Platt 1999). Recognition of these changes and the effects they have on both the habitat and wildlife has led to the use of prescribed burns to reduce brush and manage wildlife populations. Use of burns to manage fire-dependent bird populations, including species such as red-cockaded woodpeckers, northern bobwhites, and a number of Emberizid sparrows is a common practice, followed by over 70% of organizations using fire in habitat management (Engstrom and Brownlie 2002). Henslow's sparrow, like several other related Emberizid sparrows, benefits

from prescribed burning (Dickson 2002, Engstrom and Brownlie 2002, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005).

Selection and use of winter range by Henslow's sparrow

After an initial arrival period on the wintering grounds, from late October through mid-November, during which post-migration movements occur (Johnson et al. 2009), Henslow's sparrow is site faithful to its selected home range over the course of the winter (Plentovich et al. 1998, Thatcher et al. 2006, Johnson et al. 2009). These sparrows select habitats that have been burned recently (Chandler and Woodrey 1995), with the greatest density of sparrows found in areas burned one growing season earlier (Plentovich et al. 1999, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005). Sparrow density decreases in the second and third growing seasons since the last burn, and few Henslow's Sparrows are found in areas with more than three growing seasons since they were last burned (Tucker and Robinson 2003, Bechtoldt and Stouffer 2005). The sparrows do require a minimum of one season of vegetative growth to occupy an area, and are not found on sites where burning occurred less than three months earlier (Chandler and Woodrey 1995).

In addition to supporting greater densities of sparrows, birds occupying sites burned one growing season earlier have higher survival rates than those occupying older sites, likely due to differences in vegetation structure or food resources (Thatcher et al. 2006). Previous studies have shown that Henslow's Sparrow prefers wintering habitats with high densities of herbaceous vegetation (Plentovich et al. 1999, Carrie et al. 2002, Tucker and Robinson 2003) and little to no ground litter (Carrie et al. 2002). Johnson (2006) found ground-level herbaceous

density and shrub cover to be the most important factors in determining Henslow's Sparrow densities in upland and flatwood pine savannas.

Grass seeds and sedge achenes are an important resource for wintering Henslow's sparrow, and both the frequency of occurrence of grass stalks bearing seeds (Tucker and Robinson 2003) and mean abundance of seed producing grass stalks (Bechtoldt and Stouffer 2005) have also been shown to be an important predictor of Henslow's Sparrow abundance. DiMiceli et al. (2007) suggested that an increase in abundance of sparrows one growing season after a burn may be due to an increased level of preferred food items, rather than changes in seed abundance. While food choice trials indicated Henslow's Sparrows consumed greater quantities of seed from species abundant during the first growing season after a burn than from species producing seeds several years after a fire, they are generalists and body condition is not affected by living in less preferred habitats (DiMiceli et al. 2007, Johnson 2006).

Although factors related to habitat selection and use on the winter range have been previously studied, few of these studies have focused on the key period of habitat assessment that takes place after initial arrival of Henslow's sparrow on the wintering grounds in November. Previous studies have included measurements of vegetation structure taken at the end of the winter, just prior to the onset of spring growth, rather than during the initial arrival (Plentovich et al. 1999, Carrie et al. 2002, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005, Johnson 2006). This is because it has been assumed that there is no change in vegetation structure over the course of the winter, since there is no new growth. It is possible that vegetation structure may be altered considerably by litter formation over the course of the

winter, and late winter vegetation may differ significantly from that present in November when birds select winter range. Measuring vegetation at the beginning of the winter would offer a better assessment of habitat available at the time of winter range selection.

Likewise, measurement of food resources in the form of seed-producing stalks has been primarily near the end of the winter, after most seeds have dropped (Tucker and Robinson 2003 Bechtoldt and Stouffer 2005). Johnson (2006) provided an exception to this, having collected seeds from both the ground and stalks in late November, though he found that vegetation structure, rather than food resources, was most important to Henslow's sparrows. The food available over the course of the winter is limited (Hutto 1985), and low seed abundance in winter has been associated with decreased sparrow population densities (Pulliam and Dunning 1987). It is possible that minimum resource availability reached in a location, rather than mean resource availability or availability at the start of the winter, is a better predictor of habitat quality. However, previous studies have not used methods capable of measuring either mean resource availability over the course of the winter, or minimum resource availability. Therefore, resources available should be observed over the course of the winter to assess both mean and minimum resource availability.

Arthropods have been largely overlooked as potential resources for wintering sparrows, presumably because seeds make up the majority of their winter diet (Fuller 2004, DiMiceli et al. 2007). Though they only accounted for 8% of all items consumed, arthropods were the second most common food item found in a study of crop contents at the Mississippi Sandhill Crane National Wildlife Refuge (Fuller 2004). DiMiceli (2006) also found arthropods in 89% of fecal

samples in a study of Henslow's Sparrows in Louisiana, but abundance was not measured. Some authors have suggested that arthropods may be an important factor in determining Henslow's Sparrow abundance in winter habitats (Tucker and Robinson 2003, Thatcher et al. 2006), and any comprehensive analysis of winter range quality should assess availability of both seeds and arthropods.

Research Objectives

The objective of this study was to determine the relative importance of vegetation structure, seed availability, and arthropod abundance in predicting Henslow's Sparrow occupancy in areas of pine savanna on the Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR). My study focused on identifying factors that may influence site selection by Henslow's Sparrow by 1) determining the presence or absence of Henslow's Sparrows on transects representing different burn regimes, 2) quantifying vegetation structure and resource availability at the time of their arrival from the breeding grounds, 3) quantifying both total seed abundance and the abundance of seeds on standing stalks over the course of the winter, 4) determining the abundance of arthropods inhabiting the sites over the course of the winter, and 5) comparing the importance of mean vs. minimum resource availability in predicting Henslow's sparrow transect occupancy.

Though Henslow's Sparrow abundance decreases with time since burn, there can be significant variation in abundance and density of sparrows among sites of the same age (Bechtoldt and Stouffer 2005, Johnson 2006). This suggests that sites vary in quality or suitability, which is apparently not determined solely by burn age. Therefore a comparison of

vegetation structure and resources available on occupied and unoccupied transects may provide a clearer picture of factors important to winter site selection by Henslow's Sparrow. By observing differences in aspects of both vegetation structure and resource availability in sites of different ages, it should be possible to determine which factors are most important to determining Henslow's sparrow site occupation.

METHODS

Study Site

The Mississippi Sandhill Crane National Wildlife Refuge, in Jackson County, MS is a 7810-ha wildlife refuge (Figure 1) established in 1975 for the protection of the federally endangered Mississippi Sandhill Crane and to manage the area's wet pine savanna habitat (U.S. Fish and Wildlife 2007, Hereford and Billodeaux 2009). This area is managed with both dormant and growing season prescribed burns that attempt to mimic a natural fire regime, using a 2 to 3 year burn rotation for longleaf pine savannas. These burns are applied within individual management compartments on the refuge (Figure 1). The refuge supports a large wintering population of Henslow's Sparrow (Chandler and Woodrey 1995) at a high density (Burhans 2002), and recently burned savannas on the refuge generally have the highest number of observed wintering Henslow's Sparrows in the country (Hereford and Billodeaux 2009). In 2009, 48 Henslow's Sparrows were observed at MSCNWR in the Christmas Bird Survey (Hereford and Billodeaux 2009), though this method may underestimate the number of Henslow's Sparrows present (Burhans 2002).

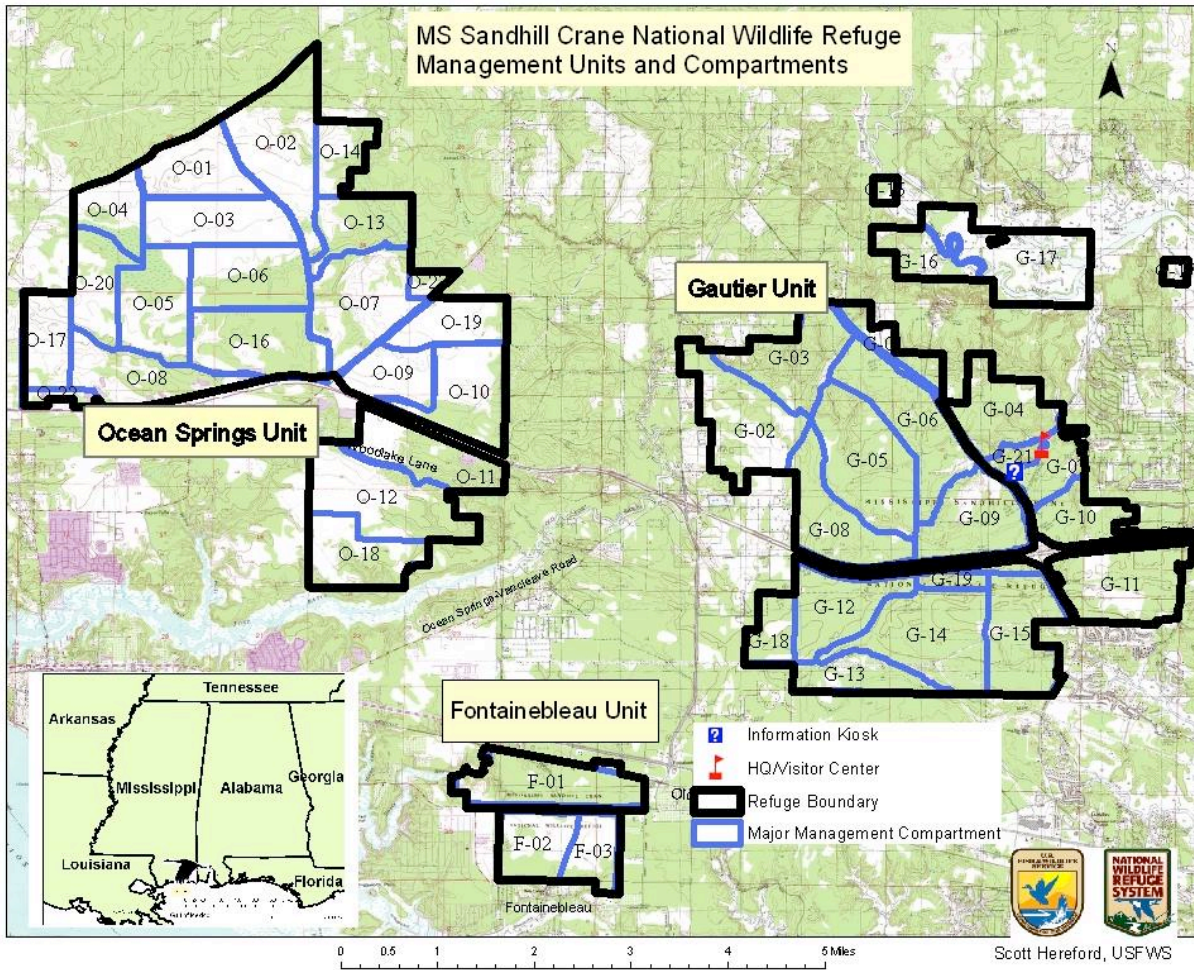


Figure 1. Map of the Mississippi Sandhill Crane National Wildlife Refuge showing management compartments.

Sampling Design

In October 2010, I set up twenty-seven 100 m transects in nine different management compartments at MSCNWR (Table 1). The selected compartments were classified into three burn treatments by the number of years since the last fire. The treatments included sites with one growing season (age-1), two growing seasons (age-2), and three or more growing seasons (age-3+) since the last controlled burn occurred. Three sites within each burn treatment were selected randomly from the available compartments, and all compartments selected were

burned during the growing season. Though previous studies have indicated that burn season does not have a strong effect on Henslow's Sparrow populations (Tucker and Robinson 2003, Thatcher et al. 2006), only growing season burns were considered in the selection of sites to prevent any possible seasonal influences.

Table 1. Management compartments with burn data and treatment category.

Compartment	Last Burn Date	Burn Treatment
O-07S	4/2010	1
G-05	4/2010	1
G-12	3/2010	1
G-19	4/2009	2
G-7	5/2009	2
G-10	5/2009	2
O-18	4/2007	3+
G-08	4/2008	3+
G-13	4/2007	3+

Three 15 m x 100 m transects were laid out in each of the nine sites, with a minimum distance of 30 m between the nearest edges of adjacent transects. The inter-transect distance was large enough to minimize that the probability that a given sparrow would be detected on more than one transect, as well as to pick up variation in vegetation within the unit. Bird abundance and food availability were assessed monthly on each transect from November 2010 to March 2011, while vegetation structure was observed in November and in March, at the beginning and end of the winter season. Bird abundance was assessed on either the first or second week of each month, and resource data was collected one week later. On months vegetation structure was observed, measurements were taken at the same time as resource data was collected.

Bird Surveys

I surveyed Henslow's Sparrows on each transect by using a modified Project Prairie Bird (PPB) method (Shackelford et al. 2001). This method is specifically designed to search for secretive wintering grassland birds, such as Henslow's Sparrow (Heath et al. 2008, Twedt et al. 2008). In Twedt et al. (2008), Henslow's Sparrow abundance using this method was several times greater than the estimated abundance using the Winter Bird Population Studies method (Anonymous 1947). The authors suggest that secretive birds are less likely to escape the active flushing of this method, relative to a passive area search by a single searcher (Twedt et al. 2008), which makes this an ideal method for measuring transect occupancy in this study.

During each survey, three individuals walked the length of a transect. Two acted as "beaters," and struck the vegetation with 4 m bamboo poles to flush any sparrows present within the transect. This pole length, and associated transect width, was less than the original PPB method due to transportation constraints. I followed these two individuals, walking the centerline and identifying all birds that flushed. In addition to Henslow's sparrows, Swamp sparrows, Sedge wrens, and a Savannah sparrow were also identified during bird surveys. All birds were observed until they landed or had flown out of view in order to prevent recounting. Henslow's sparrow generally flies only a short distance when flushed, and has a recognizable flight pattern (M. Woodrey, *personal communication*). All Henslow's sparrows observed flew a distance less than the 30+ m between transects.

Vegetation Structure

I assessed vegetation structure at five randomly chosen locations on each transect in November 2010 and again in March 2011. I classified plants into graminoids (grasses and sedges), forbs, carnivorous plants, shrubs and trees, and I assessed cover using the modified pole method used by Plentovich et al. (1999), and developed by Mills et al. (1991). Briefly, I measured standing herbaceous vegetation cover up to 1 m within height intervals of 5 cm for the first 20 cm and intervals of 10 cm from 20 cm to 1 m. Within each height interval the number of items, up to a maximum of 10, of each type of vegetation within 10 cm of the pole were recorded. In cases where more than ten items occurred in an interval, the vegetation class was assigned a score of 10 for the interval.

I developed a qualitative scale to quantify litter cover in situ, without disturbing or removing litter (Table 2). This scale ranged from 0 to 10 and increased with increasing litter density, where 0 represented bare ground, 5 indicated moderate density with some ground visible, and 10 represented full coverage of dense litter.

Table 2. Scale used to determine litter cover score within 10 cm of pole.

Litter Scale
0 – bare ground, no litter
1 – a few scattered pieces of litter, 80%+ bare ground
2 – low litter cover, >50% of ground visible, litter height of 0-10 cm
3 – low litter cover, ~50% of ground visible, litter height of 0-10 cm
4 – low litter cover, ~50% of ground visible, litter height of 10+ cm
5 – moderate litter cover, 20-50% of ground visible, litter height of 0-20 cm
6 – moderate litter cover, 10% ground visible, litter height of 0-10 cm
7 – moderate litter cover 10% ground visible, litter height of 10+ cm
8 – high litter cover, 0% ground visible, litter height of 0-10 cm
9 – high litter cover, 0% ground visible, litter height of 10-20 cm
10 – high litter cover, 0% ground visible, litter height of 20+ cm

Seed Availability

I estimated seed availability on each transect monthly from November, 2010 to March, 2011. Since Henslow's sparrows are generalists and consume both the seeds of grasses and achenes of sedges, I grouped these together for observing food resources, and refer to this grouping as "seeds" for the purposes of this study. I estimated seed availability at each site using two methods. First, I sampled the total number of available seeds from both the ground and standing stalks in three 0.25 m² quadrats on each transect by vacuuming. Quadrats were distributed across the transect by tossing a sampling frame randomly from approximately 25 m, 50 m, and 75 m along the 100 m transects. I used a leaf blower (Husqvarna 125BV) in reverse to suck up seeds from the ground and stalks within the quadrat. This continued until it was determined all areas of the ground within the quadrat had been covered. Quadrats were vacuumed for 45-60 seconds depending on the density of cover, and samples were stored in standard eight-gallon trash bags. In a second set of samples, seeds were collected from standing vegetation using a sweep net while collecting arthropods (see methods below). Seeds that were released into the net while collecting arthropods were obtained following the same procedure as arthropod sampling.

After collection, samples were returned to the lab for processing. All samples were placed in soil sieves to separate seeds from a large quantity of small debris items (grass, dirt, sand) collected in the samples. As suggested by Johnson (2006), only seeds larger than 500 µm were kept due to the likelihood that Henslow's sparrows would not be interested in such small seeds, and because they may not have been adequately sampled.

Due to the large amount of grassy debris remaining in vacuum samples after they were shaken through the sieves, only a subsample of most samples was sorted. One out of every nine samples was sorted in entirety to help assure that estimates generated from subsamples were representative of totals in the samples. In each subsample, 25% of an unsifted whole sample was weighed out and shaken through the soil sieve for two minutes. Due to the greater quantity of debris, whole samples were shaken for three minutes to assure all small debris was removed.

After samples were sorted with the soil sieves, all seeds were removed from the sample using a dissecting microscope. The seeds were then counted and weighed. Seeds collected via sweep net were separated from arthropods, counted and weighed. The number and biomass of seeds in subsamples were multiplied by four to approximate that of the full, unsifted sample. Individual seed species were not identified, since Henslow's sparrows are believed to be generalist foragers on their wintering grounds and a variety of seeds have been found in crop and fecal contents (Fuller 2004, DiMiceli 2006).

Arthropod Abundance

I estimated arthropod abundance and biomass at each site using a sweep net monthly from November, 2010 to March, 2011. While moving in a straight line from a point adjacent to where the quadrat used for seed collection was tossed, I performed 10 consecutive sweeps over a linear distance of approximately 4 m. This was repeated three times per transect. Arthropod samples and associated seeds were stored in one-gallon Ziploc bags and put on ice

until they could be placed in a freezer. This was done to kill the arthropods without introducing fluids that would make seeds difficult to remove from the sample.

Samples were frozen for several days to ensure all arthropods had died. I sorted arthropods from all samples using a dissecting microscope. I counted the number of arthropods in each order. Samples were then placed in a drying oven (VWR) for a minimum of 24 hours at 100°C. After this period, I removed them from the dryer and placed them in a desiccator (Secador) until they had cooled. Once the arthropod samples cooled I measured the dry mass of each.

Statistical Analysis

All analyses were performed in SYSTAT Version 11 (SYSTAT Software Inc., Richmond, CA). I used a Kolmogorov-Smirnov (K-S) two sample test to compare vegetation structure in November and March. For purposes of analysis I pooled density scores obtained at a given sampling point in intervals from 0-20 cm and intervals from 20-100 cm. Separate K-S tests were used to analyze the pooled density scores of graminoids, forbs, carnivorous plants, and shrubs, from 0-20cm and 20-100cm. I also used this test to analyze mean litter cover score. Due to the low number of trees encountered in the vegetation data, trees were excluded from all analyses.

I performed repeated measures analyses of variance to determine changes in potential food resources over the course of the winter on sites in each of the three age groups. Separate analyses were carried out for the number and mass of sweep net-collected seeds, vacuum-collected seeds, and arthropods.

I used two-sample t-tests to compare resources at arrival, mean resource availability over the winter season, and minimum resource availability over the winter season on transects where Henslow's Sparrows occurred to those on which they were absent. Since Henslow's Sparrows are site-faithful over the course of the winter (Thatcher 2003), I used habitat data values collected in November to compare the available resources and vegetation structure on these sites at the time of arrival. These t-tests included number and mass of net-collected seeds, vacuum-collected seeds, and arthropods. I also used two-sample t-tests to compare the mean and minimum availability of food resources on sites that were occupied vs. unoccupied. A Bonferroni correction was applied to all tests to correct for multiple comparisons.

I performed two-sample t-tests, with a Bonferroni correction, comparing the number of contacts for graminoids, forbs, carnivorous plants, and shrubs from 0-20 cm and from 20-100 cm, as well as the litter cover score on sites where Henslow's sparrow was present versus absent. I then performed ANOVAs to compare vegetation variables at sites of different age classes. For all tests performed, results were considered significant if the p-value was ≤ 0.05 .

I then performed a post-hoc analysis of habitat characteristics significant to transect occupancy using the occupancy estimation module in Program MARK, to lend additional support to my findings and attempt to determine which of the observed habitat characteristics were most important for Henslow's sparrow site selection at MSCNWR. Program MARK uses maximum likelihood techniques to estimate occupancy (Ψ) and detection (p) parameters for a given set of models and determine the most parsimonious model given the data.

The detection probability (p) of a species, is generally <1 at any given point in time (MacKenzie et al. 2002), which I accounted for by using multiple detection events (MacKenzie et al. 2002, MacKenzie and Royle 2005). Though p is not known for Henslow's sparrows using PPB methods, this method assumes approximately the same detection probability across habitats. Therefore, models were created to based upon constant detection probability across burn treatment and time (p), with either constant transect occupancy (Ψ), variation in occupancy based on burn treatment (Ψ_g), or variation based on a combination of transect characteristics (Ψ_{NovNet} , Ψ_{MinVac} , Ψ_{Litter}), which were included as independent covariates (Table 3).

I performed a goodness-of-fit test using a parametric bootstrap simulation in MARK on the global model ($p.\Psi$) to determine whether overdispersion was present. Overdispersion was estimated with the variance inflation factor (\hat{c}). When no overdispersion is present $\hat{c} = 1$, and when low levels are present \hat{c} is between 1 and 2. To calculate \hat{c} , I used two methods: 1) observed deviance / deviance expected from goodness-of-fit simulations, and 2) observed \hat{c} / expected \hat{c} from goodness-of-fit simulations, and accepted the larger value of the two (Cooch and White 2009). Overdispersion was accounted for by adjusting \hat{c} .

Models were run using the alternative optimization procedure, and individual covariates were z-transformed. Models were ranked according to Akaike's Information Criterion corrected for small sample size and over-dispersion (QAICc), which were calculated by MARK. The model with the lowest QAICc provided the most parsimonious model and a $\Delta QAICc$ of 0.00. The $\Delta QAICc$ is the difference between the model that best fits the parameters and all other models.

Models with a ΔQAICc less than 2 were considered equally well supported, while $\Delta\text{QAICc} > 2$ between two models showed considerable support for a difference between the models (Burnham and Anderson 2002).

Table 3. Models used to test for habitat variables important for site selection.

Model	Variables
1	$\rho(\cdot)\Psi(\cdot)$
2	$\rho(\cdot)\Psi(\text{g})$
3	$\rho(\cdot)\Psi(\text{novnet})$
4	$\rho(\cdot)\Psi(\text{minvac})$
5	$\rho(\cdot)\Psi(\text{litter})$
6	$\rho(\cdot)\Psi(\text{novnet minvac})$
7	$\rho(\cdot)\Psi(\text{novnet litter})$
8	$\rho(\cdot)\Psi(\text{minvac litter})$
9	$\rho(\cdot)\Psi(\text{novnet minvac litter})$

RESULTS

Bird Surveys

Henslow's sparrows (HESP) were found on 12 of 27 transects surveyed. Sparrows were observed on 78% of age-1 transects, with a mean (\pm SE) of 1.22 ± 0.155 HESP sightings per transect. In age-2 sites, HESP only occurred on 56% of transects, with a mean of 0.55 ± 0.075 sightings per transect. No Henslow's sparrows were found on any age-3+ transect (Figure 2).

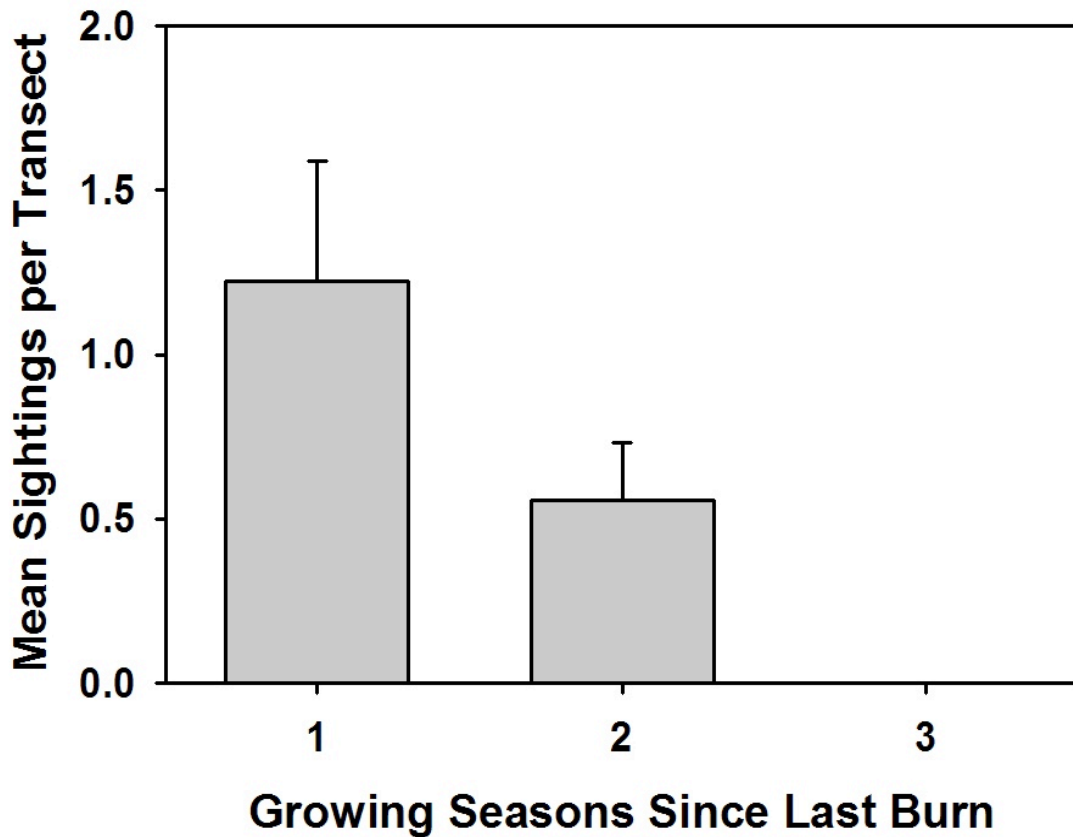


Figure 2. Mean number of Henslow's Sparrow sightings per transect in each age group (\pm SE).

Vegetation Structure

My vegetation data indicated that November and March vegetation structures were significantly different in regard to graminoid cover both below and above 20cm (Table 4). Graminoid cover was greater in November than in March both below 20 cm and above 20 cm (Figure 3). Forbs, carnivorous plants, shrubs, and litter did not differ in structure between November and March.

Table 4. Maximum differences and probabilities from a Kolmogrov-Smirnov test comparing vegetation structure between November and March. Significant P values are marked with an *.

	D_{max}	P
Graminoids 0-20cm	0.407	0.018*
Graminoids 21-100cm	0.444	0.007*
Forbs 0-20cm	0.111	0.991
Forbs 21-100cm	0.185	0.698
Carnivorous Plants 0-20cm	0.222	0.475
Carnivorous Plants 21-100cm	0.148	0.898
Shrubs 0-20cm	0.222	0.475
Shrubs 21-100cm	0.333	0.087
Litter	0.259	0.293

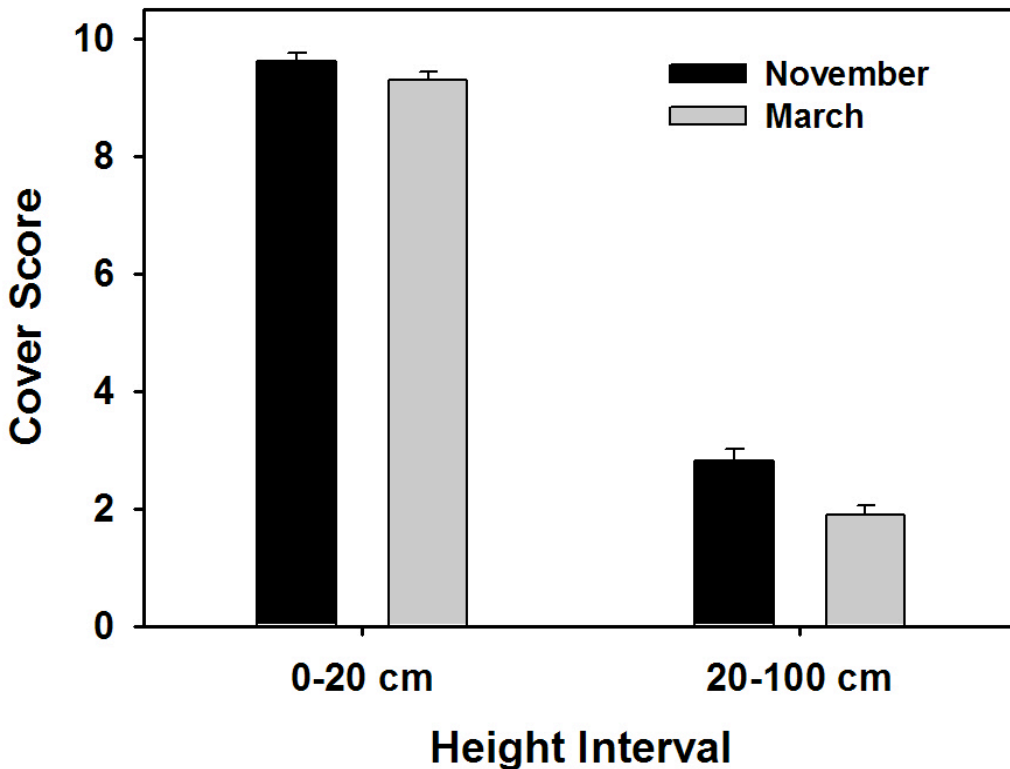


Figure 3. Difference in graminoid (grasses and sedges) cover from 0-20 cm and 21-100 cm in November and March. Cover is shown as the mean score on a 0 to 10 scale ($\pm 1SE$).

November litter cover (Table 5) was significantly different between burn treatments, increasing with time since the last burn (Figure 4). The number of forbs above 20 cm in height was also significantly different between burn treatments, with the highest number of forbs greater than 20 cm in height occurring in age-2 sites (Figure 5). No other vegetation variables were significantly different between burn treatments.

Table 5. Results of ANOVA comparing November vegetation structure among sites of different ages. Significant P values are marked with an *.

	df	f	p
Graminoids 0-20cm	2	1.402	0.266
Graminoids 21-100cm	2	3.093	0.064
Forbs 0-20cm	2	2.391	0.113
Forbs 21-100cm	2	5.787	0.009*
Carnivorous Plants 0-20cm	2	1.976	0.161
Carnivorous Plants 21-100cm	2	2.095	0.145
Shrubs 0-20cm	2	2.278	0.124
Shrubs 21-100cm	2	2.222	0.13
Litter	2	54.967	0.000*

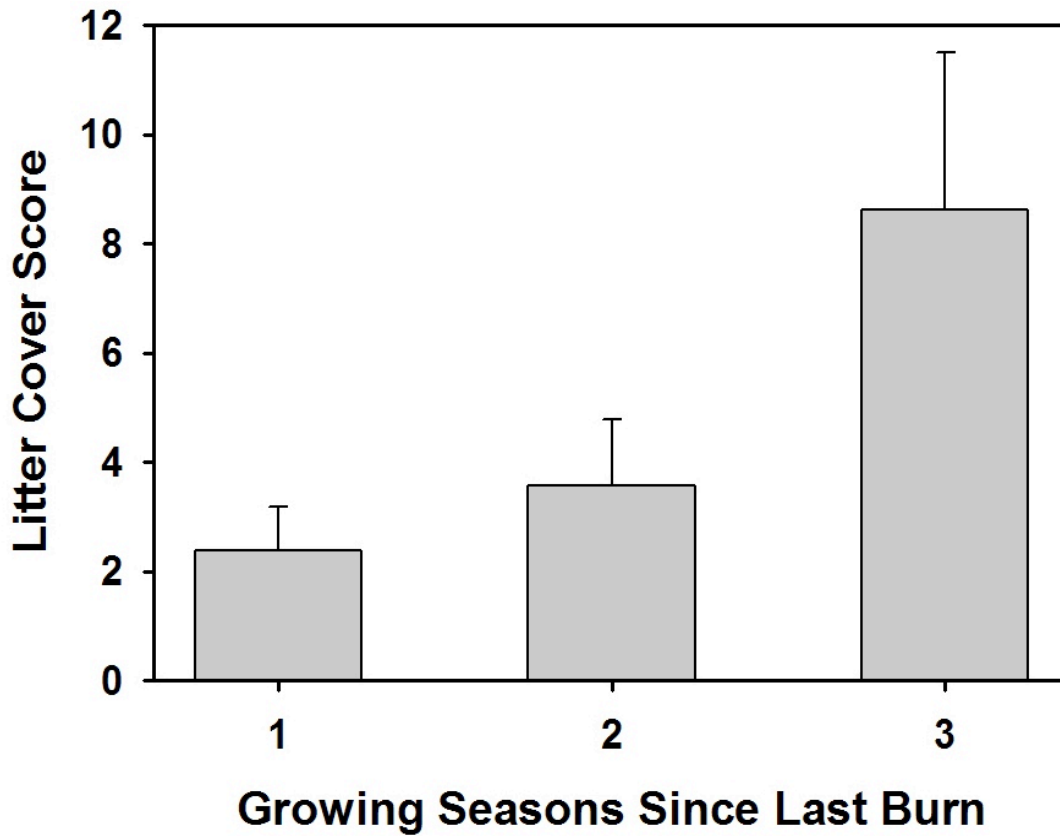


Figure 4. Mean litter cover (\pm SE) on a 0-10 scale in each burn treatment.

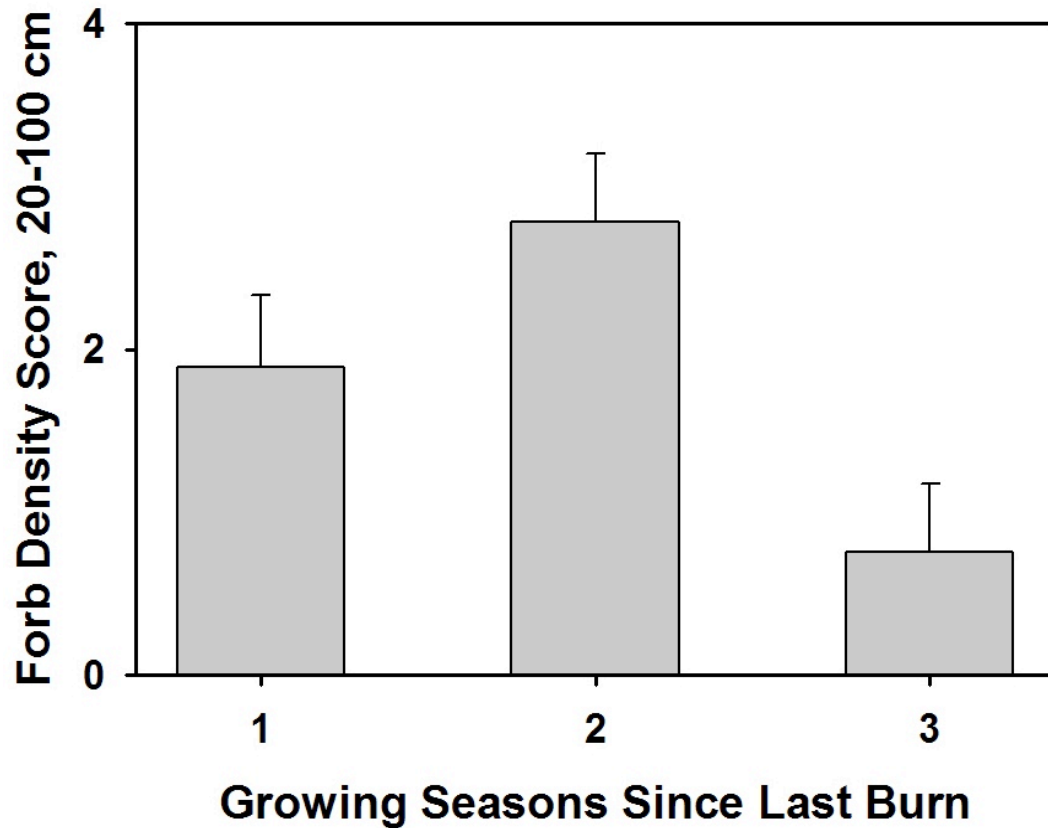


Figure 5. Mean forb density above 20 cm (\pm SE) in each burn treatment.

Food Availability

My food availability data indicated that both the number and mass of sweep-net collected seeds over the course of the winter differed significantly among burn treatments (Table 6). The greatest number of standing seeds occurred in age-2 sites, while age-3+ sites had the fewest seeds (Figure 6). In contrast, the greatest standing seed mass was found in age-1 sites, while the lowest seed mass was found in age-3+ sites (Figure 7). Neither vacuum-collected seeds nor arthropods differed significantly between burn treatments in either number or mass (Table 6).

Within transects, all measured resources showed significant changes in availability over time (Table 7). Seed number (Figure 6) and mass (Figure 7) decreased linearly over time for both net-collected seeds and vacuum-collected seeds. Arthropod mass decreased linearly over time as well (Figure 7). Changes in arthropod number over time best fit a quadratic equation (Table 8), rather than a linear decrease, since the number of arthropods increased during the month of March (Figure 6).

Table 6. Between groups results from a repeated measures ANOVA comparing potential food resource number (N) and mass. Significant P values are marked with an *.

	df	F	P
Net Seed N	2	6.337	0.006*
Net Seed Mass	2	5.601	0.01*
Vacuum Seed N	2	0.229	0.797
Vacuum Seed Mass	2	1.387	0.269
Arthropod N	2	0.241	0.788
Arthropod Mass	2	0.734	0.490

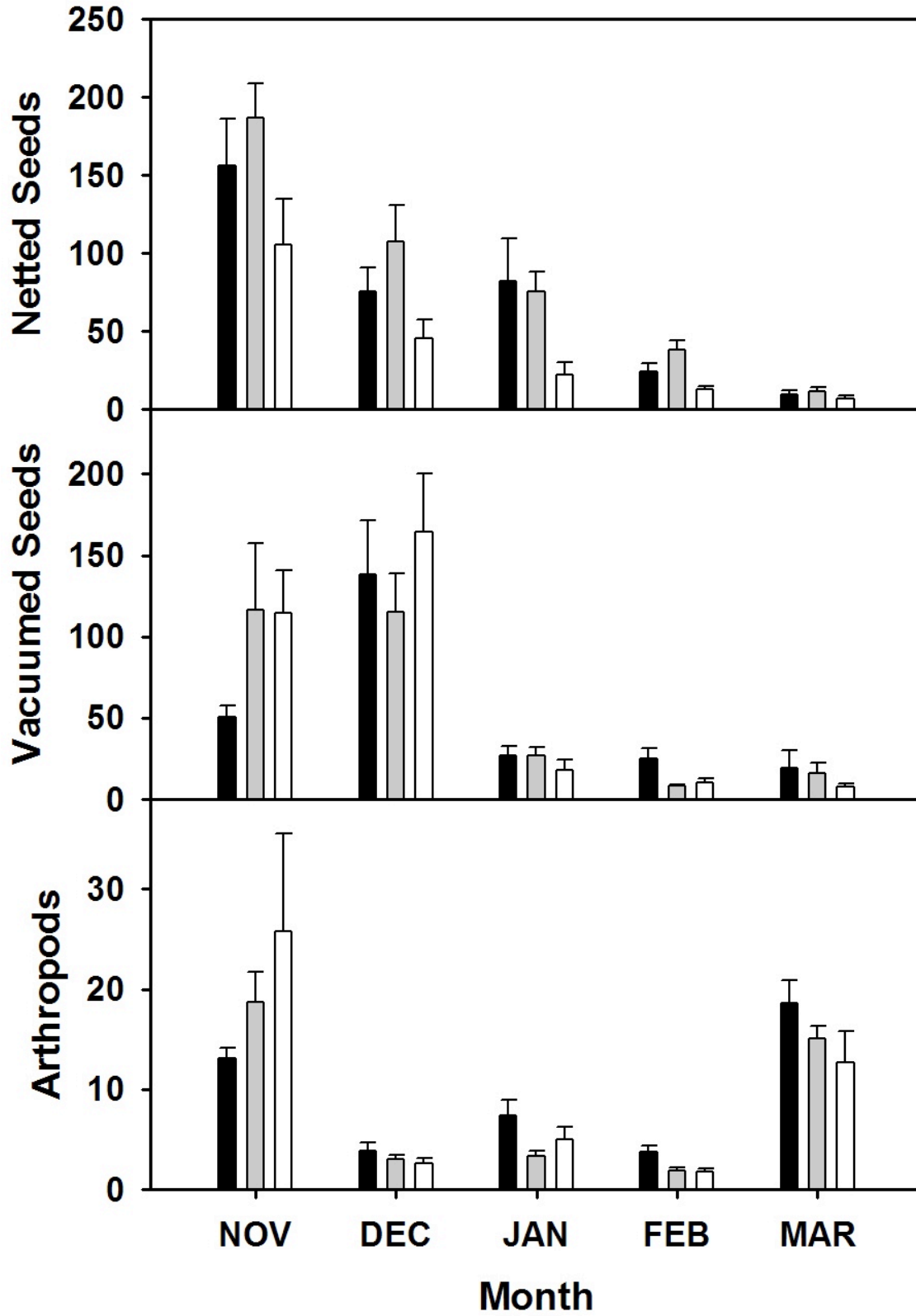


Figure 6. Mean number of netted seeds, vacuumed seeds, and arthropods over the course of the winter at sites with 1 (black), 2 (gray), and 3+ (white) growing seasons since the last burn.

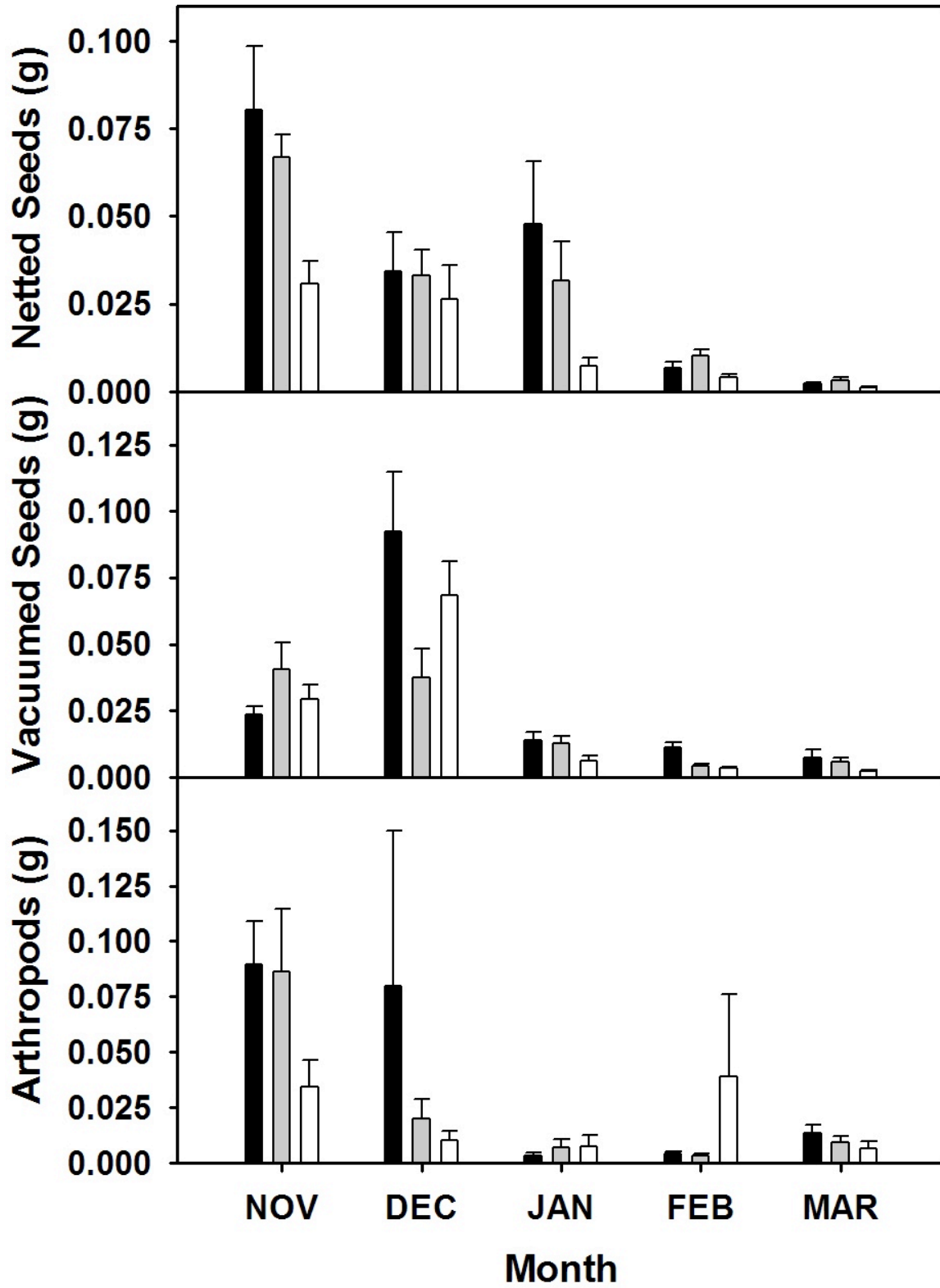


Figure 7. Mean mass of netted seeds, vacuumed seeds, and arthropods over the course of the winter at sites with 1 (black), 2 (gray), and 3+ (white) growing seasons since the last burn.

Table 7. Within groups results from a repeated measures ANOVA comparing potential food resources. Significant P values are marked with an *.

	df	F	P
Net Seed N	4	37.345	0.000*
Net Seed Mass	4	22.257	0.000*
Vacuum Seed N	4	31.678	0.000*
Vacuum Seed Mass	4	35.186	0.000*
Arthropod N	4	20.374	0.000*
Arthropod Mass	4	4.289	0.003*

Table 8. F-test results showing the significant quadratic shape of the number of arthropods over the course of the winter.

Degree	SS	df	MS	F	P
1	180.467	1	180.467	1.126	0.299
Error	3845.199	24	160.217		
2	5471.4	1	5471.4	56.24	0.000*
Error	2334.885	24	97.287		
3	13.498	1	13.498	0.306	0.585
Error	1058.143	24	44.089		

Occupied vs. Unoccupied Transects

Mass of available food resources at the time of initial occupancy in November was significantly different between the seed mass obtained via sweep net in occupied vs. unoccupied transects (Table 9). Transects on which birds were observed during the winter had higher sweep net-collected seed mass than transects on which no birds were observed (Figure 8). No significant difference was found in seed mass obtained from vacuum samples or from arthropod samples. There was also no significant difference in the number of seeds collected with the sweep net or vacuum, or in the number of arthropods among occupied and unoccupied transects.

Leaf litter in November showed differed significantly between occupied and unoccupied transects (Table 10). Transects on which birds were observed during the winter had lower litter cover scores than transects on which no birds were observed (Figure 9). No other vegetation characteristics were significantly different in occupied vs. unoccupied sites.

Table 9. T-test results of November food resources in occupied vs. unoccupied transects. Significant P values are marked with an *.

	df	t	p
Net Seed N	25	-0.964	0.344
Net Seed Mass	25	-2.505	0.019*
Vacuum Seed N	25	0.38	0.707
Vacuum Seed Mass	25	-0.662	0.514
Arthropod N	25	1.294	0.208
Arthropod Mass	25	-0.194	0.848

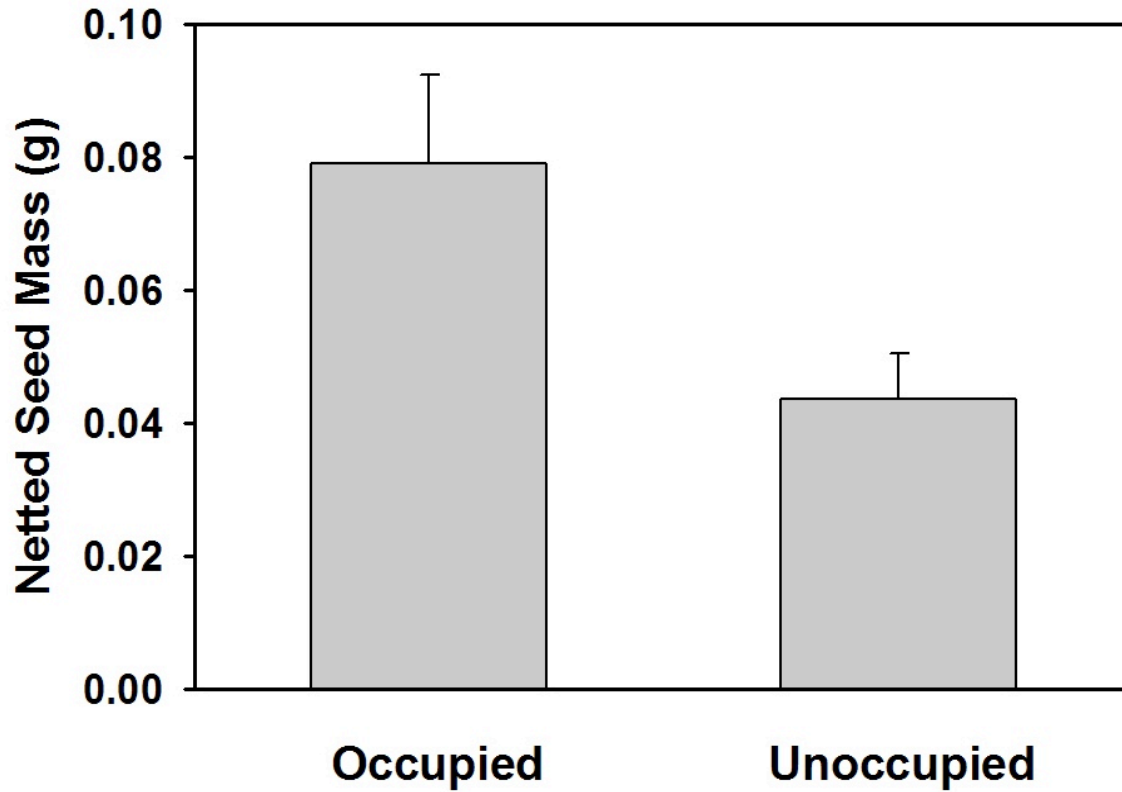


Figure 8. Mean netted seed mass (\pm SE) in occupied vs. unoccupied transects during November.

Table 10. T-test results of November vegetation structure in occupied vs. unoccupied transects. Significant P values are marked with an *.

	df	t	P
Graminoids 0-20cm	25	-0.058	0.954
Graminoids 21-100cm	25	-0.731	0.472
Forbs 0-20cm	25	-0.314	0.756
Forbs 21-100cm	25	-0.545	0.59
Carnivorous Plants 0-20cm	25	-0.117	0.908
Carnivorous Plants 21-100cm	25	0.451	0.656
Shrubs 0-20cm	25	-1.717	0.098
Shrubs 21-100cm	25	-0.393	0.698
Litter	25	4.855	0.000*



Figure 9. Mean litter cover score (\pm SE) in occupied vs. unoccupied transects in November.

While t-tests of mean available resources over the course of the winter showed that there were no significant differences in any variable for either the mass or number of seeds or arthropods, a t-test of minimum food resource mass reached on occupied vs. unoccupied transects revealed a significant difference between vacuum-collected seed samples (Table 11). The minimum mass of vacuumed seeds available was less in unoccupied than in occupied transects (Figure 10). No significant difference in minimum net-collected seed mass or minimum arthropod mass was observed on sites that were occupied vs. those that were unoccupied. T-tests of minimum seed number were not significant for either net-collected seeds or vacuum collected seeds. The difference in the number of arthropods between occupied and unoccupied transects was non-significant as well.

Table 11. T-test results of minimum food resource levels in occupied vs. unoccupied transects. Significant P values are marked with an *.

	df	t	P
Net Seed N	25	-1.013	0.321
Net Seed Mass	25	-1.09	0.286
Vacuum Seed N	25	-1.926	0.066
Vacuum Seed Mass	25	-2.893	0.008*
Arthropod N	25	0.351	0.729
Arthropod Mass	25	1.432	0.164

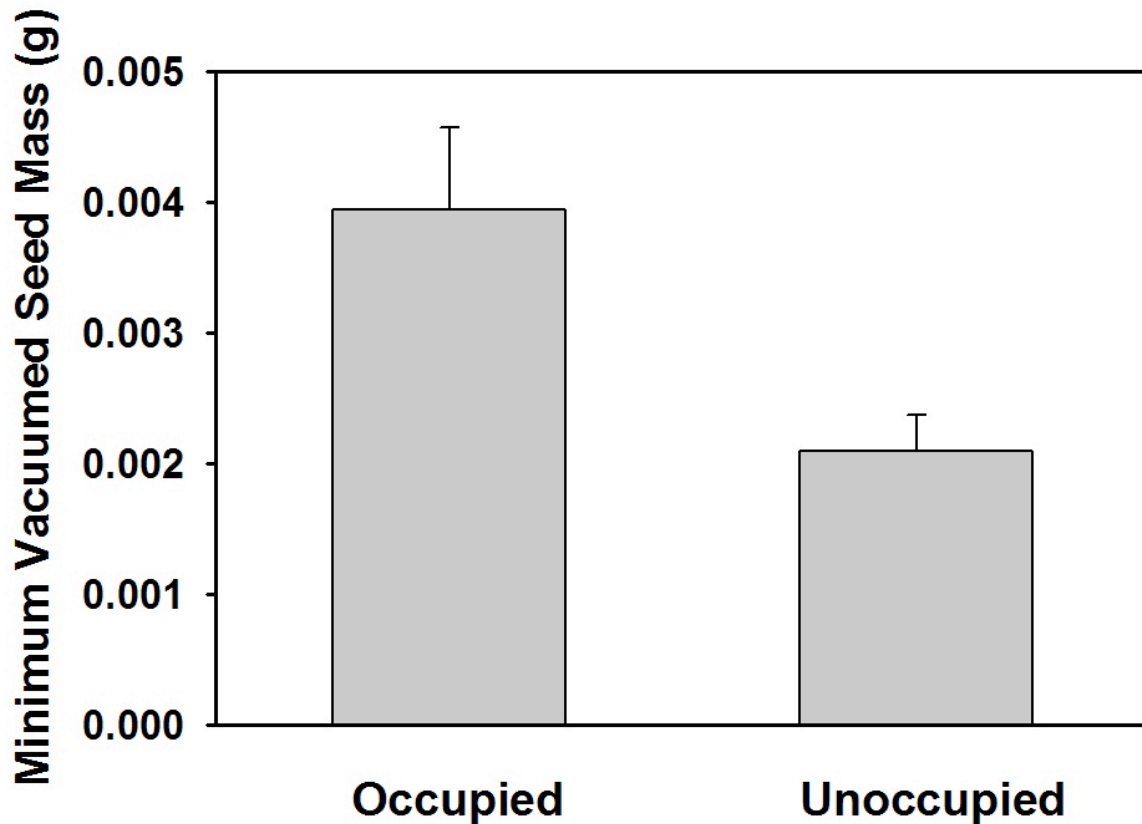


Figure 10. Minimum mass of vacuumed seeds (\pm SE) in occupied vs. unoccupied transects.

Occupancy Modeling

Models, adjusted for a $c\text{-hat} = 1.159$, indicated that model 5 (Table 3), which included litter as a covariate, was 3.97 times more likely than the second best model tested, 18.35 times more likely than a model based on burn treatment alone, and 400 times more likely than the model based on constant occupancy (Table 12). All other models had a ΔQAIC_c of at least 2.75, suggesting considerable support for model 5 providing a better fit for the data. It should be noted, however, that due to scarcity of data, confidence in the models presented is low.

Table 12. Rankings of all models used to test for occupancy, ranked by QAIC_c. All models assume constant probability of detection.

Model	QAIC _c	ΔQAIC _c	Model Weights	Model Likelihood	# Param.	QDeviance	-2log(L)
p(.)Ψ(litter)	71.1084	0	0.61078	1	3	64.065	74.2577
p(.)Ψ(minvac litter)	73.8649	2.7565	0.15393	0.252	4	64.0467	74.2365
p(.)Ψ(novnet litter)	73.8678	2.7594	0.15371	0.2517	4	64.0496	74.2399
p(.)Ψ(novnet minvac litter)	76.8831	5.7747	0.03403	0.0557	5	64.0259	74.2125
p(.)Ψ(g)	76.9289	5.8205	0.03326	0.0545	4	67.1107	77.788
p(.)Ψ(novnet minvac)	80.7022	9.5938	0.00504	0.0083	4	70.884	82.1617
p(.)Ψ(minvac)	81.3724	10.264	0.00361	0.0059	3	74.3289	86.1546
p(.)Ψ(novnet)	81.653	10.5446	0.00313	0.0051	3	74.6095	86.4799
p(.)Ψ(.)	82.1027	10.9943	0.0025	0.0041	2	77.6027	89.9493

DISCUSSION

In this study, Henslow's sparrows were most highly associated with high levels of seeds on standing stalks and low litter densities, as well as greater minimum total seed mass than unoccupied transects. This suggests that sparrows select for wintering sites where foraging efficiency can be maximized. Higher standing seed mass at the time of arrival suggests that greater resources will be available later in the winter, which is supported by the greater minimum total seed resources that occurred on these sites. Low litter densities allow more rapid movement through the vegetation and should increase foraging efficiency. Low litter density was the most important characteristic to transect occupancy based on maximum likelihood models. Overall, my results suggest that Henslow's sparrow selects sites with few impediments to foraging and high seed availability, maximizing foraging efficiency and minimizing the risk of starvation during times of low winter food availability.

Site Occupancy

As expected, Henslow's sparrows occurred on a larger number of age-1 sites and were found more frequently in these sites than on age-2 sites. This pattern of occupancy is similar to those found in other studies (Chandler and Woodrey 1995, Plentovitch et al. 1998, Plentovitch et al. 1999, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005, Johnson et al. 2009). Though the number of sparrows has been observed to decrease sharply with time since burn, this study differs from previous studies in that no sparrows were found at any age-3+ site. This result contrasts with a number of previous studies that have found a low number of Henslow's sparrows still occupy sites with three growing seasons or more since the last burn (Chandler

and Woodrey 1995, Plentovitch et al. 1999, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005). Evidence suggests that these differences may be due in part to differences in area of sampling units, which influences the sensitivity of survey methods to very low bird densities, but also suggests possible differences in habitat quality at observed locations.

While Chandler and Woodrey (1995) found Henslow's sparrows in sites on MSCNWR with as many as three growing seasons since the last burn, they used area searches, which covered a larger area than the transect method used in this study. A recent small-scale winter bird transect survey using Project Prairie Bird methods by personnel at MSCNWR located Henslow's sparrows only in an age-1 site, with none in sites age-2 or greater (Hereford and Billodeaux 2009). Using a transect method similar to the one employed in this study, Carrie et al. (2002) found Henslow's sparrows at sites burned more than two growing seasons previously. This suggests that the absence of sparrow observations in age-3+ sites is due to the lower area sampling that occurs with transect searches, as well as lower population density in older sites than has been observed in other locations.

The lack of sparrows on age-3+ sites in this study could be due to an abundance of high-quality habitat leading to lower numbers of sparrows occupying older sites. Since estimates of available habitat have suggested that as many as 2200 sparrows could be supported on age-1 sites alone without home range overlap (Thatcher 2003), it is possible that Henslow's sparrows are found at older sites more rarely at MSCNWR than in other locations where surveys have taken place. Habitat in Southeastern Louisiana contained multiple "floaters," or individuals that did not maintain a consistent home range (Johnson 2006). This indicates that the habitat, which

was also used by Bechtoldt and Stouffer (2005), was likely saturated with sparrows since not enough habitat was available to support all individuals (Sherry and Holmes 1996, Johnson 2006). A similar study at MSCNWR found no floaters and only two occasions when a movement of more than 100 m occurred (Thatcher 2003), indicating that habitat at MSCNWR is not saturated and should be capable of supporting all individuals currently occupying the refuge. This suggests that MSCNWR supports its large, high-density population of Henslow's sparrows (Chandler and Woodrey 1995, Hereford and Billodeaux 2009, Burhans 2002) primarily on high-quality, recently burned sites.

It is also possible that no sparrows occurred on age-3+ sites in this study due to a regionally lowered abundance of Henslow's Sparrows relative to other years. Emberizid sparrows are locally efficient foragers that utilize patches of abundant food resources (Gordon 2000, Grzybowski 1982), and their density in a given habitat can change dramatically between years due to fluctuations seed resources (Grzybowski 1982, Pulliam and Dunning 1987, Gordon 2000). It is possible that low levels of rainfall at MSCNWR during the growing season led to lowered seed production, and therefore lowered sparrow densities. The decrease in seed resources would have been most exaggerated in sites that had not been burned recently, leading to the absence of Henslow's sparrows on age-3+ site.

Resource Availability

Time Since Burn

Age-1 sites were associated with highest mass of net-collected seeds, while the highest number of net-collected seeds occurred on age-2 sites. This suggests that as vegetation and

seed production changes with time since a burn, a progressive shift from larger to smaller seeds occurs. Since Henslow's sparrows are known to prefer large seeds to small seeds (DiMiceli 2006, DiMiceli et al. 2007), this shift in seed size may in large part explain the preference of birds for recently burned sites.

Since fire increases herbaceous diversity and alters flowering and seed production in longleaf pine savannas (Rodgers and Provencher 1999, Gilliam and Christensen 1986, Platt et al. 1988), the observed change in seed size distribution may be due to a successional change in relative species dominance (Rodgers and Provencher 1999, Johnson 2006), or to increasing competition and resultant nutrient limitation among a single set of species (Gilliam and Christensen 1986). Though total numbers of individual seed species were not quantified in this study, the achenes of sedges *Scleria spp.* and *Rhynchospora spp.* were commonly found in samples (*personal observation*). Analyses of wintering Henslow's sparrow diets have found that *Scleria spp.* and *Rhynchospora spp.* were the most commonly found seeds in Henslow's sparrow fecal samples (DiMiceli 2006) and crop contents (Fuller 2004). *Scleria spp.* produce large seeds, and while these sedges are suppressed after fire in some areas (Buckner and Landers 1979), Fuller (2004) found that they were most common on newly burned savannas at MSCNWR. Many species of *Rhynchospora* produce small seeds that are most common on older sites (Fuller 2004). The number of *Rhynchospora* consumed is correlated with the total number of items consumed (Fuller 2004), since these smaller seeds provide less energy (DiMiceli et al. 2007). Preferred seeds used in preference trials by DiMiceli et al. (2007) were fairly large, high-energy seeds that are abundant soon after a burn. Since seed size appears to be important for Henslow's sparrows wintering in coastal Mississippi, it would be of particular interest to further

investigate the dynamics and productivity of herbaceous species relative to seed size and burn schedules in pine savannas.

Though Henslow's sparrows are generally ground foragers (Herkert et al. 2002), graminoid seeds borne on stalks at the time of arrival on the wintering grounds may be a reliable indicator of food resources available later in the winter. Sparrows may avoid age-3+ sites due to low seed mass leading to decreased feeding rates on older sites, as the availability of food resources is likely the most important factor for wintering migrant survival (Sherry and Holmes 1996, Hutto 1985), and low seed production has been shown to decrease the number of Emberizid sparrows that occur in an area relative to similar sites with greater seed production (Pulliam and Dunning 1987). It is not clear which cues Henslow's sparrow uses to select winter territories or whether they are capable of directly assessing seed availability prior to seed-fall, but by selecting sites with high standing seed crops they are selecting sites likely to maximize their probability of survival over the winter.

The mass and number of vacuum-collected seeds between sites of different ages did not differ at the time of site selection. Likewise, arthropod mass and number were not significantly different between sites of different ages. It is not surprising that arthropods would be similar in overall abundance and mass across burn treatments, because of their high dispersal ability, though it is possible that differences in abundance may exist in some groups of arthropods. Hanula et al. (2000) found high winter arthropod abundance in a longleaf pine forest, with the orders Coleoptera and Araneae representing the largest portion of available arthropod biomass. Since arthropods in these orders are consumed by Henslow's sparrow more

frequently than other arthropods (Fuller 2004, DiMiceli 2006), it may be worthwhile to focus more attention on the relationship of these groups to Henslow's sparrow site selection.

As winter progressed, the availability of all resources declined in each of the burn treatments, with resources available at sites of different ages becoming more similar by the end of the winter. This indicates that it is important to look at resources at the beginning of the wintering season, when sparrows are selecting sites, since birds will be choosing a home range based on resource cues observed at the time of arrival. In this study, resource assessment only in late winter would have been unable to distinguish patterns of resource availability among burn treatments and would have generated few insights into winter home range selection.

Transect Occupancy

Unlike arthropods or vacuum-collected seeds, transects occupied by Henslow's sparrows had a significantly higher mass of net-collected seeds at the beginning of the winter than did unoccupied sites. This indicates that not only are seed resources greater over the course of the winter in sites more frequently selected by Henslow's sparrows, but they may provide an indicator for selection of individual home ranges within a savanna when sparrows arrive after fall migration. Though litter cover was best supported by occupancy models, litter cover may be important to initial site selection, and it is possible that once on a site with acceptable levels of litter, Henslow's sparrow assesses foraging rates, which are influenced by seed abundance, to select a home range within a given location.

Minimum Seed Mass

Henslow's sparrows selected sites that provided greater total resources over the course of the winter, occupying transects with significantly higher minimum vacuum-collected seed masses. Though vacuum-collected seed mass was not greater on occupied vs. unoccupied transects at the beginning of the winter when resources were at their maximum, sparrows occupied transects with significantly greater masses of net-collected seeds at the time of site selection. This suggests that though a large portion of seeds fall from the stalk earlier in the fall, seeds remaining on the stalk during the time of site selection by Henslow's sparrows may provide an indicator of total resource availability later in the winter, as food becomes more scarce.

Vegetation Structure

Seasonal change in vegetation structure

While previous studies have found that high densities of herbaceous vegetation such as grasses and pitcher plants (Plentovich et al. 1999, Carrie et al. 2002, Tucker and Robinson 2003, Johnson 2006) and little to no ground litter (Carrie et al. 2002), are associated with site occupancy by wintering Henslow's sparrows, these studies observed vegetation at the end of the winter. In this study graminoid density scores up to 1 m decreased significantly between November and March, suggesting that declines due to litter formation and flattening by wind significantly changed vegetation structure. Although other vegetation types (forbs, carnivorous plants, shrubs) did not change significantly over the winter, this change is important because perennial grasses dominate the sparrow's winter range, accounting for 87% of vegetation

contacts in all transect samples. Grasses also provide both essential seed resources and cover from predators, and should be of particular importance in the site preferences of wintering grassland birds. My results suggest that though no new growth occurs, vegetation structure changes over the course of the winter in this habitat. Vegetation surveys at the time of arrival on the wintering grounds are therefore most relevant to understanding site selection by Henslow's sparrow.

Transect Occupancy and Time Since Burn

In contrast to food resources, there were few differences in vegetation structure between occupied and unoccupied transects. Of the vegetation characteristics observed, only litter cover at the start of the winter differed significantly between transects. Litter cover was also the most important habitat characteristic in maximum likelihood analysis, though confidence in these models is low due to scarcity of data. Carrie et al. (2002) also found that Henslow's sparrows were associated with low levels of litter. This indicates that, like standing seed mass, litter cover serves as an important indicator for Henslow's sparrow habitat selection. Frequently burned savannas burn patchily (Slocum et al. 2003), so the density of litter can vary within a given savanna, which may make vegetation structure in some areas more suitable than others for habitation by Henslow's sparrow.

When comparing vegetation structure on sites of different ages, only litter cover and forb height varied based on age class. As expected, litter cover was lowest in age-1 sites, with density increasing along with time since the last burn. Litter provides fuel for fires in pine savannas (Slocum et al. 2003), which leads to a decreased litter layer in more recently burned

sites. Though forb height is greatest in age-2 sites, this difference does not appear to effect transect occupancy. Since Henslow's sparrow is a ground dweller, it may be expected that vegetation structure closest to the ground (0 – 20 cm) would have a greater effect on transect occupancy than vegetation density above 20 cm. Therefore, Henslow's sparrows may select more recently burned sites because low levels of litter may make it easier to navigate the underbrush, providing greater access to forage on the ground for available food resources (Carrie et al. 2002) as well as increased protection from predators (Thatcher et al. 2006).

Conclusions

Henslow's sparrows utilizing longleaf pine savannas of the Mississippi Sandhill Crane National Wildlife Refuge occupied sites with two or fewer growing seasons since the last burn at a given location, and had the highest densities on age-1 sites. Though Henslow's sparrow population density is known to decrease to near zero after three growing seasons since the last burn (Chandler and Woodrey 1995, Plentovitch et al. 1999, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005), no sparrows in this study occupied any age-3+ site. This suggests that MSCNWR provides an abundance of high quality habitat for these sparrows. The maintenance of high quality habitat is essential, due to the large reduction in Henslow's sparrow populations over the last half-century (Sauer et al. 2008). Therefore the continuation of the two to three-year burn cycle implemented at MSCNWR (Hereford and Billodeaux 2009) is vital to providing ample habitat for Henslow's sparrow.

My study indicated that Henslow's sparrow occupied transects that displayed high levels of standing seed mass on stalks at the time of home range selection. As resources decreased

over the course of the winter, these transects also maintained a higher total available seed mass, as indicated by a higher minimum seed mass reached on occupied relative to unoccupied transects. Given that standing seed mass at the time of arrival may provide an indicator of available seed resources later in the winter, which were important to Henslow's sparrow survival, observation of standing seed mass in November may provide an indicator of sites likely to be occupied by Henslow's sparrows.

Litter cover in this study was important to Henslow's sparrow transect occupancy, as it was in a study of Henslow's sparrow in upland pine forest (Carrie et al. 2002). Post-hoc analysis suggested that litter may be the most important factor in determining home range selection. Low litter levels occur in recently burned sites, and as time since the last burn increases, so does the density of litter. This gradual transformation of the ground-level vegetation structure may hinder movement by Henslow's sparrows, which can negatively impact foraging efficiency.

Henslow's sparrow home range selection appears to be based largely upon maximizing foraging efficiency. Since food resources are always limited (Hutto 1985), the selection of a home range with an abundant food supply is essential to sparrow survival. By selecting sites with high levels of standing seed mass at arrival, Henslow's sparrow maximizes foraging efficiency later in the winter by occupying sites that have higher seed availability when resources are scarce. Choosing sites with low litter cover may similarly increase foraging efficiency by allowing more rapid movement at ground level. Though litter was suggested as the most important factor in transect occupancy, it is likely that a combination of these two habitat characteristics are used by Henslow's sparrow to select home ranges.

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