APPROVAL SHEET

Title of Dissertation: NESTING HABITAT, FOOD RESOURCE AVAILABILITY, AND LONG-TERM OCCUPANCY DYNAMICS IN THE ENDANGERED FLORIDA GRASSHOPPER SPARROW (*AMMODRAMUS SAVANNARUM FLORIDANUS*)

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ABSTRACT

Title of Document:	NESTING HABITAT, FOOD RESOURCE AVAILABILITY, AND LONG-TERM OCCUPANCY DYNAMICS IN THE ENDANGERED FLORIDA GRASSHOPPER SPARROW (*AMMODRAMUS SAVANNARUM FLORIDANUS*).
	Archer Freni Larned, PhD, 2020
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Determining the cues by which an organism selects habitat for nesting or territory occupancy is important for conservation of endangered or threatened species. Understanding the role of vegetation and resources in habitat selection enables land managers to maintain preferred habitat. The Florida Grasshopper Sparrow is an endangered non-migratory grassland bird that resides in fire adapted habitat in Florida. To understand the influence of vegetation on nest site selection and nest success I measured microhabitat around Florida Grasshopper Sparrow nests at two sites, dry prairie and a private cattle ranch (Ch. 1 and Ch. 4) for managing the habitat for this endangered bird. Territory occupancy is determined by multiple factors, but one of those is likely food availability. I sampled arthropods, the primary food resource for Florida Grasshopper Sparrows, in different fire treatments to examine the effect of fire on

abundance and the influence arthropods have on occupancy use of Florida Grasshopper Sparrows (Ch. 2). Accurate population assessment is important for monitoring endangered organisms over time. I looked at the impact that time since the last fire using different fire metrics (maximum, minimum, and mean) has on Florida Grasshopper Sparrow occupancy at different spatial scales (Ch. 3). Using a misclassification occupancy model also allowed us to control for the presence of eastern Grasshopper Sparrows, which are difficult to differentiate in the field. I found that Florida Grasshopper Sparrows select certain microhabitat characteristics when nesting in the dry prairie, but not the cattle pasture. Nest success at both sites seem to be influenced by factors other than microhabitat. There is a difference in arthropod abundance between fire treatments with the most recent fires having the most arthropods, which may explain why Florida Grasshopper Sparrows prefer recently burned habitat. Recent fires (<1 year) do not influence the probability of Florida Grasshopper Sparrows colonizing a new area, but they do influence the probability of remaining in an area. All of these studies contribute and provide information for the ongoing monitoring of this critically endangered bird.

NESTING HABITAT, FOOD RESOURCE AVAILABILITY, AND LONG-TERM OCCUPANCY DYNAMICS IN THE ENDANGERED FLORIDA GRASSHOPPER SPARROW (*AMMODRAMUS SAVANNARUM FLORIDANUS*).

By

Archer Freni Larned.

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General Introduction

Habitat selection and the cues used to determine habitat quality are important factors in understanding the relevant behavioral and ecological issues for animals of conservation concern. Habitat selection is the behavioral decision process by which an animal selects an area to occupy, which can have an important effect on its fitness (Jones 2001). The quality of a habitat is generally inferred by correlating environmental measurements with population density or reproductive success, although population density may not always accurately reflect habitat quality (Van Horne 1983). A focal species may also use criteria for assessing habitat quality that differ from what researchers at the time consider to be important. When a species declines to a low population density, it can become difficult for researchers to determine suitable habitat characteristics since comparisons to unused habitat can lead to incorrect generalizations if the unused habitat is empty solely due to a lack of individuals available to colonize it (Johnson 1980).

Habitat selection is also likely to be based on multiple cues for different components of what that habitat is used for by a focal species. The cues an animal uses for selecting a particular habitat in which to breed range from social cues, such as conspecific attraction (Stamps 1988), vegetation structure for determining nesting sites (Cody 1981), food availability (Hamer et al. 2006, Martinez et al. 2010, Coudrain et al. 2010), cover from predators, and even cues retained from their natal habitat (Davis and Stamps 2004). Some birds select different habitat for breeding and for foraging, and also reside in different habitat types at different ages (Small et al. 2015), which can make an overall assessment of preferred habitat difficult to determine. It is especially important to form an accurate assessment of the cues used for different activities and different life stages to determine what constitutes a "high-quality" habitat for the purpose of reintroductions of captive reared individuals of conservation concern.

Organisms use certain cues to determine habitat quality and when these do not correlate with the actual quality of the habitat, the attraction to a habitat becomes maladaptive (Schlaepfer et al. 2002). When an animal's fitness is reduced in a certain habitat, but the attraction to the habitat remains this mismatch is considered to be an "ecological trap." In that case, the actual quality of the habitat that is selected by an animal is decoupled from the behavioral selection process leading the animal to incorrectly identify that habitat as appropriate (Kokko and Sutherland 2001). Sometimes indirect cues are used by an organism to determine habitat quality, but these may not always be accurate representations of habitat quality if recent anthropogenic events lead to deleterious changes, such as when grassland birds are attracted to hay-fields and suffer nest loss due to harvesting (Bollinger et al. 1990). Ecological traps are an especially important issue for endangered species, where high-quality habitat is vitally important, as is the ability to recognize it.

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is a non-migratory songbird endemic to the dry prairie habitat of southcentral Florida. The Florida Grasshopper Sparrow is also critically endangered, with only a few small populations remaining. They were reported as relatively abundant in the early 1900s, although populations were not regularly censused until the 1980's and 1990's when population numbers ranged from 182-600 (Delany et al. 1985, Delany and Cox 1986). However, population numbers as of 2018 are estimated at only about 75 total individuals (FWC Annual Report to USFWS 2018, unpublished). The Florida Grasshopper Sparrow was originally listed in1986 as federally endangered because of habitat degradation due to conversion of native dry prairie habitat to pasture for cattle and for agriculture, and loss of habitat due to development (USFWS Federal Register 1986). Following the listing and subsequent recommendations for protecting habitat and adopting what seemed like sensible fire management regimes, the sparrow populations continued to decline, and in some areas their decline has appeared to accelerate. Determining more specific habitat preferences and criteria of suitable and high-quality habitat remains an important issue for the Florida Grasshopper Sparrow as the population continues to decline for unknown reasons.

One of the more important management techniques for creating and maintaining suitable habitat for the Florida Grasshopper Sparrow is prescribed fire. Prescribed fires have been used to replace natural lightning strike fires to maintain the dry prairies of central Florida in an early successional stage and to keep trees and large shrubs from invading. The timing of prescribed fires has changed following numerous population surveys and demographic studies completed over the last three decades (Walsh et al. 1995, Shriver et al. 1996, Shriver and Vickery 2001, Delany et al. 2002, Hewett Ragheb et al. 2019). Prescribed fires set by ranchers to improve pasture were generally ignited during the winter dry season, although it is thought that natural lightning strike fires occurred most often at the beginning of the summer growing season, during what is referred to as the “fire or transition season” (Platt et al. 2015). Dry prairie habitat was maintained for the Florida Grasshopper Sparrows with winter fires, but now prescribed fires are also ignited during the summer growing season in an effort to return to a more natural fire regime and to extend the breeding season into August or September (Shriver et al. 1996). However, Hewett Ragheb et al. (2019) found no evidence that growing season fires extended the breeding season and routinely found nests into August in all prescribed burn treatments. Hewett Ragheb et al. (2019) also found after a 4-year demographic study that the Florida Grasshopper Sparrows preferred areas burned during the current dormant (dry) season or previous growing season, but that there was no difference in reproductive indices in any of the different burn treatments. Thus, prescribed fires remain an important management tool for maintaining habitat, but more information is necessary to ensure that they are used appropriately.

In the following chapters, I examine Florida Grasshopper Sparrow preferences for nesting habitat, territory settlement based on available food resources, and long-term population dynamics following prescribed burns. In chapter one, I measured vegetation variables around Florida Grasshopper Sparrow nests and compared those characteristics with habitat nearby at two different sites where the birds are currently found. My work substantially increases the nest sample size and expands upon prior studies (Delany and Linda 1998a; b; Nicholson 1936) to monitor these endangered birds and ensure that preferred habitat is being adequately maintained. I also provide the first comparison between nesting habitat in two important remaining populations of the Florida Grasshopper Sparrow: 1) a managed native dry prairie habitat, and 2) a privately owned semi-improved cattle pasture. I found that the nesting habitat is very different between the sites in vegetation composition, but my results suggest that grass height surrounding nests, which did not differ between sites, is probably an important feature in selecting nesting habitat. Florida Grasshopper Sparrows also select nest sites in portions of the habitat with less bare ground and more grass than non-nest areas in the managed dry prairie habitat which, of the two sites, had a higher diversity in overall vegetative structure and composition.

In chapter two, I collected arthropods in different prescribed fire treatments and at the semi-improved pasture to understand if Florida Grasshopper Sparrows are selecting territories based on potential resource availability, and if those resources differ between treatments. It seems likely that Florida Grasshopper Sparrows may be using multiple cues to determine habitat quality when establishing territories. Food resource availability is most likely an important cue in that context, given its importance in contributing to a bird's fitness. I sampled arthropods in the dry prairie habitat, but only included the total counts for arthropods that were most likely to be consumed by Florida Grasshopper Sparrows. I also sampled arthropods in the semi-improved cattle pasture (though this habitat was not burned during the course of my work) to understand how arthropod numbers compared to those in native dry prairie. From my results, the prescribed burn treatment that occurred in the current year during the transition (spring) season had the highest arthropod numbers, while the sparrows mostly occupied territories in areas burned during the current dormant (dry) season, suggesting that current year burn treatments were preferred by both sparrows and arthropods. This result reflects a tradeoff between food availability and sufficient vegetation coverage for nesting, since units burned during the current transition season were burned at the same time that male sparrows are establishing their territories.

In chapter three I used occupancy modeling to look at long-term (1996-2011) population dynamics at the dry prairie site that until the early 2000s held one of the largest populations of Florida Grasshopper Sparrows. Point count surveys have been standardized for several remaining sites and used since the 1990's to determine population numbers, but the first round of those surveys (March – April) is completed when the eastern subspecies (*A. s. pratensis*) is still present on the dry prairie habitat (prior to migrating northward). It is very difficult to distinguish between the two subspecies in the field either by song or visually from a distance but removing the first round of point count survey records would result in a huge loss of information. Grasshopper Sparrow males sing more frequently in the early part of the season as compared to later in the season (Lohr et al. 2013). In order to account for the presence of migratory eastern Grasshopper Sparrows during early point counts at this site, my co-authors and I added a misclassification probability to an existing occupancy model (Chambert et al. 2015). This model operates in a Bayesian framework to look at population dynamics and determine the influence of time since the last prescribed burn on persistence and colonization in an area. We looked at point count data at two different spatial scales; one approximately the size of individual territories, and a larger scale approximately the size of several territories and closer to home range size, (Dean 2001).

Finally, I have also included a short chapter four that examines the spatial orientation of Florida Grasshopper Sparrow nests. Grasshopper Sparrows build domed nests on the ground with an opening whose circular direction can be quantified. Previous work found no apparent consistent direction of the nest entrances with respect to circular orientation (Delany and Linda 1998). Using a sufficiently large sample, I found that Florida Grasshopper Sparrows orient their nests primarily to the northeast, similar to other grassland birds and Grasshopper Sparrow subspecies (Hartman and Oring 2003, Long et al. 2009, Ruth and Skagen 2017). I also included nests from two sites with very different vegetation characteristics and determined that since nest opening orientation does not differ between the sites, it is most likely oriented with respect to solar radiation and storm avoidance.

Overall, these chapters build upon prior work to expand our knowledge of habitat selection preferences and our ability to determine high-quality habitat for the endangered Florida Grasshopper Sparrow. Furthermore, they can also provide additional information relevant to habitat selection in other grassland songbirds and increase our understanding about key management issues affecting endangered species in different habitats.

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Chapter 1: **Nest microhabitat influences nest site selection in dry prairie but not in pasture habitat for the endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*)**

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Archer F. Larned, Erin L. Hewett Ragheb, Karl E. Miller, Bernard Lohr

Abstract

Vegetation characteristics can influence nest-site selection and nest survival of birds. The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is a critically endangered ground nesting grassland bird endemic to central Florida. Currently, the two largest remaining populations are found on sites with differently managed habitats. One site is burned regularly to maintain native dry prairie habitat and the other is a cattle pasture that is mowed and burned to optimize cattle forage. Little is known about how vegetation influences Florida Grasshopper Sparrow nest-site selection and nest success in these different habitats. We measured microhabitat characteristics (percent vegetation cover and grass height) at Florida Grasshopper Sparrow nests and paired random plots at both sites for three breeding seasons (2014- 2016). Percent cover differed significantly between the sites for 7 of 8 vegetation types, with the cattle pasture characterized primarily by grasses and dry prairie characterized by more diverse native vegetation. Despite these vegetative differences, grass height did not differ at the two locations, suggesting that plant height, rather than plant species composition, may be more important for nest site selection in this bird. Microhabitats around nests at the dry prairie site had 31% less bare ground and 32% more grass than non-nest plots. No variables predicted the placement of nests at the cattle pasture, possibly due to the more homogenous habitat at that site. We did not find a vegetative component of nest success, which suggests that other non-vegetative factors may

influence nest predation. Understanding the vegetation characteristics associated with Florida Grasshopper Sparrow nests will help inform habitat management strategies for maintaining vegetation height for nest-site habitat of this critically endangered subspecies.

Introduction

Habitat loss and degradation have contributed to the loss of biodiversity in grasslands (Noss et al. 1995). In North America, grasslands have lost more than 80% of their original area since the 1800s, making them one of the most endangered ecosystems in the United States (Samson and Knopf 1994, Noss et al. 1995). As a result, plants and animals associated with grasslands are also in decline (Brennan and Kuvlesky 2005, Askins et al. 2007). In particular, grassland birds have experienced steep population declines, with more recent declines attributed to intensification of agriculture (Murphy 2003, North American Bird Conservation Initiative 2016, Stanton et al. 2018). Historically, fire and herbivores naturally maintained grasslands by preventing the growth of trees and large shrubs (Noss 2013). A concerted effort has been made to restore or maintain grasslands for birds and other native wildlife in the United States using prescribed fires and grazing by cattle or bison (Schramm 1990, Gill et al. 2006, Vogel et al. 2007).

Determining the specific vegetative cues that birds seek out for nesting is important for land management, especially for birds with small or declining populations. There is evidence that birds select certain structural characteristics of vegetation within their territories to place their nests, rather than selecting random locations within the habitat (Cody 1981, Gjerdrum et al. 2005, Winter et al. 2005a). Disturbance from grazing and fire applied at the local level generally results in a mosaic of habitat structure and increased heterogeneity of grassland birds and vegetation (Fuhlendorf et al. 2006). Whereas some birds prefer recently burned habitat (Johnson 1997, Hewett Ragheb et al. 2019a.), others, such as Henslow's Sparrow (*Centronyx henslowii*) prefer vegetation containing more dead plant material resulting from longer burn intervals (Zimmerman 1988). Grasshopper Sparrows (*Ammodramus savannarum*) responded positively with increased survival and site fidelity to prescribed fire management practices that restored a degraded agricultural field to grassland habitat (Gill et al. 2006). Prescribed fire is a commonly used management tool in prairie habitat, and it is important to understand the effects at the microhabitat scale since the vegetation composition may have varying impacts on different grassland bird species (Grant et al. 2010).

The scale at which the vegetation is assessed is critical for management decisions, as avian preferences for territory formation and nest site selection operate on both macro and microhabitat levels (Pribil and Picman 1997, Chalfoun and Martin 2007, Ruth and Skagen 2017). For understanding nest habitat preferences, the microhabitat spatial scale is more ecologically relevant since preferences may differ between the nest site and other locations within the territory due to different resource needs, for example the presence of singing perches to define territory boundaries, or vegetation for concealment at nest sites (Chalfoun and Martin 2007). Determining habitat preferences around the nest at the microhabitat scale can also provide clues to habitat quality, though occasionally there is a mismatch between habitat quality and fitness. This mismatch may reflect a lack of information in our understanding of habitat suitability at the territory vs. nest site scale (Arlt and Pärt 2007, Chalfoun and Martin 2007, Chalfoun and Schmidt 2012), or because human modification of habitat negatively affects nest success (Kokko and Sutherland 2001, Shochat et al. 2005). A lack of variation in microhabitat around the nest may also obscure a significant relationship between microhabitat and predation due to the parent's adaptive response to predators when they select only well-concealed nest sites, without less-concealed nest sites for comparison (Latif et al. 2012).

Vegetation immediately surrounding the nest provides cover to protect adults and nest contents from predators and maintain a suitable microclimate for many bird species. These factors may have implications for reproductive success (Dion et al. 2000, Arlt and Pärt 2007, Small et al. 2015). While some studies show a relationship between nest success and microhabitat vegetation variables (Taylor et al. 1999, Winter et al. 2005b.), others show no relationship (Vickery et al. 1992a, Rodewald and Yahner 2001, Winter et al. 2005b.). It is unlikely that a single vegetation component influences nesting success and may be a combination of different vegetation variables. Grasshopper Sparrows (*Ammodramus savannarum*) and Henslow's Sparrows showed no change in daily nest survival after removing woody vegetation within the entire study plot, despite the supposed association between woody vegetation and nest success (Hill and Diefenbach 2013). For Grasshopper Sparrows, an increase in vegetative cover was associated in at least one study with decreased nesting success, attributed to the additional cover for predators to remain hidden (Hovick et al. 2012). Thus, it appears that in a number of grassland bird species the relationship between nest success and vegetation variables is not always clear.

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is currently one of the most critically endangered birds in North America. It is endemic to the dry prairie in central Florida and was federally listed as endangered in 1986 due to rapid declines and a dramatic loss of habitat (USFWS Federal Register 1986). For example, at one site (Three Lakes Wildlife Management Area, Osceola County, Florida) the population dropped from approximately 142 singing males in 2008 to only 67 singing males in 2013 (FGSP Working

Group, unpublished data). The largest two populations of Florida Grasshopper Sparrow are found in a public conservation area containing dry prairie habitat and a privately owned semi-improved cattle pasture. Semi-improved pasture in Florida consists of a combination of non-native forage species and native grasses and forbs (Willcox et al. 2010). Historically, dry prairie covered much of south-central Florida but has since mostly been converted to pasture for cattle grazing, sod farms, agriculture, and housing developments (Stephenson 2011). Dry prairie and improved pasture habitats appear compositionally and structurally very different, yet Florida Grasshopper Sparrows occupy and nest in both. Florida Grasshopper Sparrows nest on the ground in well-concealed nests usually on the edge of a clump of grass or at the base of a small shrub for structural support (Nicholson 1936, Vickery 1996, Delany and Linda 1998a). Despite having well-concealed nests, Florida Grasshopper Sparrows have low cumulative nest success, with an average of only 12.7% in dry prairie habitat and 5.9% in semi-improved pasture (Hewett Ragheb et al. 2019b).

Here we attempted to quantify the differences in nesting microhabitats used by Florida Grasshopper Sparrows at both sites and relate these differences to nest site selection and the probability of nest success. Specifically, we asked: (1) Does the microhabitat of territories differ between the two sites?, (2) Does microhabitat influence nest location within a male’s territory and does this differ between sites?, and (3) Does microhabitat predict nesting success? This study aims to expand upon previous work describing Florida Grasshopper Sparrow nest microhabitat in dry prairie habitat by increasing our ability to draw significant conclusions (larger sample size) and including a comparison with nests of known fate (Nicholson 1936, Delany and Linda 1998a, 1998b). We also provide the first description of Florida Grasshopper Sparrow nest site characteristics in semi-improved cattle pasture habitat.

Methods

Study Sites

We investigated the microhabitat characteristics around Florida Grasshopper Sparrow nests in 2014-2016 at two study sites: Three Lakes Wildlife Management Area (Three Lakes) and a private ranch (the Ranch) in Osceola County, Florida. Both areas had low elevation (range 16-21m) and flat topology. The average annual temperature was 22° C and the average annual precipitation was 1321 mm (1981-2010). The study area at Three Lakes was the Route 60 Unit near Kenansville, FL (27.876°, -80.988°) and was approximately 3,000 ha in size, which included a 1,728 ha area of relic dry prairie (Figure 1). The Florida Fish and Wildlife Conservation Commission manages Three Lakes for Florida Grasshopper Sparrows and other wildlife by frequent prescribed burning (ca. 2-year interval), mechanical roller chopping to reduce shrub density (prior to burning), and tree removal when necessary (Hewett Ragheb et al. 2019a). The dry prairie habitat at Three Lakes was characterized by low shrubs, pyrogenic grasses, and herbaceous forbs with small patches of bare ground (Florida Natural Areas Inventory 2010). The dominant shrubs in dry prairie habitat were saw palmetto (*Serenoa repens*) and dwarf oak (*Quercus minima*). Generally, wiregrass (*Aristida stricta*) was the predominant grass, but many other species (for example *Andropogon spp*) were present, as were numerous herbaceous forbs (Florida Natural Areas Inventory 2010).

The study area at the Ranch was 1,012 ha in size and consisted of semi-improved pasture interspersed with small ponds and hammocks (Figure 2). The Ranch had been privately managed for cattle grazing for at least 12 years by mowing every 2-3 years during the dry season (Jan-Apr) and occasional prescribed burning. Cattle foraged at the Ranch site at approximately 1 animal unit per 8-9 ha (G. Hendricks, Florida Eco Enterprises, LLC, unpublished data). Semi-improved pasture was previously covered in a monoculture grass (bahiagrass [*Paspalum notatum*]), for cattle forage, and now has some native dry prairie plants recolonizing the site, such as bluestem grasses (*Andropogon spp*) and saw palmetto (*Serenoa repens*; G. Hendricks, Florida Eco Enterprises, LLC, unpublished data, Willcox et al. 2010). Shrubs consisted mostly of large clumps of saw palmetto with lesser amounts of southern wax myrtle (*Myrica cerifera*), gallberry (*Ilex glabra*), and rarely dwarf oak (G. Hendricks, Florida Eco Enterprises, LLC, unpublished data).

Nest searching and monitoring

We searched for Florida Grasshopper Sparrow nests from April to August at both sites during the years 2014-2016 as part of concurrent demographic studies (Hewett Ragheb et al. 2019a, 2019b). We found nests during all stages of the breeding cycle by observing adult behavioral cues, including singing behavior (Lohr et al. 2013), or by occasionally flushing females off of nests when walking in the habitat. Nearly all male territories were known at both sites each year and nest searching occurred daily, with each territory visited repeatedly for that purpose. The proportion of total nest attempts discovered per breeding pair each season was unknown, but we attempted to find as many nests as possible. We monitored nests at both sites by carefully checking nest contents every 2-3 days until nestlings were 5 days old, then daily until nestlings fledged at 7-8 days old or the nest failed. Empty nests were considered successful if ≥ 1 fledgling was sighted or if nestlings were fledging age and the parents were seen carrying food or heard producing alarm calls. We banded all males at both sites with a unique color combination and an aluminum federal band. The sites were treated as separate populations, with limited movement of individuals between sites based on previous observations (Delany et al. 1995, Miller 2005, Tucker et al. 2010). For nests found by A.L., all relevant animal care and use protocols were followed as designated by Institutional Animal Care and Use Committee at the University of Maryland Baltimore County (BL010591215).

Microhabitat attributes

We measured microhabitat characteristics around each nest within 2 weeks (mean of 8.6 days, range 2 – 15 days) following nest completion (fledged or failed). First, we identified the vegetation type(s) (grass, dwarf oak, saw palmetto, forb, and non-oak shrubs) that the nest was built into to provide a general, qualitative comparison of nest locations between sites. Second, we measured the visual obstruction of the vegetation surrounding the nest using a modified Robel pole (measuring tape with decimeter increments marked with alternating white and grey; Robel et al. 1970). The amount of visual obstruction was determined by recording the lowest decimeter section visible while standing at a distance of 4 meters from the nest viewing from a height of 1 meter to the south of the nest (Robel et al. 1970). We restricted the measurement to the south to minimize trampling of vegetation and to reduce the amount of time spent at each plot to minimize stress of Florida Grasshopper Sparrows tending young fledglings or re-nesting nearby. We acknowledge that grassland birds often have one side of the nest that is less obstructed to provide an escape to facilitate anti-predator displays (Delany and Linda 1998b). Florida Grasshopper Sparrow nests are generally oriented to the north-east (A. Larned *unpublished data)*, so by only measuring to the south it is likely that we did not include the side with the shortest vegetation, which may have biased the results.

Third, we estimated the percent cover of different vegetation categories at the nest using a 50cm x 50cm plot frame made from PVC pipe centered over the nest. The eight vegetation categories included: bare ground, dead flat litter, prostrate saw palmetto trunks, saw palmetto leaves, grasses and sedges, herbaceous forbs, dwarf oak, and non-oak shrubs. Most of these categories were identified as important to nesting in previous studies with Florida Grasshopper Sparrows (Delany and Linda 1998b, Fisher and Davis 2010), however, we added the categories of prostrate saw palmetto trunks and separated dwarf oak from non-oak woody shrubs because of their potential importance for nesting. We did not measure litter depth at the dry prairie because there was very little standing litter due to the frequent fires, although it is an important nesting component for other grassland bird species (Fisher and Davis 2010). We also did not measure litter depth at the cattle pasture for the sake of consistent methodology between sites and because of the high density of the live grass. We estimated each vegetation category to the nearest 5% (Dion et al. 2000). The percent cover for each vegetation category was measured independently of other categories, so the total could be greater than 100%. Fourth, we measured the tallest free-standing grass specimen, alive or dead, because tall grass provides singing perches and cover in the environment and was the only vegetation type that was present across all nests.

For the percent cover and grass height variables, we also surveyed a random non-nest plot 50 m away from the nest in the direction of a randomly chosen compass bearing to allow for a comparison of used and available nesting habitat (Johnson 1980). A random number generator was used to determine a compass bearing between 0 and 359 for the paired non-nest plot. If the random point was in a non-grassland habitat type within the territory (e.g. wetland, gravel road, or stand of trees) a new point was selected. We considered the non-nest plot as available habitat within the male's territory since the average size of a Florida Grasshopper Sparrow male's territory is approximately 135 m in diameter (Delany et al. 1995).

Site comparison

We conducted nine separate Mann-Whitney U-tests with a Bonferroni correction (α=0.005) to examine the differences in vegetation variables (eight percent cover categories and grass height) between sites. We pooled nest and non-nest plots within sites and pooled across years (2014-2016). We used the Mann-Whitney U-test, which is the nonparametric equivalent of a t-test, because each of our vegetation variables was non-normally distributed (Fay and Proschan 2010). We ran all Mann-Whitney U-tests in *stats* package in R (R Core Team 2016).

Nest site selection

We compared the vegetation characteristics of nest and non-nest plots to examine the role of microhabitat on Florida Grasshopper Sparrow nest site selection. For these models, we used nest vs. non-nest as the binary response variable and the eight percent cover variables and grass height as the fixed effect covariates. We first checked fixed effect covariates for multicollinearity by looking at a correlation matrix of all covariates for each site and then removed one of the variables if a pair were highly correlated ($r > 0.7$; Dormann et al. 2013). Not one of the variables was highly correlated at Three Lakes, so no variables were removed. The covariates for percent bare ground and litter were correlated for the Ranch, so we removed bare ground because few nest plots contained this variable. We also chose to exclude covariates for percent saw palmetto leaves and saw palmetto trunks from the Ranch models because they were only present in two nest plots and were therefore assumed not to be ecologically relevant at this site.

We then generated a series of generalized linear models with a binomial response distribution and a logit link function for each site separately in the *stats* package in R (R Core Team 2016). We compared models in several stages in an exploratory approach using a hierarchical method to avoid over-parameterization. In Stage 1, we created and compared models representing all univariate and additive multivariate combinations of percent cover covariates related to ground cover (bare ground, litter, and palmetto trunks) and included a null (intercept-only) model. Candidate models at this and subsequent stages were ranked by differences in Akaike Information Criteria values adjusted for small sample size (ΔAICc) with the most-supported model having the lowest value (Akaike 1973). Models within 2 AICc units of the top model were considered to be parsimonious and carried over to the next stage unless an examination of the 90% confidence intervals for the coefficient estimates revealed uninformative parameters (Burnham and Anderson 2002, Arnold 2010). If the confidence interval for a parameter estimate included 0 it was deemed uninformative. Stage 2 included all univariate and additive multivariate combinations of the percent cover covariates related to standing vegetation (palmetto leaves, grass, forbs, dwarf oak, and non-oak shrubs). Stage 3 included a model with the grass height covariate. We created a total of 36 models for Three Lakes and 17 for the Ranch plus an intercept-only (null) model at each site. For the final top model at each site, we calculated the 95% confidence intervals for the parameters to determine if they were informative and to determine the strength of effect as recommended by Arnold (2010). Model fit was tested using the Hosmer and Lemeshow goodness of fit test (α=0.05; *ResourceSelection* package in RStudio; Lele et al. 2019). We also checked the variation inflation factor (VIF) of parameters in the top model for collinearity, with VIF < 4 indicating no major collinearity, using the *car* package in RStudio (Fox and Weisberg 2019).

As a preliminary exploratory step, we also created a series of models using the same hierarchical stages using generalized linear mixed models (GLMER; *lme4* package; Bates et al. 2015). For these models, we included the identification of the breeder male and year as random effects terms to examine the potential for psudoreplication of nests from the same breeding male and a possible year effect. The variance attributed to the breeder male and year was 0 or close to 0 for all models, suggesting no support for those random effect covariates. Therefore, we used generalized linear models instead of the generalized linear mixed models for the final analysis.

Nest success

To evaluate the influence of microhabitat on nest success we used a generalized linear model with Shaffer (2004) logistic exposure link function using *stats* package (R Core Team 2016). The dataset for this analysis was restricted to nests at Three Lakes in 2014 and the first half of 2015, and the Ranch in 2015 because nests after those dates were protected with experimental predator exclosure fences that may have altered their probability of success (Hewett Ragheb et al. 2019b). We used the eight percent cover categories, grass height, site, and visual obstruction index as the fixed-effect covariates. We compared 48 models and a null in three stages to avoid over-parameterization. For Stage 1, we compared the null model with a model containing only a fixed-effect covariate for site (Three Lakes, Ranch), and the same ground cover variables in the nest site selection analysis. Model composition and ranking (AICc) for Stage 2 (standing vegetation percent cover), and Stage 3 were similar to the nest site selection analysis except that Stage 3 included models containing both the grass height and visual obstruction covariates. Covariates were checked for multicollinearity using the same methods as the nest site selection analysis and since no variables were correlated, all were retained.

As a preliminary exploratory step, we also created a series of nest survival models with the same hierarchical stages in generalized linear mixed models for the Three Lakes data only (GLMER; *lme4* package in R; Bates et al. 2015) using the identification of the breeder male and year as random effects terms. The variance attributed to year was 0 or close to 0 for all models so it was not retained. Models containing the identification of the breeder male as a random effect would not converge. The differences in microhabitat covariates between renests of the same male were often as great or greater than the differences between males, suggesting that there may be little to no bias created by including multiple nests from individual males. Considering this, we used generalized linear models instead of the generalized linear mixed models for the final analysis.

Results

A total of 154 and 52 Florida Grasshopper Sparrow nests were monitored at Three Lakes and the Ranch. We measured microhabitat data for a total of 91 nests at Three Lakes and 32 nests at the Ranch (Table 1). We were unable to collect microhabitat data at 83 nests because either a re-nesting attempt or fledglings were too close to the target nest or flooding made the area inaccessible. Sampled nests were attributed to 51 different males at Three Lakes and 18 different males at the Ranch over three years.

Microhabitat attributes

Most nests were built into grass clumps (75% of nests at Three Lakes and 100% of nests at the Ranch). At Three Lakes, supporting nest material also included: dwarf oak (43.9%), saw palmetto (16.5%), non-oak shrubs (15.4%), and forbs (4.3%). Almost all of the nests were built into multiple vegetation types.

Site comparison

Microhabitat characteristics at Florida Grasshopper Sparrow nests and non-nest plots varied between the two sites for all variables except percent cover for forbs and grass height (Table 2). Microhabitat at nests and non-nest plots at Three Lakes was primarily composed of grass (36.4%), bare ground (34.0%), and dwarf oak (23.7%). At the Ranch, grass showed an average of 84% cover in all plots.

Nest site selection

For nests at Three Lakes the top model for nest-site selection after Stage 3 contained covariates for percent bare ground, percent grass, and grass height (Table 3). We concluded that the top model was a good fit ($x_2 = 8.153$, $P = 0.419$). However, we determined that grass height was not informative because the 90% confidence interval associated with the beta estimate contained zero (Arnold 2010). The second-ranked model was within 2 AICc values of the top model (245.66 vs. 245.14) and contained only percent bare ground and percent grass. After Stage 1, the model containing covariate for percent bare ground was retained, and after Stage 2 we retained the model containing percent bare ground and percent grass (Table 3). After Stage 2, there were 3 models within 2 AICc values of the top model, but we concluded that none of the variables were informative because the 90% confidence intervals all contained 0 (Arnold 2010). Based on the second-ranking model, the probability that a plot would contain a nest increased with decreasing bare ground (odds ratio: 0.081; Fig. 3a) and increasing grass cover (odds ratio: 9.274; Fig. 3b). The variance inflation factor for the covariates were: percent bare ground = 1.05, percent grass = 1.09, neither showing any evidence of collinearity. The parameter estimates for the intercept, percent bare ground, and percent grass were 0.889 (CI -0.231, 2.041), -2.514 (CI -4.055, -1.058), and 2.227 (CI 0.912, 3.601), respectively.

For the Ranch, no microhabitat variables predicted nest site selection as the null model was the highest-ranking model for all three stages (Table 4). The second-ranking model was within 0.35 AICc values from the top model and contained the grass height covariate (Table 4). However, the 90% confidence interval for the grass height parameter estimate (0.016) contained zero (-0.0003, 0.0361) suggesting that it was not informative.

Nest success

At Three Lakes, there were 15 successful nests out of a total of 43 with microhabitat measurements in 2014 and the first half of 2015. At the Ranch, there were 4 successful nests out of 24 with microhabitat measurements in 2015. A total of 105 nest-check intervals from Three Lakes and 76 from the Ranch were used in the Shaffer logistic exposure analysis for nest survival. The null model was the highest-ranking model for nest success for all three stages (Table 5) meaning our dataset revealed no difference between sites and no vegetation variables distinguished successful and unsuccessful nests. All of the variables in the models after each stage that were within 2 AICc values of the null were determined to be uninformative by examining the 90% confidence intervals associated with the beta estimates (Arnold 2010). The mean daily nest survival for all nests was 87.8% (95% CI = 84.4% - 90.9%) and the mean probability that a nest would survive the entire 21-day nesting cycle was 6.6% (95% CI = 2.8% - 13.4%).

Discussion

Determining the vegetation characteristics that influence nest site selection can contribute to the management and conservation for endangered bird species (Cody 1981, Askins et al. 2007). Overall, we found that the microhabitat composition of Florida Grasshopper Sparrow nesting habitat at the two sites was quantifiably distinct for most measured variables, with differences in the composition of vegetation at the two sites likely a result of differences in land management regimes. Females prefer less bare ground, and more grass cover at dry prairie habitat when selecting locations to build a nest. However, females preferentially selected none of our measured vegetation features at the cattle pasture site. Despite plasticity in nest site selection in terms of vegetation composition, there was no difference in mean grass height at nest locations between Three Lakes (56 cm) and the Ranch (59 cm). However, this result only compared sites where Florida Grasshopper Sparrows currently nest. To assess the importance of grass height more thoroughly, we recommend additional work comparing grass height in sites with and without Florida Grasshopper Sparrows.

Florida Grasshopper Sparrow nests in dry prairie were not randomly placed within available habitat, and our results suggest that specific vegetative characteristics can predict nest placement in this habitat. The presence of increased amounts of grass cover around nests as compared to non-nest areas is not surprising, as most other North American grasshopper sparrow subspecies also build their nests into clumps of grass (Vickery 1996). We found that Florida Grasshopper Sparrow nest locations had less bare ground than a random plot in available adjacent habitat, similar to Le Conte's Sparrows (*Ammospiza leconteii;* Winter et al. 2005a.). Although bare ground in front of a nest entrance may facilitate anti-predator distraction displays (Delany and Linda 1998b), too much would leave a nest without enough concealment for the adults to hide from predators. In contrast to our results, Delany and Linda (1998b) found no difference in the amount of bare ground between nest and non-nest areas. However, their study was at a different site (Avon Park Air Force Range in Highlands County, Florida) that was burned and grazed by cattle, which may have contributed to more homogenous bare ground coverage (Delany and Linda 1998b).

The entire nesting cycle for Florida Grasshopper Sparrows lasts ca. 21 days (Vickery 1996). It is unclear how long the female takes to determine a suitable nesting site, but re-nesting can happen within a few days following a predation event (A. Larned, personal observation), implying that the selection process may only take a day or two. We measured vegetation characteristics around all nests within 2 weeks after nest completion (the average time between nest completion and data collection was 8.6 days). While it is possible that the vegetation changed somewhat since the nest was built, some vegetation characteristics, such as height and composition, most likely changed only minimally. Many plants in the habitat reach a maximum height and do not continue growing taller throughout the breeding season, such as dwarf oak (typically 15-45 cm) and many forbs (Orzell and Bridges 2006). In addition, the tallest standing grass specimen was often dead, so the height was relatively fixed until the habitat was burned at a later point.

Florida Grasshopper Sparrow nesting habitat at the cattle pasture was homogenous in comparison with that at the dry prairie. The lack of variability of the nesting habitat at the cattle pasture was likely a consequence of management, as it is semi-improved pasture that had previously been planted with non-native grasses and now also contains interspersed native grasses and forbs. Grassland birds in tallgrass prairie habitat had decreased nest success and increased rates of brood parasitism associated with habitat homogeneity as a result of grazing alone (Rahmig et al. 2009). Generally grazing and burning was associated with higher vegetation heterogeneity, which leads to increased biodiversity for bird communities (Fuhlendorf and Engle 2004, Hovick et al. 2015). The habitat at the cattle pasture, however, was mainly grazed and only occasionally burned, and it did not appear to have substantial vegetative heterogeneity. Grazing and burning are generally applied simultaneously to create a mosaic of different structural components in the habitat, which are associated with increased reproductive productivity for some grassland birds (Rohrbaugh et al. 1999). Patch-burn treatment, which increases vegetation heterogeneity, has been shown to increase nest success for Dickcissels (*Spiza americana*) in tallgrass prairie (Churchwell et al. 2008), by increasing the vegetative cover for nests. Historically, Florida Grasshopper Sparrows have been occasionally found on improved cattle pasture, provided that the cattle density was low (Delany et al. 1985). Grasshopper Sparrows in grasslands in the Midwest responded positively to grazing and burning with low to moderate stocking density (3.5-5.9 animal units per month per ha; Hovick et al. 2012), although overgrazing was associated with reduced clutch size and nest success in Kentucky (Sutter and Ritchison 2005). Grazing and mowing at the cattle pasture in this study appears to keep the grass at a similar height to areas burned ≤ 2 years prior at the dry prairie. Habitat abandoned by Florida Grasshopper Sparrows in the past also had a high percentage of grass cover (83%), similar to the Ranch habitat (Delany and Linda 1994). The principal difference between the abandoned habitat of Delany and Linda (1994) and the semi-improved pasture of the Ranch was the height of grass. The grass at the abandoned habitat was much shorter (mean = 11 cm), than at the Ranch (mean = 59.8 cm) and could explain why the Ranch is occupied.

The presence of a Florida Grasshopper Sparrow population at the cattle pasture instead of dry prairie suggests a possible mismatch between habitat preference and fitness (Delibes et al. 2001, Chalfoun and Schmidt 2012), especially with the very low nest success at the cattle pasture as evidenced from a study by Hewett Ragheb et al. (2019b). While our nest success data did not show a site effect, evidence from Hewett Ragheb et al. (2019b) did show reduced nest success at the cattle pasture as compared to the dry prairie site. Grazing on semi-improved pasture in Florida is associated with decreases in vegetation height and grass cover (Willcox et al. 2010), attributes that can contribute to reduced cover for nesting birds (Sutter and Ritchison 2005). It is possible that birds at the cattle pasture are selecting habitat based on other factors, such as food availability or site fidelity, when assessing areas for nesting (Shochat et al. 2005). The apparent attractiveness of the site coupled with the low apparent nesting success suggests that this site may be acting as an ecological trap (Schlaepfer et al. 2002). Florida Grasshopper Sparrows do not disperse long distances between years very often (Miller 2005). Once a population is established in an area there may be a tendency for it to remain established at that site (Delany et al. 1995, Tucker et al. 2010). It is intriguing that the remaining population on non-native habitat, the cattle pasture, is adjacent to Kissimmee Prairie Preserve State Park, Okeechobee County, Florida, which is managed dry prairie habitat where this subspecies formerly occupied in large numbers. It is unclear why a population initially became established at the cattle pasture (perhaps historically this population existed in that location before the site was managed for cattle), but the low nest success rate (Hewett Ragheb et al., 2019b), and rate of decline in the population as a whole (Florida Grasshopper Sparrow Working Group; unpublished data) suggest it might not persist there.

Microhabitat characteristics around the nest did not appear to influence nest success based on our data, which suggests that another factor may drive nest predation rates. Nests at the dry prairie that failed did so predominantly due to depredation caused by mammals and snakes, while nests at the cattle pasture were primarily depredated by fire ants (*Solenopsis invicta*; Hewett Ragheb et al. 2019b). Fire ant density is greater in cattle grazed areas in central Florida and was previously attributed as a cause of nestling deaths in Florida Grasshopper Sparrows and

Northern Bobwhite (*Colinus virginianus;* Mueller et al. 1999, Tucker et al. 2010). There is some evidence of structural differences in vegetation between successful and unsuccessful nests for other grassland birds (Dion et al., 2000, Gjerdrum et al. 2005, Sutter and Ritchison 2005), although it is not always possible to determine specific vegetative components that may contribute to nest success (Winter et al. 2005b, Hill and Diefenbach 2013). Our lack of association between nest fate and measured microhabitat variables could be due in part to an insufficient number of variables that were measured or a high predator density, whereby the effects of vegetation can be negated (Vickery et al. 1992b).

Conclusion

Florida Grasshopper Sparrow nesting habitat differs compositionally between dry prairie and semi-improved cattle pasture. This result suggests some plasticity in nest site selection in terms of plant species and bare ground cover, but not grass height in this declining sparrow. Florida Grasshopper Sparrows nest in areas in dry prairie with more grass and less bare ground than in surrounding areas of available habitat. However, we did not find a vegetative component to nest placement in semi-improved cattle pasture, which tends to be homogenous and primarily covered in grass. It is difficult to ascertain, however, if Florida Grasshopper Sparrows are demonstrating a willingness to settle in cattle pasture habitat with low nesting success (in which case it may be acting as an ecological trap), or if their continued occupation at the cattle pasture is a consequence of high site fidelity and a general tendency not to move even relatively short distances in establishing new breeding populations. The dry prairie habitat is generally preferred by Florida Grasshopper Sparrows (Delany et al. 1985), but they can nest in semi-improved pasture habitats provided that the vegetation height is moderate. For management purposes, vegetation height appears to be more important for nesting than providing areas of bare ground or a particular plant species composition. Since sparrows are seen foraging in areas of bare ground, it is recommended that managers maintain a habitat mosaic consisting of areas of bare ground and denser grass for nesting. The Florida grasshopper sparrow population has reached a critically low number and continues to decline. This study can help identify suitable nesting habitat and can provide information for land managers to improve it in areas currently maintained for this bird.

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Table 1.1. Total number of Florida Grasshopper Sparrow nests found at both sites, Three Lakes and the Ranch, Osceola County, Florida. The number of nests with microhabitat characteristics measured each year is in parentheses.

Year	Three Lakes	Ranch
2014	43 (32)	3 (3)
2015	61 (34)	29 (24)
2016	50 (25)	20 (5)
Total	154 (91)	52 (32)

Table 1.2. All but two microhabitat variables near Florida grasshopper sparrow nests differ between Three Lakes (n=182), Osceola County, Florida and the Ranch (*n*=64), Osceola County, Florida during 2014-2016. α= 0.005, * *P* < 0.0005

		Three Lakes	Ranch
Variable	U	Mean (SE)	Mean (SE)
Bare Ground (%)	946.5	34.0(1.4) *	7.6 (1.5) *
Litter (%)	2818.5	14.5 (1.0) *	5.8 (1.0) *
Saw palmetto trunks (%)	4087.5	4.1 (0.5) *	0.5 (0.3) *
Saw palmetto leaves (%)	2381	12.0 (1.1) *	1.8 (0.9) *
Grass (%)	10906.5	36.4 (1.5) *	84.0 (2.6) *
Forbs (%)	6222	8.7 (0.6)	9.0 (1.2)
Dwarf oak (%)	1082.5	23.7 (1.5) *	1.1 (0.5) *
Non-oak shrubs (%)	3161.5	9.8 (1.1) *	0.9 (0.3) *
Grass height (cm)	6241.5	56.1 (1.3)	59.8 (2.7)

Table 1.3. Model selection table for generalized linear models representing the influence of vegetation on Florida Grasshopper Sparrow nest site selection at Three Lakes (*n*=91), Osceola County, Florida in 2014-2016. Models are ranked according to the difference in Akaike Information Criterion score corrected for small sample size (AICc) from the lowest scoring model within each of three stages in a hierarchical, additive selection process. Models shown here are highly supported models (ΔAICc $\leq$ 2) plus the null (intercept only) and full models at each step.

Model	*k*	ΔAICc	w_i	*logLikelihood*
Stage 1: Ground cover variables				
Bare ground	2	0	0.448	-120.875
Bare ground + palmetto trunks	3	0.92	0.283	-120.303
Bare ground + palmetto trunks + litter	4	3.00	0.100	-120.294
Null	1	9.89	0.003	-126.843
Stage 2: Vegetation cover variables				
Bare ground + grass	3	0.00	0.236	-117.660
Bare ground + grass + palmetto leaves	4	1.63	0.105	-117.427
Bare ground + grass + forbs	4	1.75	0.098	-117.491
Bare ground + grass + non-oak shrubs	4	1.85	0.094	-117.540
Bare ground	2	4.36	0.027	-120.875
Bare ground + grass + palmetto leaves + forbs + dwarf oak + non-oak shrubs + site	7	7.43	0.006	-117.122
Stage 3: Height				
Bare ground + grass + grass height	4	0.00	0.57	-116.334
Bare ground + grass	3	0.56	0.43	-117.660

Table 1.4. Model selection table for generalized linear models representing the influence of vegetation on Florida Grasshopper Sparrow nest site selection at the Ranch (*n*=32), Osceola County, Florida (2014-2016). Models are ranked by using the difference in Akaike Information Criterion score corrected for small sample size (AICc) against the lowest score. Models shown here are top models only (ΔAICc ≤ 2) plus the null (intercept only) and full models in three stages in a hierarchical, additive selection process.

Model	*k*	ΔAICc	w_i	*logLikelihood*
Stage 1: Ground cover variables				
Null	1	0.00	0.707	-44.361
Litter	2	1.76	0.293	-44.175
Stage 2: Vegetation cover variables				
Null	1	0.00	0.213	-44.361
Forbs	2	0.85	0.139	-43.722
Grass	2	1.07	0.125	-43.830
Forbs+ grass+ oak+ non-oak shrubs	5	6.24	0.015	-42.995
Stage 3: Height				
Null	1	0.00	0.544	-44.361
Grass height	2	0.35	0.456	-43.471

Table 1.5. Model selection table for Shaffer logistic exposure models representing the influence of vegetation on Florida Grasshopper Sparrow nest success at Three Lakes and the Ranch (*n*=67), Osceola County, Florida in 2014 and 2015. Models are ranked by using the difference in Akaike Information Criterion score corrected for small sample size (AICc) against the lowest score. Models shown here are top models only (ΔAICc≤2) plus the null (intercept only) and full models in three stages in a hierarchical, additive selection process.

Model	*k*	ΔAICc	w_i	*logLikelihood*
Stage 1: Ground cover variables and Site				
Null	1	0.00	0.301	-100.299
Saw palmetto trunk	2	1.19	0.166	-99.869
Litter	2	1.82	0.121	-100.185
Site	2	2.01	0.110	-100.283
Litter + bare ground + saw palmetto trunks	4	5.16	0.023	-99.774
Stage 2: Vegetation cover variables				
Null	1	0.00	0.121	-100.299
Non-oak shrubs	2	0.51	0.094	-99.531
Forbs	2	1.03	0.072	-99.791
Palmetto leaves	2	1.15	0.068	-99.852
Forbs + non-oak shrubs	3	1.49	0.057	-98.987
Palmetto leaves + non-oak shrubs	3	1.57	0.055	-99.025
Grass	2	1.78	0.050	-100.165
Dwarf oak	2	1.99	0.045	-100.272
Non-oak shrubs+ palmetto leaves+ forbs+ dwarf oak+ grass	6	6.59	0.004	-98.364
Stage 3: Height and Visual Obstruction				
Null	1	0.00	0.367	-99.155
Visual obstruction	2	0.28	0.318	-98.275
Grass height	2	1.27	0.194	-98.768
Visual obstruction + grass height	3	2.23	0.120	-98.213

Figure 1.1. Dry prairie habitat at Three Lakes Wildlife Management Area, Osceola County, Florida.

Figure 1.2. Cattle pasture habitat at the Ranch, Osceola County, Florida.

Figure 1.3a. Modeled estimates of the probability that a plot would be selected for nest placement based on the percent cover of bare ground. Dotted lines are upper and lower 90% confidence intervals.

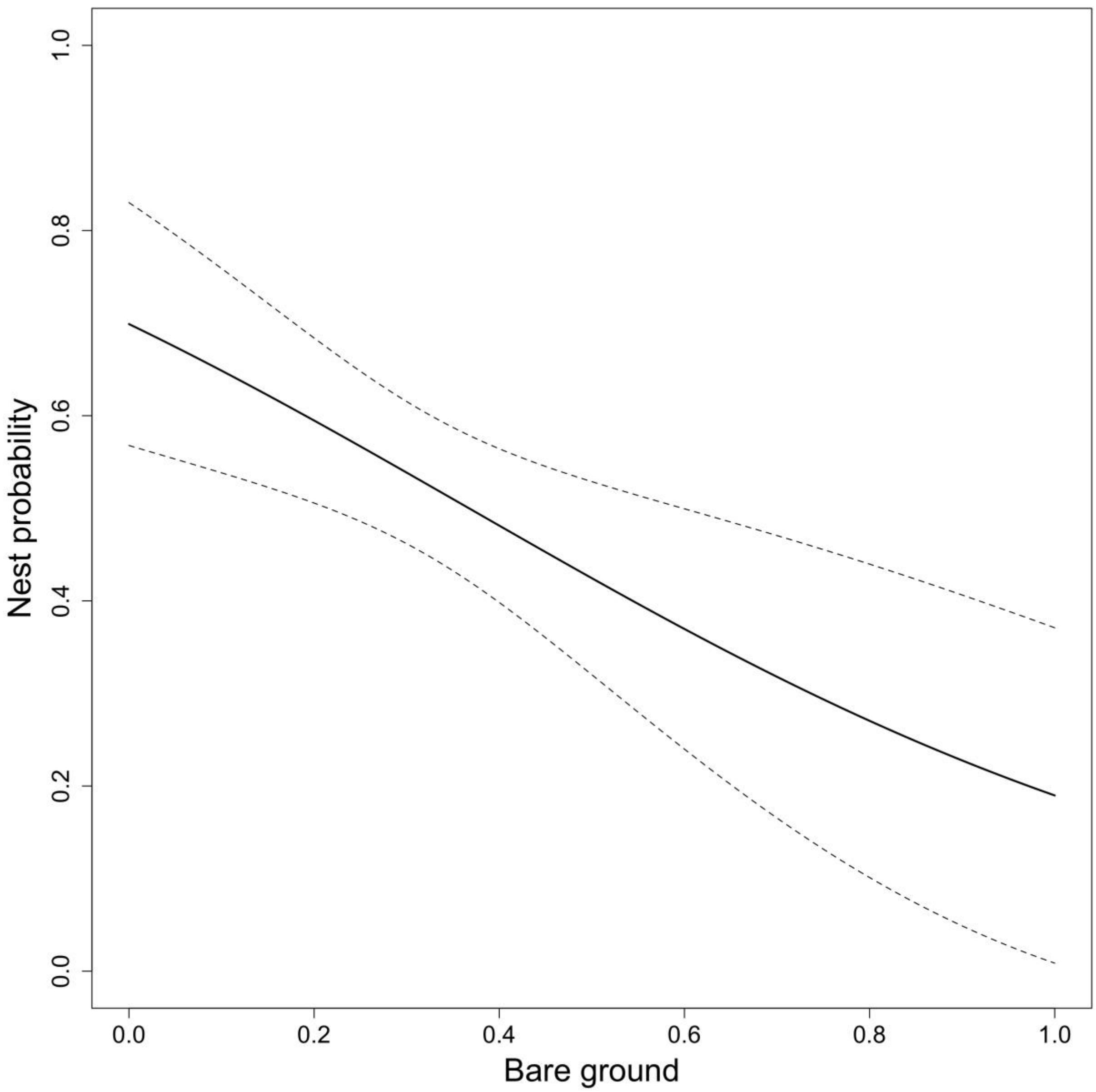
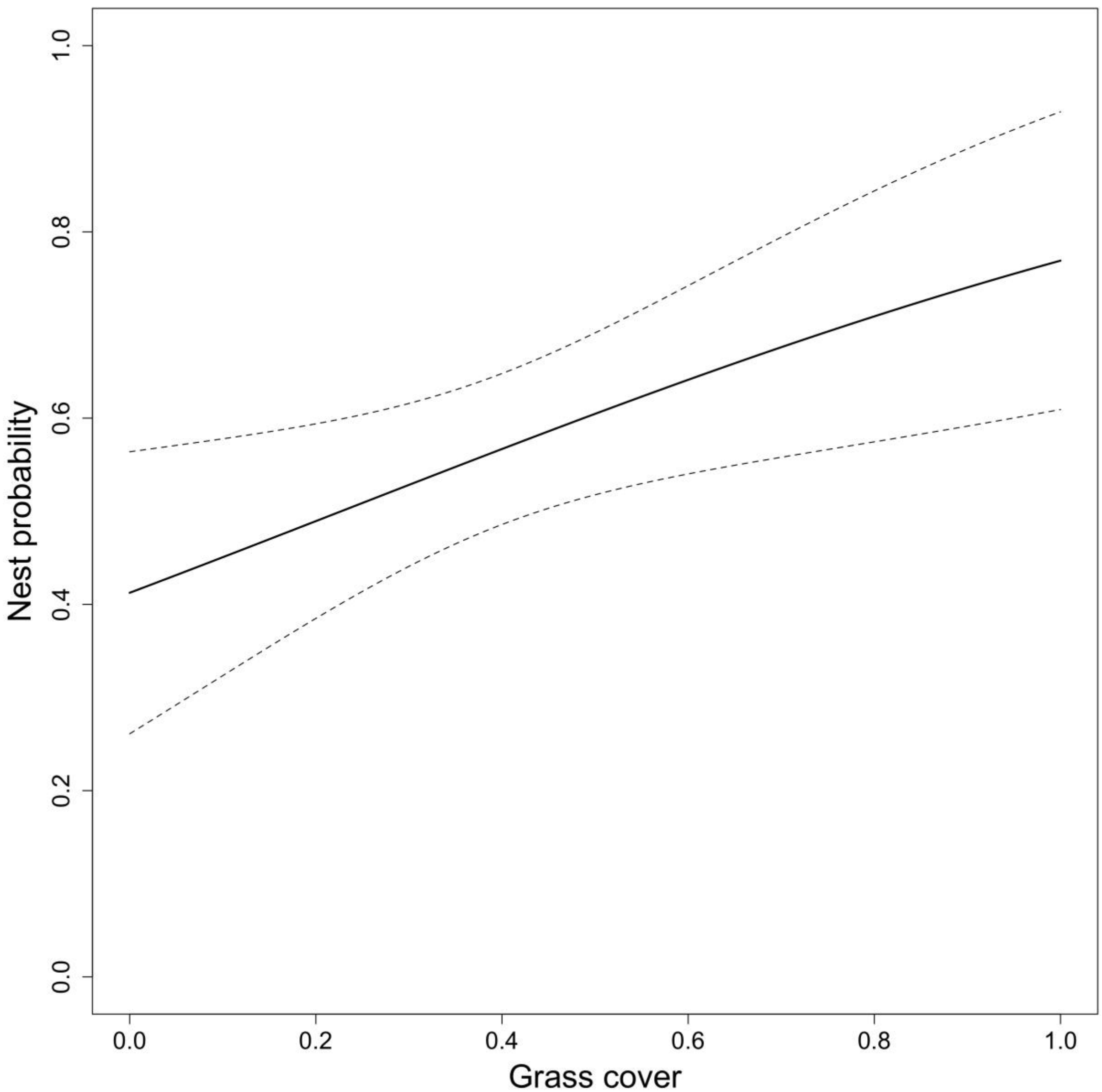


Figure 1.3b. Modeled estimates of the probability that a plot would be selected for nest placement based on the percent cover of grasses. Dotted lines are upper and lower 90% confidence intervals.



Chapter 2: Prescribed fire frequency and season influences arthropod abundance and Florida Grasshopper Sparrow occupancy

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Abstract

Availability of food resources is an important element in determining where birds establish territories. The Florida Grasshopper Sparrow is a critically endangered bird endemic to dry prairie in Central Florida. This subspecies prefers prairies burned < 2 years ago, but it is not yet clear which factors drive this preference. We tested the hypotheses that the most recently burned prairies would contain more arthropods and be more likely to be occupied by Florida Grasshopper Sparrows. We also tested the hypothesis that Florida Grasshopper Sparrow occupancy area would be higher in prairies with greater arthropod abundance. We assessed arthropod abundance and occupancy during 2015 and 2016 at two sites in Osceola County, Florida containing the two largest remaining populations of Florida Grasshopper Sparrows. Fire units burned during the current dormant season (Feb.-Mar.) were used by Florida Grasshopper Sparrows in 2015 and 2016 more than expected based on the availability of that fire treatment on the landscape. In 2015 prairies burned during the current transition season (Apr.- Jun.) had the highest abundance of arthropods, but in 2016, when there were no transition season fires, prairies burned during the current dormant season had the highest abundance. We also found a positive relationship between the density of Florida Grasshopper Sparrow occupancy and arthropod abundance during a year when arthropod abundance was reduced (2016). The difference in

arthropod abundance between the different fire treatments suggests that resource availability may be one reason that Florida Grasshopper Sparrows settle in recently burned habitat.

Introduction

Birds may rely on a number of factors when determining where to establish territories, including the vegetative composition of the landscape, food availability, and predator avoidance (Hamer *et al.*, 2006). Territories often contain resources such as food, access to mates, and nesting sites, and high-quality resources generally lead to higher fitness (Matthysen, 1990; Naef-Daenzer *et al.*, 2000). The quality of a territory is often directly determined by food availability (Golawski and Golawska, 2008) because it can effect clutch size (Sutter and Ritchison, 2005), offspring growth and number of nest attempts (Rodenhouse and Holmes, 1992), or number of fledglings (Kaspari, 1991). Decreased food availability can also have important population and community level impacts. For example, decreased arthropod abundance, which is a primary food resource for many temperate, territorial birds during the breeding season, results in a lower abundance and diversity of birds in the area (Hickman *et al.*, 2006). Thus, understanding food availability is important if we wish to evaluate territory selection and habitat quality for species of conservation concern.

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is a critically endangered non-migratory bird endemic to dry prairie of southcentral Florida (Delany *et al.*, 1985; Vickery, 1996). Territories are maintained throughout the breeding season (Mar. – Aug.) and are found predominantly in habitat burned during the current or preceding year (Walsh *et al.*, 1995; Shriver and Vickery, 2001; Hewett Ragheb *et al.*, 2019a). This preference for recently burned dry prairie is presumed to result from the maintenance of bare ground by fires, which is thought to be optimal for foraging on arthropods, although this hypothesis has not been studied in depth (Delany *et al.*, 1985). Florida Grasshopper Sparrow populations have been declining since the 1990s (Florida Grasshopper Sparrow Working Group, unpublished data), but it is unclear if overall arthropod abundance or species composition has changed during that time.

Dry prairie habitat in Florida is dominated by pyrogenic plants, historically adapted to frequent fires set by lightning (Platt *et al.*, 2006). These lightning-strike fires predominantly occurred during the transition period (Apr. – Jun.) between the winter dormant season (Dec. – Mar.) and the summer growing season (Jul. – Aug.; Abrahamson, 1984; Platt et al. 2015). Modern dry prairie is managed by prescribed fire every 1-3 years, often during the dormant or transition seasons, which maintains the prairie in an early successional stage (Delany *et al.*, 2002; Platt *et al.*, 2015). The season of a prescribed fire can have a large impact on plant diversity and biomass. For example, the dominant dry prairie grass, wiregrass (*Aristida stricta*) flowers and goes to seed only after spring fires (Streng *et al.*, 1993; Brockway and Lewis, 1997). The season of prescribed fire may also have an impact on Orthoptera (grasshopper, crickets, and katydids) populations, which are presumed to be the primary food source for Florida Grasshopper Sparrows (Vickery, 1996; Delany *et al.*, 2000; Korosy, 2013), because certain age classes of grasshoppers may be more sensitive to the direct effects of fire (Knight and Holt, 2005). Because Florida is relatively warm year-round, many grasshoppers overwinter as both adults and nymphs (Squitier and Capinera, 2002), and the flightless nymph stages may be less likely to survive winter season fires.

In order to restore Florida Grasshopper Sparrow populations, we need to better understand the relationship between prescribed fire management and arthropod abundance, and whether this relationship influences sparrow breeding habitat selection. Currently, the largest population of Florida Grasshopper Sparrows is found at Three Lakes Wildlife Management Area (hereafter Three Lakes), and this site contained only 64 singing males and an unknown number of females in 2015 (Florida Grasshopper Sparrow Working Group, unpublished data). Three Lakes consists of dry prairie habitat managed by prescribed fire on a 2-year cycle. The second largest population is pasture habitat on a private cattle ranch (hereafter the Ranch) that is regularly mowed (every 2-3 years), grazed by cattle, and only infrequently burned. We assessed arthropod abundance during the middle of the breeding season to address the following questions at Three Lakes: 1) which fire treatments are preferred for sparrow territory occupancy?; 2) how do different fire treatments affect arthropod abundance?; 3) is arthropod abundance associated with sparrow occupancy area?; and 4) is there a direct relationship between arthropod abundance and sparrow occupancy density? We also sought to address whether arthropod abundance was associated with sparrow occupancy area at the Ranch and to compare abundance between study sites. Results from this study may help to explain one factor that attracts the Florida Grasshopper Sparrows to certain fire treatments and could provide insights into appropriate land management policies to help ensure adequate food resources for this endangered sparrow.

Methods

Study sites

We assessed arthropod abundance at two study sites that contain the largest remaining populations of Florida Grasshopper Sparrows: Three Lakes (27°37’ N 81°19’ W) and the Ranch, both in Osceola County, Florida. Three Lakes (approximately 3,000 ha) contained 1,728 ha of remnant dry prairie habitat managed by the Florida Fish and Wildlife Conservation Commission. Dry prairie in south-central Florida is treeless, flat grassland populated mainly with shrubs such as saw palmetto (*Serenoa repens*) and dwarf oak (*Quercus minima*), grasses such as wiregrass (*Aristida stricta*) and broomsedge bluestem (*Andropogon virginicus*), as well as numerous herbaceous forbs (Florida Natural Areas Inventory 2010). The Ranch (1,012 ha) was semi-improved cattle pasture, historically planted with non-native bahiagrass (*Paspalum notatum*), but has now been colonized by native prairie plants, such as saw palmetto and broomsedge bluestem (G. Hendricks, Florida Eco Enterprises, LLC, unpublished data).

Three Lakes consisted of 64 separate prescribed fire management units ranging from 12-109 ha. Individual units were burned on a staggered 2-3-year rotation, so that in any year there were units burned that year, the previous year, and 2 years prior. These fire units were separated by fire breaks or gravel roads. Prescribed fires occurred during a portion of the dormant season (Feb. – Mar.), transition season (Apr. – Jun.), and growing season (Jul. – Aug.; Shriver and Vickery, 2001; Hewett Ragheb *et al.*, 2019a). Not all fire units were burned in equal numbers in any given year and not all were represented each year, as fire regimes depended on management decisions and weather.

The Ranch was divided into management units (range = 176-493 ha) separated by breaks or roads and consisted of semi-improved pasture habitat interspersed with small stands of trees and ponds. Management units at the Ranch were mowed every 2-3 years during the dormant season (Jan. – Apr.) to maintain the habitat for cattle. Cattle density throughout the site was approximately 1 animal per 8-9 ha (G. Hendricks, Florida Eco Enterprises, LLC, unpublished data). Prescribed fire at the Ranch was applied irregularly during the dormant season only. A small portion of the site (approx. 168 ha) was burned in 2015 and then grazed, and another portion was burned in 2016 (approx. 280 ha) but was not grazed during the breeding season (E. Myers, pers. comm.).

Arthropod Sampling

To estimate arthropod abundance, we sweep net sampled along transects in June and July (2015, 2016) at both sites. We established 18 transects within 18 different fire units at Three Lakes with an east-west orientation. Sixteen transects were 200 m in length and two transects were 100 m in length (fire units that were > 30 ha contained transects 200 m in length and burn units < 25 ha had transects 100 m in length). We located transects 100 m from a road or fire break to minimize potential edge effects and only sampled in dry prairie habitat. We avoided transects through wetlands or ponds where Florida Grasshopper Sparrows were unlikely to occur. We located transects in at least one unit representing each of the available fire treatments each year (Table 1). The same fire units were surveyed in both years, except for two units that were flooded and inaccessible in 2016. The flooded fire units were replaced with units that were also burned two years earlier during the growing season. Although the same fire units were surveyed both years, they represented different fire treatments each year due to the staggered prescribed fire schedule. As a result, they were not treated as replicates of the same experimental unit. For example, if a fire unit was burned in February 2015 (current year dormant season) then in 2016 that unit would become classified as previous year dormant season. We assumed that the abundance of arthropods within a fire unit would be relatively uniform throughout the fire unit, regardless of whether it was within or outside a territory.

We established 17 arthropod sampling transects at the Ranch, each 100 m in length. This site was smaller than Three Lakes and had fewer and more homogenous management units. Therefore, we placed transects based on proximity to a male's occupancy area rather than targeting units with specific management treatments. We placed eight transects in areas that overlapped several males and nine transects ≥ 300 m away from any male's occupancy area in similar, but unoccupied adjacent habitat. Transects were oriented east-west, except for two transects that were oriented north-south to avoid hammocks and very wet habitat, because we do not have evidence that Florida Grasshopper Sparrows forage in those areas. The same transects were used for both 2015 and 2016.

We used a standard 38 cm diameter canvas sweep net for arthropod sampling. Sweep net sampling was done with one sweep per 1 m interval for each transect with the total transect length distance recorded using a handheld GPS unit (Garmin 72H). We sweep net sampled while walking and kept the nets as close to the ground as possible while sweeping quickly at an 180° arc (O'Neill *et al.*, 2002, Gardiner *et al.*, 2005). This enabled us to collect the majority of the jumping orthopterans, as well as some crawling arthropods (such as Lepidoptera larvae and spiders). Arthropods were collected into a plastic specimen bag after every 20 - 40 sweeps. Southern two-striped walking sticks (*Anisomorpha buprestoides*) adults were counted and then returned alive to the habitat, since it is unlikely that the adults are consumed by Florida Grasshopper Sparrows due to their large size (ca. 40-67 mm in length). The counts were used in determining frequency of orders present at both sites but were not included in arthropod abundance for prey analysis. Specimen bags were put into a cooler with ice packs while in the field and placed into a freezer at approximately -18 C once the sweep netting was completed for the day. Arthropods were separated from vegetation and other debris by hand after the specimen bags had been frozen at least 24 hours. Arthropods were identified to order, then counted. Total counts for June and July were pooled for each transect. Arthropods were keyed out when identification was questionable or counted as "other" if identification to order was not possible (Choate 2011, Florida Insect Family Keys).

At both sites, arthropods were collected between 1000 hrs. and 1700 hrs. This time frame allowed the dew on vegetation to dry and ensured that arthropods were active. We only sweep net sampled on sunny or cloudy days with no rain, and only when winds were less than 15 km per hour. Wind speed was approximated using descriptions from the Beaufort Scale (1970).

Occupancy Area Assessment

Both of the study sites were systematically searched along a point count grid throughout the breeding season. All males were individually marked with a unique color-band combination and an aluminum USGS band. Territories were visited repeatedly during the breeding season and perch points (ca. 1-5) were recorded with a handheld GPS unit at each visit. The perch points were collected opportunistically during ongoing demographic studies and we did not systematically collect enough territory points to adequately identify territory boundaries (Odum and Kuenzler 1955).

Individual fire units were distinct and separated by either a road or fire break, but some Florida Grasshopper Sparrows were found in multiple adjacent fire units, since they were often the same fire treatment (e.g. current dormant). Occupancy area at Three Lakes was assessed as male presence in each fire unit as determined by singing perch points collected during May, June, and July. In 2015, 34% of males had occupancy area in more than 1 fire unit and in 2016, 46% of males had occupancy area in more than 1 fire unit. If a male occupied area in more than 1 fire unit, we used singing perch points and counted the male in each fire unit that contained >1 perch point during May, June, and July, since the male utilized habitat in each fire unit (mean points collected in May-July 2015 per male= 14, range= 4 – 43; 2016 per male= 16, range= 3 – 27). Males with perch points only in May were omitted from the analysis because we could not be certain as to their location in June and July.

Statistical Analysis

Fire Unit Occupancy Area

We used a multinomial goodness of fit test to determine if the distribution of Florida Grasshopper Sparrow occupancy area in the different fire treatments varied from expected based on availability at Three Lakes for each year. The expected distribution for the fire treatments was based on the proportion of area available for each fire treatment within the total dry prairie habitat of the site (see methods from Hewett Ragheb *et al.,* 2019a for more detail). The different fire treatments were based on the month and year of the most recent burn for each year (see Table 1). The multinomial test was completed using RStudio package *EMT* (Uwe, 2013). The occupancy area for each male for this test only is the fire treatment that has the most singing perch points in May, June, and July. If two fire treatments had an equal number of perch points collected, we assigned the male in the fire treatment with the largest occupancy area measured in square meters from a convex polygon created using perch points. We also calculated selection ratios, which represent the resource use divided by the proportion available, to determine which burn treatments were used more than expected (Manly 2010). A selection ratio >1 indicated that the burn treatment area was used more than expected and <1 indicated that it was used less than expected based on availability. If the 95% confidence interval of the selection ratio values included 1 then we determined that the selection ratio was not significant. We calculated selection ratios using RStudio package *adehabitat* (Calenge, 2006).

Fire Treatment and Arthropod Abundance

We used an ANOVA to test if the different fire treatments (current transition, current dormant, previous transition, previous dormant, and 2 years previous growing) and year affected arthropod abundance and if there was an interaction between fire treatment and year. We calculated effect sizes using eta squared to determine the variation attributed to each variable. We determined a small effect as between 0.01 – 0.06 and a large effect as anything > 0.14 (Cohen 1988). We calculated post hoc Tukey Honest Significant Differences values with an alpha level of 0.05 to determine which fire treatments were significantly different from each other after accounting for year. We used the *stats* package in R (R Core Team 2019) for running the ANOVA and the *multcomp* package in RStudio (Hothorn *et al*., 2008) for posthoc tests.

Florida Grasshopper Sparrow Occupancy and Arthropod Abundance

We used a generalized linear model with binary distribution and logit link function to determine if the presence of at least one portion of a Florida Grasshopper Sparrow male occupancy area within a fire unit at Three Lakes and the Ranch varied with arthropod abundance. Occupancy area presence was assessed by male usage determined by singing perch points recorded during May – July within each fire unit at Three Lakes. At the Ranch we determined occupancy area presence if a male had perch points located within 300 m of a transect. We created five models for each site, each with the presence or absence of Florida Grasshopper Sparrows as the binary response variable and the abundance of all arthropods per sweep (orders pooled) or the abundance of the Orthoptera, Coleoptera, Araneae, or Lepidoptera orders individually as the predictor variables. Florida Grasshopper Sparrows have been documented to consume species from the following orders Orthoptera, Araneae, Coleoptera, Lepidoptera, and Odonata (Delany *et al.*, 2000; Korosy, 2013), however, Odonata were rarely captured in our sweep nets and were therefore not retained as an important prey item in this study. We tested the four arthropod orders in separate models because arthropod abundance and the abundance of individual orders were correlated ($r_2 \geq 0.70$). During preliminary analysis we used a generalized linear mixed model and added year as a random effect, but the variance was 0 or close to 0, therefore, the random effect was excluded and used generalized linear models instead. We created and compared models using the *lme4* package in RStudio (Bates *et al*., 2015) and *stats* package (R Core Team 2019).

We assessed relative model support by using the ΔAICc (Akaike Information Criteria, corrected for small sample size; Burnham and Anderson, 2002). If ΔAICc was within 2 values, we examined the 95% confidence interval of the parameter estimates and if they included 0, we determined the parameter to be uninformative (Arnold, 2010). We validated model fit of the top model using the Hosmer-Lemeshow Goodness of Fit test (α= 0.05) in the *ResourceSelection* package in RStudio (Lele *et al*., 2019).

Florida Grasshopper Sparrow Occupancy

We used linear regression models to examine the effect of arthropod abundance on Florida Grasshopper Sparrow male occupancy density in the sampled fire units at Three Lakes each year (2015, 2016). We defined Florida Grasshopper Sparrow male occupancy density as the total number of males that occupied each fire unit for at least one day for each fire unit sampled per hectare. We used two models each year, the first with Florida Grasshopper Sparrow male occupancy density as the response variable and total arthropod abundance (average per sweep; all orders pooled) as the predictor variable. The second model was a multiple linear regression model with Florida Grasshopper Sparrow occupancy density as the dependent variable and the abundance of individual arthropod orders (Orthoptera, Coleoptera, Araneae, or Lepidoptera) in each burn unit as the independent variables. We created and analyzed models using the *stats* package (R Core Team, 2019). We used a log transformation to normalize the data because the Florida Grasshopper Sparrow response variable was not normally distributed and skewed to the right due to the large number of zero entries. We assessed the effect size using Cohen's d using the thresholds 0.2 as small, 0.05 as medium, and 0.08 or greater as large (Cohen 1988).

Results

Arthropod Abundance

We identified 10 different arthropod orders from both sites, including: Araneae (spiders), Coleoptera (beetles), Hemiptera (true bugs), Lepidoptera (butterflies and moths, including larvae), Mantidae (praying mantis), Odonata (dragonfly and damselfly), Orthoptera (grasshopper, crickets, and katydids), and Phasmatodea (walking sticks; Table 2). We grouped the two least common arthropod orders (Hymenoptera - bees, wasps, and ants, Diptera - flies, and any unidentified arthropods as "Other" (Table 2). The mean arthropod abundance (arthropods per sweep) in 2015 for all transects at Three Lakes was 0.77 (SE = 0.05) and at the Ranch was 1.20 (SE = 0.10: t= 3.88, P< 0.001). The mean arthropod abundance in 2016 for all transects at Three Lakes was 0.52 (SE = 0.05) and at the Ranch was 0.87 (SE = 0.13: t= 2.43, P= 0.02). Orthoptera was the most abundant order at Three Lakes (35.16% and 28.6%, in 2015 and 2016, respectively) while Hemiptera was most abundant order at the Ranch (34.04% and 39.6%, in 2015 and 2016, respectively; Table 2).

Fire Unit and Occupancy Area

At Three Lakes, Florida Grasshopper Sparrow males did not occupy area in fire treatments as expected based on availability (Table 3). In 2015 and 2016, male Florida Grasshopper Sparrows occupied area in current dormant season fire treatments more than expected based on availability (Table 4a, b). In 2015 males used previous transition and 2 year fire treatments less than expected based on availability. In 2016 males used previous transition and previous dormant less than expected. No males used 2 year fire treatments in 2016.

Fire Treatment and Arthropod Abundance

Arthropod abundance varied significantly by year and fire treatment. Fire units burned during the current transition season in 2015 had the most arthropods (Fig. 1, Table 5). However, the interaction between fire treatment and year was not significant ($P = 0.498$; Table 5), so we analyzed the main effects of fire treatment and year separately in post-hoc tests. Effect sizes (using eta-squared) for the variables tested were: year (0.25), fire treatment (0.29), both of which had a large effect and the interaction (0.03), which has a small effect. Post hoc tests showed that units burned in the current transition season had more arthropods than units burned in the current dormant season, previous transition season, previous dormant season, and growing season 2-years prior.

Florida Grasshopper Sparrow Occupancy and Arthropod Abundance

The arthropod abundance did not predict the presence of Florida Grasshopper Sparrow male occupancy area in a fire unit at Three Lakes in 2015 and 2016. The top model was the null model and had the lowest ΔAICc score (Table 6). The model containing Araneae was within 2 AICc units of the top model (AICc = 51.5 vs. 50.6; Table 6), but the 95% CI for the intercept included 0 (-18.86, 4.39; Arnold, 2010).

At the Ranch, total arthropod abundance did not predict the presence of Florida Grasshopper Sparrow males' occupancy area (Table 7). The null model had the lowest ΔAICc value and although the models with total arthropods, Orthoptera and Lepidoptera were within 2 AICc units (ΔAICc = 48.8 vs 50.5, 50.5, 50.7, respectively), all had 95% CI that included 0, so we determined that they were all uninformative (total arthropods= -0.82, 2.11; Orthoptera= -1.41, 3.56; Lepidoptera= -26.67, 54.91; Arnold, 2010).

Florida Grasshopper Sparrow Occupancy

There was no relationship between Florida Grasshopper Sparrow occupancy density and arthropod abundance (orders pooled) in each fire unit at Three Lakes in 2015 (adjusted $r^2 = -0.06$, $P = 0.88$, Fig. 2), but there was a positive relationship in 2016 (adjusted $r^2 = 0.37$, $P = 0.006$, Fig. 3). The effect size (Cohen's d) for 2015 was medium (0.64) and for 2016 was large (0.86). In both years, there was no relationship between Florida Grasshopper Sparrow occupancy density and the abundance of the arthropod orders ($P > 0.09$) at Three Lakes.

Discussion

Our results showed that Florida Grasshopper Sparrows at Three Lakes occupied dry prairies burned during the current dormant season (Feb. – Mar.) more often than expected based on fire treatment availability. Our finding corresponds with results from previous studies (Delany *et al.*, 1985, 2002; Perkins *et al.*, 2009; Hewett Ragheb *et al.*, 2019a). Total arthropod abundance at Three Lakes was highest in dry prairies burned during the current transition season in 2015 and highest in current dormant season in 2016. Spring or summer fires show little fire induced mortality because generally most arthropods are in more mobile adult stages able to escape the fire and herbivorous arthropods respond positively to the increased herbaceous growth following fires (Hartley *et al.*, 2007, Johnson *et al.*, 2008).

Orthopterans were the most frequently captured arthropod at Three Lakes, an order that was previously found to make up the majority of a Florida Grasshopper Sparrow's diet (Delany *et al.*, 2000; Korosy, 2013). In contrast, at the Ranch Hemiptera was the order most frequently captured during both years, but Orthoptera was second in 2015 and Coleoptera second in 2016. The majority of Hemiptera collected at the Ranch were seed bugs (family Lygaeidae). Delany et al. (2000) showed evidence of Florida Grasshopper Sparrow fledglings consuming one species from the order Hemiptera, the two-lined spittle bug (*Prosapia bicincta*), but there was no direct evidence of them eating any other Hemiptera. Orthoptera and total arthropod abundance were higher overall at the Ranch compared with Three Lakes, a potential consequence of the amount of grass and grazing at the former site. Grazing and burning in a grassland increases the vegetation heterogeneity and diversity, which in turn increases grasshopper diversity and abundance (Joern, 2005; Anderson, 2006). Many grasshopper species in Florida overwinter as adults (36%), a much greater percentage than at higher latitudes in North America where most overwinter underground in the egg stage (Squitier and Capinera, 2002). Prescribed fires at the Ranch were conducted during the dormant fire season, when adult grasshoppers would be able to escape a fire and may contribute to the higher numbers found at that site.

In contrast to our general finding that arthropod numbers and Florida Grasshopper Sparrow occupancy were most associated with habitats during the first year after a burn, we did not find that arthropod abundance or the abundance of individual orders predicted the presence of Florida Grasshopper Sparrow occupancy area in specific fire units. At Three Lakes, this lack of concordance was most likely due to current transition fire units having had the highest arthropod abundance, but current dormant season fire units having been the ones more likely to contain Florida Grasshopper Sparrow territories. While fires may initially reduce orthopteran populations through direct mortality, the new grass and forb growth after fire can be beneficial to herbivorous arthropods, such as orthopterans. The higher arthropod abundance in current transition fire treatment units may result from the new herbaceous plant growth that happens following a fire (Evans, 1984; Bock and Bock, 1991). Given that arthropods sampled 1-2 years following a fire continued to show differences in abundance in other studies (Kral *et al*., 2017), we assumed that abundance patterns would also be present in our samples, given that the youngest fire units were sampled as soon as three months after a fire. Male Florida Grasshopper Sparrows establish territories in March, and nesting typically begins in April, which is the same time when current transition fire units are burned, so there would likely not be enough vegetated cover for nesting at that time (Hewett Ragheb *et al*., 2019a). There may be differences in arthropod abundances in March and April between the fire treatments that we were not able to distinguish by sampling in June. Wrynecks (*Jynx torquilla*) in Switzerland, for example, were more likely to select territories near higher densities of insect food resources, provided that nest cavities were available (Coudrain *et al*., 2010). In that species, territory settlement patterns appeared to involve a trade-off between food resources and nest site availability, suggesting that birds may need to balance these two factors in particular when choosing where to establish territories. It is not yet known whether the lack of congruence between male Florida Grasshopper Sparrow occupancy and fire treatments with highest arthropod abundance represent a trade-off between food resources and vegetative cover for nesting. It is possible that these birds may be balancing other factors as well, for example, making a choice between leaving an established territory and nest, and moving to a newly burned unit with more food but less cover.

There was a positive relationship between Florida Grasshopper Sparrow occupancy density within a fire unit and arthropod abundance at Three Lakes during 2016, when arthropod abundance was reduced compared to 2015. The fire treatment with the highest arthropod abundance, current transition season, was not available in 2016, but arthropods were lower in the all fire treatments in 2016 vs. 2015. Arthropod abundance was also lower at the Ranch in 2016 vs. 2015, suggesting that 2016 might have been a poor insect year overall. Food limitations can be detrimental to reproductive output and lead to decreased egg production or nesting attempts (Martin, 1987). During years when arthropod abundance is lower it may be especially important to select areas where arthropods are found in higher densities and are therefore easier to capture. The time parents spend searching for prey increases the time spent away from nests and could leave nestlings more susceptible to predators, as shown by a food supplementation study with Song Sparrows (*Melospiza melodia*) (Duncan Rastogi et al. 2006). Red-backed Shrikes (*Lanius collurio*) have been shown to establish territories in habitat having the highest number and biomass of preferred invertebrate food resources so they do not have to travel as far to forage (Golawski and Golawska, 2008). Food resources in grasslands are generally not considered limiting during most years, but there are between-year fluctuations of prey items, which could impact bird species not adapted to consuming multiple different types of prey (Wiens and Rotenberry 1979, Pulliam and Dunning 1987). Our results suggest that during a year when arthropod numbers are lower overall, Florida Grasshopper Sparrows may be more likely to occupy areas where food resources are highest.

Arthropod abundance at the Ranch also did not predict the presence of Florida Grasshopper Sparrow occupancy, which might be due to the higher arthropod abundance (and in particular, Orthoptera) for all of the transects there. Some of the transects with high arthropod abundance may not have had Florida Grasshopper Sparrows present merely because there were not enough birds remaining to occupy all the preferred habitat. Florida Grasshopper Sparrows may be assessing overall arthropod abundance when making breeding habitat settlement decisions (as early as February or March), as Aldredge (2009) found higher abundance of Orthoptera, Araneae (spiders), and Odonata (dragonflies and damselflies) in Florida Grasshopper

Sparrow territories as compared to unoccupied habitat. Greater numbers of arthropods at our semi-improved pasture site are therefore a possible explanation for why this site continues to maintain a small population of Florida Grasshopper Sparrows, despite proving to be less favorable in terms of nesting habitat. The Ranch may thus be acting as an ecological trap because while the available food resources attract Florida Grasshopper Sparrows (Shochat *et al.*, 2005), the population experiences reduced reproductive output as evidenced by low nest survival (5.9% in 2015 for a 21-day cycle; Hewett Ragheb *et al*. 2019b).

Conclusion

Florida Grasshopper Sparrows generally selected breeding habitat burned during the current year, which also contained the highest average arthropod abundance. Although Florida Grasshopper Sparrows are mainly found in native dry prairie habitat, one remaining population also resides in semi-improved pasture adjacent to the dry prairie, while much of this bird's historical range is unoccupied. Previous populations also have been found to exist on pasture adjacent to dry prairie (Delany *et al.*, 1985; Delany and Cox, 1986). One potential reason for Florida Grasshopper Sparrows selecting recently burned habitat is that it contains more arthropods. Selecting breeding habitat, especially during years when food abundance is reduced, appears to coincide broadly with areas having high arthropod abundance, provided that there is also adequate cover for nesting from predators. It is unlikely that the Florida Grasshopper Sparrows are utilizing only one factor (resource availability) when determining breeding habitat (Both and Visser, 2003). The specific timing of prescribed fires in the habitat has an impact on arthropod abundance both directly and indirectly (in plant growth and flowering) and needs further study to ensure that adequate resources are maintained for this critically endangered sparrow.

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Table 2.1. The number of fire units with various fire season treatments available at Three Lakes Wildlife Management Area, Osceola County, Florida (2015-2016). The units sampled for arthropods each year are in parentheses.

Prescribed fire treatment	**Year**	
	2015	**2016**
Current growing	0	0
Current transition	18 (4)	0
Current dormant	20 (4)	24 (11)
Previous growing	0	0
Previous transition	11 (3)	18 (4)
Previous dormant	4 (3)	11 (1)
2 years previous growing	10 (4)	8 (1)
2 years previous transition	0	0
2 years previous dormant	0	0

Table 2.2. The number of arthropods per sweep (by order) collected in 2015 and 2016 at Three Lakes Wildlife Management Area and the Ranch, Osceola County, Florida, pooled for June and July. Frequencies are in parentheses.

	2015		2016	
Arthropod order	**Three Lakes** Number per sweep (frequency)	**The Ranch** Number per sweep (frequency)	**Three Lakes** Number per sweep (frequency)	**The Ranch** Number per sweep (frequency)
Phasmatodea	0.06 (0.3%)	0.17 (0.5%)	0.01 (0.09%)	0.28 (1.0%)
Araneae	3.53 (20.8%)	4.17 (13.6%)	2.69 (21.6%)	3.33 (14.0%)
Odonata	0.09 (0.6%)	0.27 (0.9%)	0.64 (5.0%)	0.94 (3.8%)
Lepidoptera	0.56 (3.5%)	0.38 (1.2%)	0.24 (1.9%)	0.14 (0.6%)
Mantid	0.05 (0.3%)	0.04 (0.1%)	0.04 (0.4%)	0.09 (0.4%)
Coleoptera	2.54 (14.9%)	4.51 (13.4%)	0.86 (7.5%)	5.41 (20.6%)
Hemiptera	2.81 (16.0%)	11.37 (34.0%)	3.39 (27.0%)	9.99 (39.6%)
Orthoptera	5.74 (35.2%)	9.92 (32.0%)	3.43 (28.6%)	3.81 (15.1%)
Ensifera (crickets and katydids)	1.19 (7.3%)	2.36 (7.1%)	1.28 (9.9%)	2.02 (7.9%)
Caelifera (grasshoppers)	4.55 (27.9%)	7.56 (24.9%)	2.15 (18.7%)	1.79 (7.2%)
Other	1.41 (8.4%)	1.18 (4.2%)	0.97 (7.7%)	1.19 (4.7%)

Table 2.3. The proportion of the total available habitat of in each fire treatment out of the total available habitat and the number of Florida Grasshopper Sparrow (FGSP) male occupancy in each at Three Lakes Wildlife Management Area, Osceola County, Florida. The number of male occupancies in the burn units were based on locations in June and July, and in parentheses is the actual number of total males. $\alpha = 0.05$

	2015		2016	
Burn type	Proportion of total area	FGSP male occupancy	Proportion of total area	FGSP male occupancy
Current transition	0.24	11		
Current dormant	0.36	30	0.43	37
Previous transition	0.17	4	0.24	1
Previous dormant	0.08	6	0.23	2
2 years previous growing	0.16	3	0.11	0
n		54 (64 males)		40 (48 males)
P		0.0078		<0.001

Table 2.4a. Selection of fire treatments by Florida Grasshopper Sparrow males for occupancy during 2015 at Three Lakes Wildlife Management Area, Osceola County, Florida. Confidence intervals (±95%) not including 1 are significant.

Fire treatment	Wi (selection ratio)	SE	95% CI (lower)	95% CI (upper)
Current transition	0.857	0.231	0.404	1.310
Current dormant	1.559	0.190	1.187	1.931
Previous transition	0.440	0.212	0.024	0.855
Previous dormant	1.403	0.540	0.345	2.461
2 year	0.351	0.197	-0.035	0.737

Table 2.4b. Selection of fire treatments by Florida Grasshopper Sparrow males for occupancy during 2016 at Three Lakes Wildlife Management Area, Osceola County, Florida. Confidence intervals (±95%) not including 1 are significant.

Fire treatment	Wi (selection ratio)	SE	95% CI (lower)	95% CI (upper)
Current dormant	2.17	0.10	1.98	2.36
Previous transition	0.11	0.10	0.10	0.31
Previous dormant	0.22	0.15	-0.08	0.52
2 year	0.00	0.00	0.0	0.0

Table 2.5. Arthropod abundance by the different prescribed fire treatments sampled and year at Three Lakes Wildlife Management Area, Osceola County, Florida. The post-hoc Tukey results includes columns for the difference in means and the adjusted p-value.

ANOVA	**df**	**F**	**P**
Fire treatment	4	5.76	0.002
Year	1	16.97	0.0003
Fire treatment x Year	3	0.70	0.56
Post-hoc Tukey Honest tests	**Difference**		**P**
Current transition- current dormant	0.301		**0.012**
Current transition- 2 year grow	0.407		**0.0037**
Current dormant- 2 year grow	0.107		0.65
Previous transition-current transition	-0.422		**0.0012**
Previous transition-current dormant	-0.121		0.423
Previous transition-previous dormant	-0.073		0.937
Previous transition- 2 year grow	-0.048		0.999
Previous dormant-current transition	-0.348		**0.023**
Previous dormant- current dormant	-0.048		0.979
Previous dormant- 2 year grow	0.059		0.98

Table 2.6. Model selection table for the influence of arthropod abundance on Florida Grasshopper Sparrow male territory occupancy at Three Lakes Wildlife Management Area, Osceola County, Florida. Models are ranked by ΔAICc values.

Model	*k*	ΔAICc	w_i	logLikelihood
Null (intercept only)	1	0.0	0.33	-24.25
Araneae	2	0.92	0.21	-23.58
Orthoptera	2	2.06	0.12	-24.15
Lepidoptera	2	2.08	0.12	-24.16
Total arthropods	2	2.22	0.11	-24.23
Coleoptera	2	2.22	0.11	-24.23

Table 2.7. Model selection table for the influence of arthropod abundance on Florida Grasshopper Sparrow male territory occupancy at the Ranch, Osceola County, Florida. Models are ranked by ΔAICc values.

Model	*k*	ΔAICc	w_i	logLikelihood
Null (intercept only)	1	0.00	0.34	-23.33
Total arthropods	2	1.68	0.15	-23.04
Orthoptera	2	1.75	0.14	-23.08
Lepidoptera	2	1.95	0.13	-23.17
Coleoptera	2	2.07	0.12	-23.23
Araneae	2	2.23	0.11	-23.32

Figure 2.1. Arthropod abundance in different fire treatments at Three Lakes Wildlife Management Area, Osceola County, Florida in 2015, 2016. Letters above the bars denote the significance of the means, with different letters showing significant differences between pairs of burn treatments determined by ANOVA followed by a post hoc Tukey test. $\alpha = 0.05$

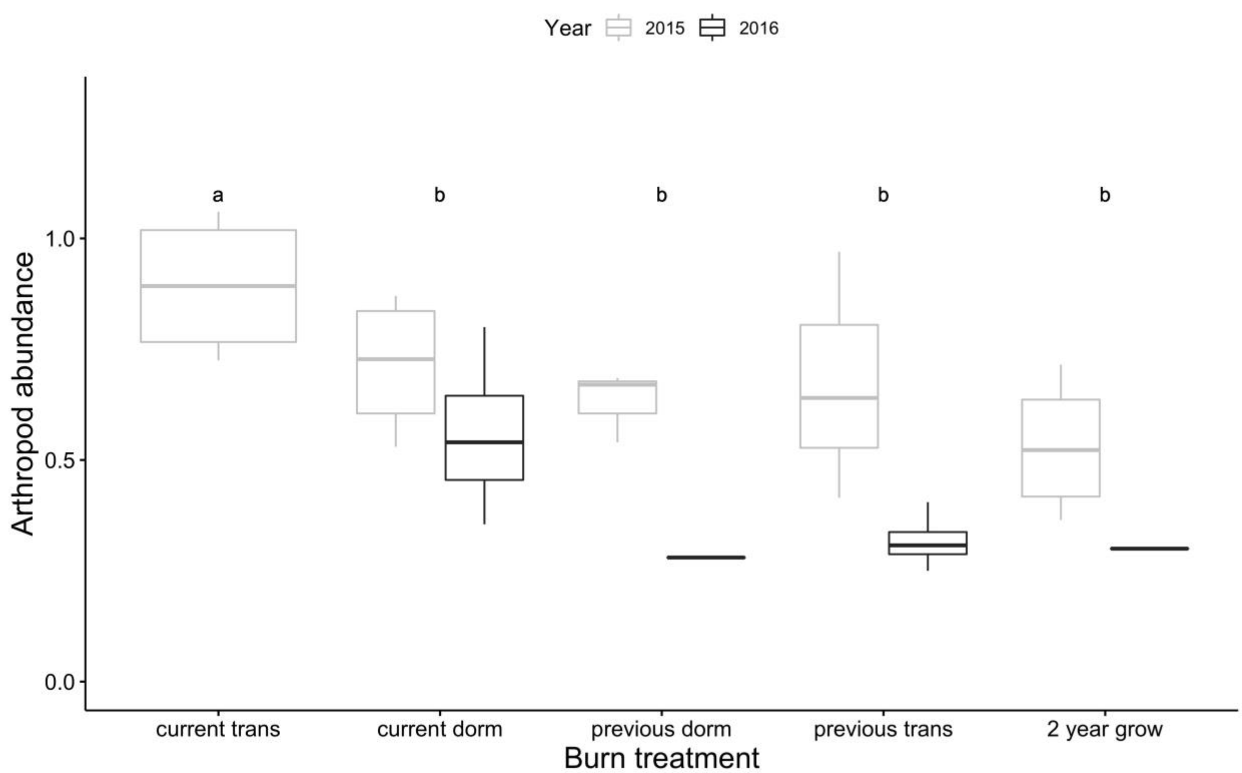


Figure 2.2. Florida Grasshopper Sparrow occupancy density (males per ha) and arthropod abundance (arthropods per sweep) at Three Lakes WMA, Osceola County, FL in 2015.

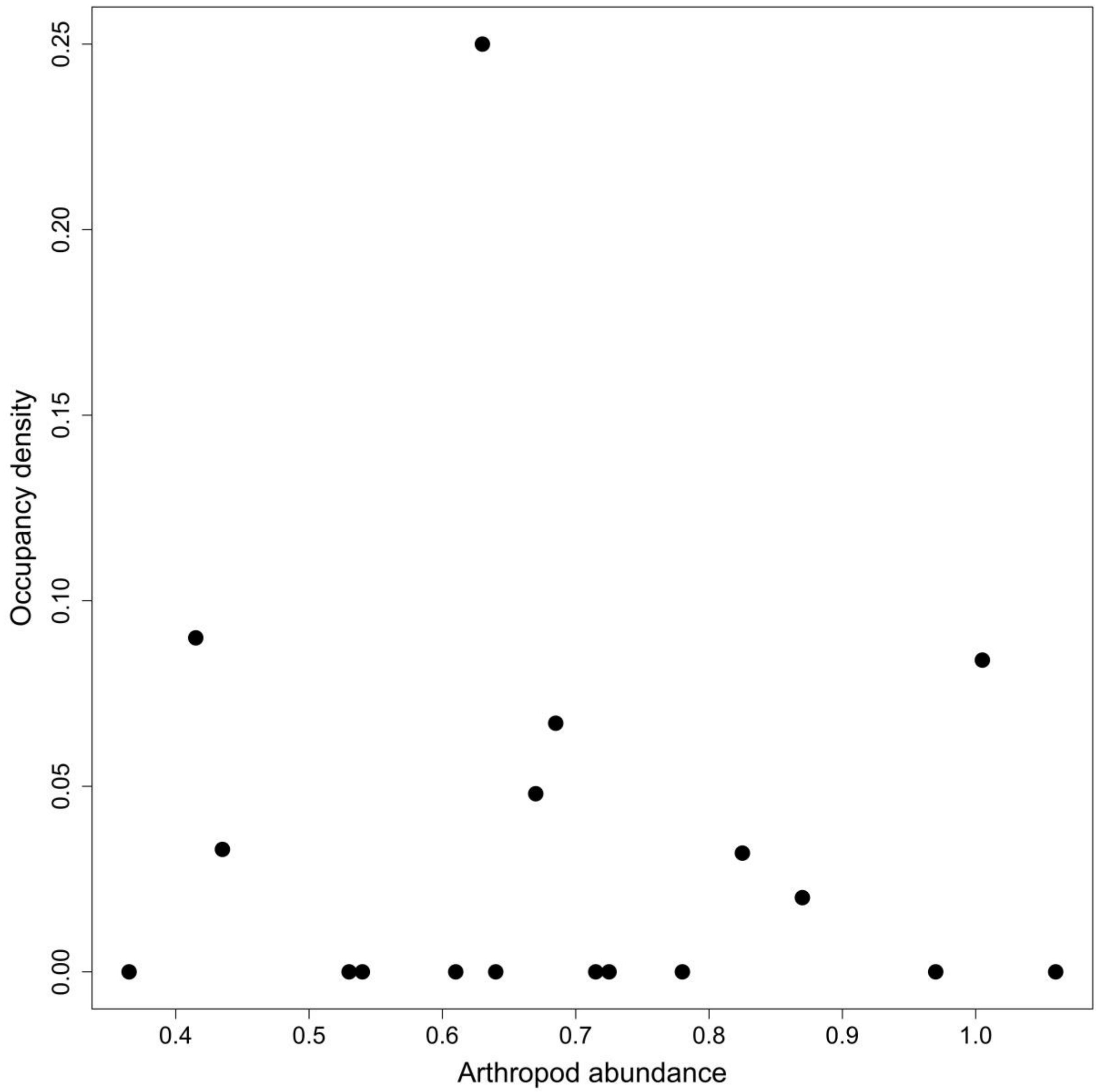
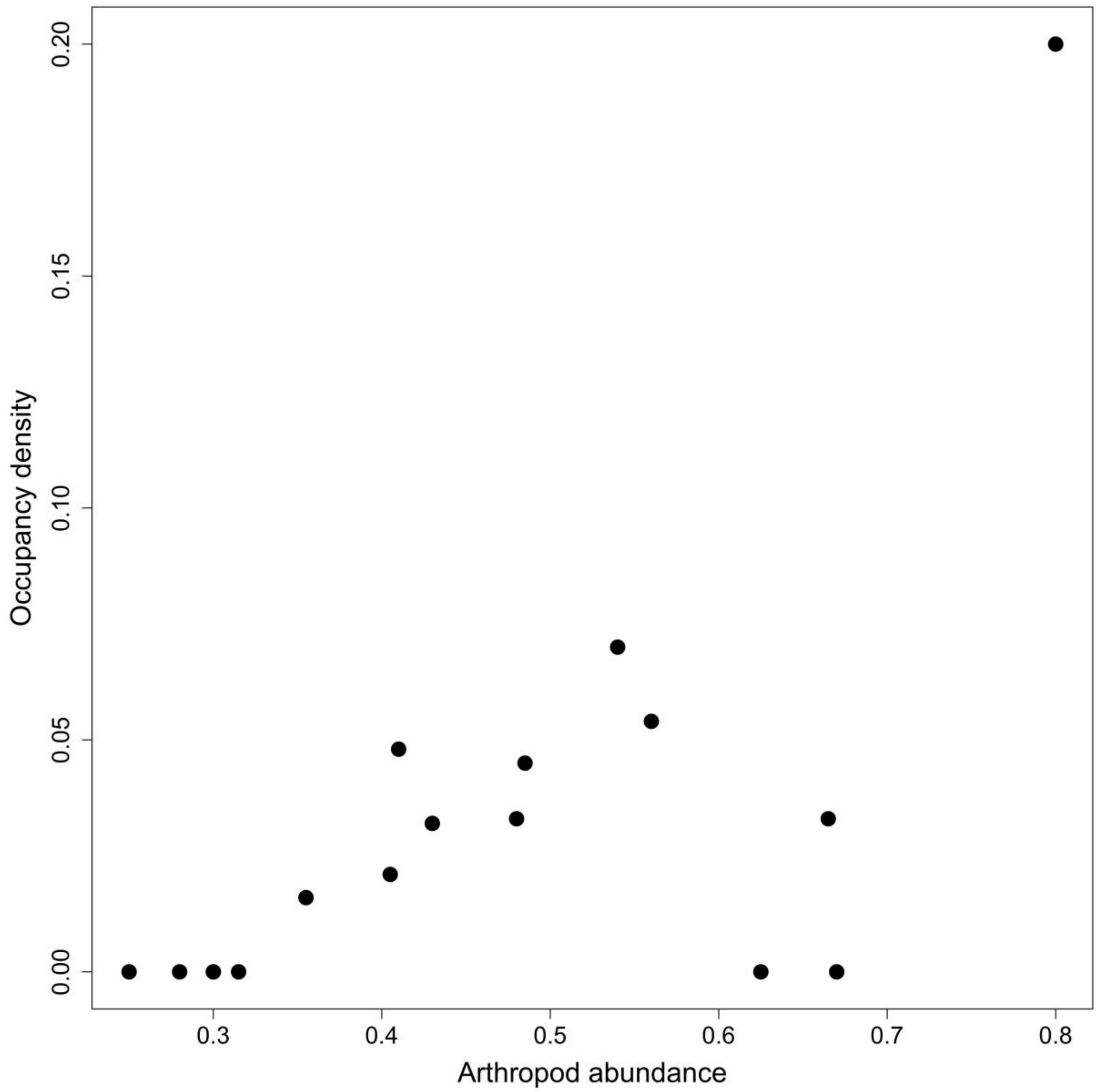


Figure 2.3. Florida Grasshopper Sparrow occupancy density (males per ha) and arthropod abundance (arthropods per sweep) at Three Lakes WMA, Osceola County, FL in 2016.



Chapter 3: Dynamic misclassification models to estimate occupancy after fires for an endangered passerine, the Florida Grasshopper Sparrow

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Abstract

Monitoring populations is critical to understanding occupancy, especially for endangered or threatened species, and is important for determining the effectiveness of land management strategies. The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is a critically Endangered non-migratory grassland bird that has been monitored since the 1990's. The Florida Grasshopper Sparrow resides primarily in early successional dry prairie habitat that is managed by frequent (2-3 years) prescribed fires. Monitoring Florida Grasshopper Sparrows is confounded by the presence of the migratory and winter resident eastern Grasshopper Sparrow (*A. s. pratensis*), which has vocalization and morphological similarities that can lead to misclassifications and erroneous conclusions about land management. Our goal was to determine the impact of fires on Florida Grasshopper Sparrow occupancy at two spatial scales while controlling for the presence of the eastern Grasshopper Sparrow. We used point count data (1996-2011) with Bayesian misclassification occupancy models to evaluate Florida Grasshopper Sparrow occupancy with respect to fires. We found that the probability of detecting Florida Grasshopper Sparrows at point counts decreased after a peak at civil dawn. We also found that the probability of persistence at a point count station decreased as the year since fire increased, but colonization of points was not influenced by temporal patterns of prescribed fire. Our results suggest that the probability of an area remaining occupied by Florida Grasshopper Sparrows is

greatest for recent fires (<1 year) at the larger spatial scale, but there did not appear to be any influence of fire season. During the time period over which these data were collected populations of Florida Grasshopper Sparrows were declining so the number of unoccupied point count stations increased, which may explain the lack of a significant effect of colonization. This is the first long-term study to look at the effect of prescribed burning on Florida Grasshopper Sparrow occupancy that takes into account the presence of wintering eastern Grasshopper Sparrows. Our dynamic occupancy model that accounts for misclassifications provides a more accurate population assessment while incorporating management strategies, which has utility for other species where misclassification might occur.

Introduction

Accurate assessment of populations is important for conservation of species and is often used to determine Endangered or Threatened status (e.g., listed by Endangered Species Act [ESA]). Population change over time is one of the main criteria for deciding the level of protection needed for the ESA. Many different methods exist for surveying populations, but presence-absence models are among the most widely used given their logistical ease with typical time and budget constraints.

Population monitoring surveys for birds and other animals, such as frogs, usually uses an indirect means of assessment such as acoustic cues, as this allows researchers to quickly assess presence or absence of single or multiple species during the breeding season (Gibbs 2000). Conducting surveys using acoustic and visual signals, such as point count assessments for birds, however, can introduce errors in species identification due to mistakes made by surveyors. The use of autonomous recording units (ARUs) or other automated recording/storage devices for acoustic surveys can facilitate the accuracy of species-level assessments, but it is not always possible to employ such devices. When the use of ARUs is not possible or practical, surveying at the most appropriate time of day or year for the target species reduces errors for not detecting a species when it is present (Hochachka et al. 2009). Mistakes in species identification, however, can still occur due to species with vocal similarities or during times when multiple species vocalize simultaneously. Surveys also use visual cues, but neither may be reliable when species or subspecies share vocal or morphological characteristics. Adequate training for surveyors is one way to address this issue, but for species that are not reliably distinguished in the field, training may be inadequate to eliminate misclassifications.

Two common issues that occur during surveys are counting a species as absent when it is present (false negative) and counting a species as present when it is actually absent (false positive), and both can lead to incorrect population estimates (Tyre et al. 2003, McClintock et al. 2010, Farmer et al. 2012). Repeating surveys can reduce false negative rates but with similar species where one may be rarer than the other, repeated surveys are likely to increase false positive rates for the rarer species via misclassification with the more abundant species (Tyre et al. 2003, Gu and Swihart 2004, Miller et al. 2012), i. e. inflate their population estimates. Such misclassifications lead to overestimates of the number of the rarer species, which can also lead to incorrect assumptions about habitat usage, preferences, and management.

Statistical methods for occupancy modeling can improve accuracy of population estimates and account for errors in surveys (Gu and Swihart 2004). MacKenzie et al. (2002) and Tyre et al. (2003) devised a statistical method to increase the accuracy of occupancy estimations by including a detection probability that accounts for missing observations and non-detection of a species. Occupancy models assume that detecting a species where it is not present is not possible. Some controversy exists about whether false positives affect occupancy estimates.

Royle and Link (2006) extended occupancy models to account for misclassifications and concluded that false positives had small effects on occupancy estimates. However, several papers concluded that the effects of false positives are significant (McClintock et al. 2010, Miller et al. 2011), and that even small errors in misclassification can lead to large estimator biases and incorrect conclusions regarding occupancy (McClintock et al. 2010). Thus, this misclassification occupancy model is useful to decrease the impact of such problems.

The critically endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) provides an excellent case study to evaluate the utility of occupancy models that account for misclassification. Between 1998- 2017 Florida Grasshopper Sparrow populations at three public sites declined by 89% (Florida Grasshopper Sparrow Working Group, unpublished data). Given this bird's continuing population decline it is imperative to have accurate population estimates (USFWS Federal Register 1986). Point count surveys have been used since the 1990s to monitor the declining populations at three main sites (Tucker et al. 2010) in central Florida. Point count surveys that target resident Florida Grasshopper Sparrows are confounded with detections of the eastern Grasshopper Sparrow subspecies (*A. s. pratensis*) that winters in the same dry prairie habitat. These two subspecies are not reliably distinguishable in the field. Male Florida Grasshopper Sparrows begin establishing territories in early March, which coincides with the onset of point count surveys. The last round of surveys is completed before the end of July. Eastern Grasshopper Sparrows wintering in the same habitat migrate north in the spring before May and are sometimes singing prior to departure (Vickery 1996). Thus, the potential exists for incorrect identification of Florida Grasshopper Sparrows during point count surveys. As early season nesting attempts are more synchronous, male Grasshopper Sparrows sing more reliably at the beginning of the breeding season and singing decreases in frequency once nesting occurs

(Lohr et al. 2013). Florida Grasshopper Sparrows are therefore more likely to be recorded as present on the first or second round of point counts, even without misidentifications of the wintering eastern subspecies. The presence of eastern Grasshopper Sparrows therefore may bias the results for monitoring populations of the Florida Grasshopper Sparrow (Miller et al. 2015), particularly with respect to the potential for false positives.

An important monitoring goal with the remaining populations of Florida Grasshopper Sparrows is their relationship to habitat use relative to the prescribed fires used to maintain their preferred dry prairie habitat (Walsh et al. 1995, Shriver et al. 1996, Shriver and Vickery 2001, Delany et al. 2002, Hewett Ragheb et al. 2019). Short-term responses to prescribed fires have been examined with respect to their timing, which includes both the time between fires and the month or season in which those fires occurred (Shriver et al. 1996, Shriver and Vickery 2001, Delany et al. 2002). Prescribed fire seasons are split up into 3-season models, which include: dormant (Oct-Mar), transition (Apr-Jun), and growing (Jul-Sept) seasons (Platt et al. 2015). Long-term studies on the responses of Florida Grasshopper Sparrows to fires (including both colonizing new areas or persisting in an area) are needed to fully address the role that fire plays in determining occupancy. Although numerous studies have examined Florida Grasshopper Sparrow responses to fires, none have investigated the effects of fire at multiple spatial scales and using different fire metrics (minimum, maximum, or mean time since fire) to assess the effects on occupancy.

Using historic point count survey results and utilizing a misclassification modeling framework (an extension of the site confirmation model (Chambert et al. 2015b)) we evaluated occupancy over time with respect to fires. We specifically asked if fire seasonality or the time since the last fire influenced Florida Grasshopper Sparrow occupancy, while accounting for the presence of the eastern Grasshopper Sparrow. Our goal was to improve the accuracy of the occupancy population estimates using a Bayesian misclassification framework for the Florida Grasshopper Sparrow, that could then be extended for use with other species where misidentification is an issue. In addition, using the misclassification occupancy model to predict the probability of false positives and false negatives allowed for a more accurate assessment of the population, which has the prospect of aiding both state and federal agencies deciding future prescribed fire management goals.

Methods

Study site

We gathered point count data from 1996-2011 for Florida Grasshopper Sparrows from field sites located in Polk and Highlands Counties in Florida, USA with a mean center located at 27.647188°N and -81.278268°W. We standardized point count survey data from Avon Park Air Force Range (hereafter "Avon Park"), in which three separate sub-populations of Florida Grasshopper Sparrows occur (Delta/ OQ Range = 1224 ha, Charlie/ Echo Range = 2991 ha, and Bravo/ Foxtrot Range = 382 ha). This property contained areas of Florida dry prairie that is considered the primary habitat of Florida Grasshopper Sparrow and prior to the steep declines in the late 1990s and early 2000s, contained one of the largest known extant populations of Florida Grasshopper Sparrows (Pranty and Tucker 2006). Florida dry prairie is flat and treeless habitat dominated by pyrogenic wiregrass (*Aristida stricta*), shrubs such as saw palmetto (*Serenoa repens*), and dwarf oak (*Quercus minima*), and numerous herbaceous forbs. Avon Park was also lightly grazed by cattle at 1 cow / calf per 8 ha until 2013. From 1998 to 2003, the population on this property declined from 255 birds to 2 birds in 2012 but rebounded to 12 birds by 2019 (R.

Bowman, unpubl. data). Despite this decline, the property remains an important source of habitat and potential habitat for this subspecies' recovery.

Point count surveys

We selected a subset of 173 point count locations at Avon Park where adequate long-term fire data existed. We also selected point count locations where surveys were conducted for at least 90% of all surveys, and where Grasshopper Sparrows were detected on at least one occasion.

Point count locations within each grid were separated by 300–400 m. Surveys were conducted between 1 March and 31 July during the Florida Grasshopper Sparrow breeding season. Most surveys (95%) were conducted within 3 hours of civil dawn. Each point count survey was conducted for a duration of 5 minutes. Ideally, surveyors visited sites three times during each breeding season and observers were alternated at least once per season. However, several point count locations were not surveyed during some years or for all repeated visits within years and we assigned missing values for those instances. We did not truncate Florida Grasshopper Sparrow detections at any distance to maintain consistency among years of study, because most point count surveys did not record distance to detection. Florida Grasshopper Sparrows have a high-pitched (~ 8 kHz) song that cannot be heard by human listeners at greater distances, and previous studies suggest a detection radius of <200 m for surveyors (Delany et al. 2013).

Detection data

We used point count survey data to categorize Florida Grasshopper Sparrow detections ($Y_{i,j}$) at site (i) during survey visit (j) into three categories (1) no Grasshopper Sparrows detected;

(2) Grasshopper Sparrows detected but subspecies uncertain; and (3) Florida Grasshopper Sparrows detected with certainty. We used date of point count surveys to improve estimates of certainty of subspecies identification, because eastern Grasshopper Sparrows are present in winter and migrate northward in late spring. We designated detections from point count surveys as certain when >99% percent (1506 of 1511 detections, Appendix A) of eastern Grasshopper Sparrows had departed on the first of May. To identify this threshold date when detections of Florida Grasshopper Sparrows would be relatively unambiguous (i.e. there is no confusion about which subspecies the detection might represent), we used eBird data (Sullivan et al. 2009) from 1995-2012 within the state of Florida from counties where Florida Grasshopper Sparrows are not known to persist (excluding Highlands, Okeechobee, Osceola, and Polk counties). We also categorized detections as certain when surveyors observed and recorded colored leg bands in this region where many known Florida Grasshopper Sparrows are color-banded.

Fire variables

We compiled fire data from Avon Park from 1977 to 2012, when adequate fire data existed. We used ArcGIS version 10.6.1 (ESRI, Redlands, CA, USA) to create spatial layers (gridded shapefiles) from prescribed fire data maps and added point count station locations from Avon Park. We created 5m grid shapefiles to estimate years-since-fire for each 5 m pixel each year. We summarized years-since-fire as the mean, maximum, and minimum for all 5 m pixels within two spatial scales (that included 100 m and 400 m circular buffers) around each point count location, i.e. each point count location included 2 buffers, each of which had a mean, maximum, and minimum years-since-fire value depending on the timing of the last fire at the 5 m pixel scale. The 100 m circular buffer was roughly equivalent in area to a male Florida Grasshopper Sparrow's territory (Delany et al. 1995, Aldredge 2009). The 400 m buffer was the distance between point count stations, which represents the maximum distance that a male typically moves when establishing a new territory and is an area that can encompass several territories (Dean et al. 1998).

Statistical Analysis

Misclassification model. We created a dynamic occupancy model to account for false negatives (MacKenzie et al. 2002, Tyre et al. 2003) and false positives (Miller et al. 2013) within a Bayesian framework, thereby extending the "site confirmation" design described by Chambert et al. (2015) with temporal dynamics (Miller et al. 2013). The model used robust design with samples at two temporal scales: 1) a closed period during each breeding season when occupancy was assumed to be stable, and 2) an open period between each year that allowed for changes in occupancy, persistence, and colonization (Mackenzie et al. 2006). We recognized that closure during the breeding season may be improbable given previously observed movements of marked Florida Grasshopper Sparrows; therefore, occupancy must be interpreted as the probability of site use during a breeding season in the context of our study.

We modeled survey data (**Y**) of Florida Grasshopper Sparrow observations at point count sites (i) during visit (j) and for the first year ($t = 1$) as

$$Y_{i,j,t=1} \sim Categorical(\pi_{i,j,1})$$

$$\pi_{i,j,t=1,1} = z_{i,1}(1 - p11_{i,j,1}) + (1 - z_{i,1})(1 - p10_{i,j,1})$$

$$\pi_{i,j,t=1,2} = z_{i,1}(1 - b_{i,j,1})p11_{i,j,1} + (1 - z_{i,1})p10_{i,j,1}$$

$$\pi_{i,j,t=1,3} = z_{i,1}b_{i,j,1}p11_{i,j,1}$$

where $z_{i,1} \sim Bernoulli(\psi_{i,1})$ and ψ was initial occupancy, $p11$ was detection probability that accounted for false negatives, i.e., the probability that a bird was detected given that a site was occupied. $p10$ was misclassification probability that accounts for false positives, i.e., when a bird was detected but the site was unoccupied, and b was the certainty of detections. The model included additional years of survey data ($t = 2, 3, 4, \dots T$) as

$$Y_{i,j,t} \sim Categorical(\pi_{i,j,t})$$

$$\pi_{i,j,t,1} = z_{i,1}(1 - p11_{i,j,t}) + (1 - z_{i,t})(1 - p10_{i,j,t})$$

$$\pi_{i,j,t,2} = z_{i,t}(1 - b_{i,j,t})p11_{i,j,t} + (1 - z_{i,t})p10_{i,j,t}$$

$$\pi_{i,j,t,3} = z_{i,t} b_{i,j,t} p11_{i,j,t}$$

Temporal dynamics were specified as a Markovian autoregressive structure where occupancy at subsequent time steps were a function of site persistence (ϕ) and colonization (γ)

$$z_{i,t+1} | z_{i,t} \sim Bernoulli(z_{i,t}\phi_{i,t} + (1 - z_{i,t})\gamma_{i,t})$$

We present the global model that includes all covariates for each response variable hereafter. Detection probability was a function of ordinal date (DATE) and hours after civil twilight (HOUR) where numerical suffixes indicated exponentiation (e.g., DATE2 was date squared centered and scaled).

$$logit(p11_{i,j,t}) \sim \beta_0 + \beta_1 DATE_{i,j,t} + \beta_2 DATE2_{i,j,t} + \beta_3 HOUR_{i,j,t} + \beta_4 HOUR2_{i,j,t} + \varepsilon_{p10,t}$$

$$\varepsilon_{p11,t} \sim Normal(0, \sigma_{p11})$$

Probability of misclassification varied as a function of covariates and had a random effect for year

$$logit(p10_{i,j,t}) \sim \delta_0 + \delta_1 DATE_{i,j,t} + \delta_2 DATE2_{i,j,t} + \varepsilon_{p10,t}$$

$$\varepsilon_{p10,t} \sim Normal(0, \sigma_{p10})$$

Certainty varied as a function of DATE because eBird data indicated that most eastern Grasshopper Sparrows (>99%) had departed by 1 May.

$$logit\left(b_{i,j,t}\right) = \alpha_0 + \alpha_1 DATE_{i,j,t} + \alpha_2 DATE2_{i,j,t} + \alpha_3 DATE3_{i,j,t}$$

We specified initial occupancy state as

$$logit(\psi_{i,t=1}) = \ \mu_{\psi,t=1}$$

We included a single years-since-fire (YSF) and seasonality (SEAS) measure as covariates for persistence and colonization as

$$logit(\phi_{i,t}) = \rho_0 + \rho_1 YSF_{i,t} + \ \rho_2 YSF2_{i,t}$$

$$\rho_3 \sin\left(SEAS_{i,t}\right) * 2 * 3.14 + \rho_4 \cos\left(SEAS_{i,t}\right) * 2 * 3.14 +$$

$$\rho_5 YSF_{i,t} \sin\left(SEAS_{i,t}\right) * 2 * 3.14 + \rho_6 YSF_{i,t} \cos\left(SEAS_{i,t}\right) * 2 * 3.14 +$$

$$\rho_7 YSF2_{i,t} \sin\left(SEAS_{i,t}\right) * 2 * 3.14 + \rho_8 YSF2_{i,t} \cos\left(SEAS_{i,t}\right) * 2 * 3.14 + \varepsilon_{\phi,t}$$

$$\varepsilon_{\phi,t} \sim normal(0, \sigma_\phi)$$

$$logit(\gamma_{i,t}) = \ \omega_0 + \omega_1 YSF_{i,t} + \ \omega_2 YSF2_{i,t}$$

$$\omega_3 \sin\left(SEAS_{i,t}\right) * 2 * 3.14 + \omega_4 \cos\left(SEAS_{i,t}\right) * 2 * 3.14 +$$

$$\omega_5 YSF_{i,t} \sin\left(SEAS_{i,t}\right) * 2 * 3.14 + \omega_6 YSF_{i,t} \cos\left(SEAS_{i,t}\right) * 2 * 3.14 +$$

$$\omega_7 YSF_{i,t} \sin\left(SEAS_{i,t}\right) * 2 * 3.14 + \omega_8 YSF_{i,t} \cos\left(SEAS_{i,t}\right) * 2 * 3.14 + \varepsilon_{\gamma,t}$$

$$\varepsilon_{\gamma,t} \sim normal(0, \sigma_\gamma)$$

where seasonality was a covariate for persistence or colonization that has a wave-like response over the duration of a year. We included interaction terms for both persistence and colonization between YSF and SEAS, YSF2 and SEAS, and included random effects for year (ε_t).

Covariate and Model Selection

We reduced the number of covariates using three stages of covariate selection: assessment of detection covariates using CIs, Bayesian latent indicator scale selection of correlated covariates (hereafter, BLISS) (Stuber et al. 2017), and Gibb's variable selection (hereafter, GVS) (Ntzoufras 2002). During the first stage, we implemented a global detection model that included all covariates for the probability of detection, certainty of subspecies classification, and probability of subspecies misclassification. We retained detection covariates when 85% CIs did not intersect zero. We allowed an 85% CIs threshold because covariates could become significant as we built more complex models.

During the second stage, we used BLISS as a variable reduction method that enabled a comparison of correlated covariates (Stuber et al. 2017), such as related YSF (minimum, maximum, and mean) that we measured at multiple nested spatial scales (100m and 400m buffers). We included two spatial scales of YSF and seasonality covariates using 100m and 400m buffers for both persistence and colonization. We included each YSF covariate as both linear and quadratic covariates. We retained covariates with the greatest probability of being selected for further analyses (Stuber et al. 2017).

During the third stage of model selection, we used GVS to assess the probability of inclusion for the most supported variables from BLISS variable reduction. GVS uses a Bernoulli indicator variable to estimate the probability of inclusion for each covariate. Implementation of GVS is complex and beyond the scope of this manuscript but is fully described elsewhere (Ntzoufras 2002). We included YSF (linear and quadratic terms) and SEAS in addition to interactions.

Model Implementation

We performed analyses using R v3.6.1 (R Core Team 2019) and the R package NIMBLE v0.8.0 (NIMBLE Development Team 2019). The R package NIMBLE obtains parameter estimates using Markov Chain Monte-Carlo within a Bayesian framework. We used six Markov chains, each having 100,000 iterations for the posterior distribution and a burn in period of 100,000 iterations. Traceplots of Markov Chain Monte-Carlo were visually inspected to assess convergence for each parameter. We used vague priors for all estimated parameters including Uniform (a=0, b=1) for intercepts on the probability scale; Normal (mean=0, precision=0.001) for coefficients on the logit scale; and Uniform (a=0, b=20) for sigma parameters of random effects. Prior probabilities for GVS were assigned using methods that are fully described by Ntzoufras (2002). We used 95% credible intervals to determine statistical significance of covariates.

Results

We detected 943 Grasshopper Sparrows from 7,938 point counts. Of these, 456 were uncertain detections and 487 were certain Florida Grasshopper Sparrow detections.

Covariate Selection and Reduction

We retained DATE as a covariate for both misclassification and certainty, and HOUR as a covariate for detection. Both misclassification and certainty had quadratic relationships with DATE (Table 1). However, the quadratic response by certainty with DATE predicted implausibly low certainty values early in the breeding season; therefore, we included a cubic term (Table 1) to more adequately describe the relationship between certainty and DATE, and this change increased certainty during the earliest period of the breeding season while maintaining a peak during the period with the greatest number of migrants. We present coefficient estimates below from final results using GVS.

Using BLISS variable reduction (Table 2), the covariates and spatial scales that received the most support for persistence included maximum YSF at 400m (0.85 probability) and SEAS at 100m (1.0). Covariates that received the greatest support for colonization included minimum YSF at 400m (0.16) and SEAS at 100m (0.81). We retained covariates receiving the greatest support from BLISS for subsequent analysis using GVS.

Detection probability, certainty, and misclassification

The probability of misclassification had a quadratic relationship with DATE (Table 3), increasing through March, peaking in April (0.05), and decreasing through May to near zero (Fig. 3). The probability of misclassification across the entire breeding season was relatively low and stable across years and average estimates ranged from 0.001–0.003 (Fig. 2). The probability of detection decreased with HOUR (Table 3, Fig. 1), and detection decreased over time coinciding with periods when occupancy was low (Fig. 2). Certainty included a cubic association with DATE and was nearly perfect (1.0) until late March when it decreased to zero by late April, then recovered to nearly perfect again by the second week of May (Table 3, Fig. 3).

Occupancy and dynamics: persistence and colonization

GVS identified maximum YSF within a 400m buffer as an important predictor for persistence (1.0 probability of inclusion, Table 3), and persistence decreased as maximum YSF increased (Fig. 4). The mean probability of persistence was approximately 0.93 when all pixels within 400m of the point count location were recently burned (i.e., YSF=0) and decreased to 0.18 when any pixel within 400m was not burned for 35 years. Other covariates for persistence and colonization estimated a probability of inclusion <0.04 (Table 3) and we deemed these unimportant. Site use (occupancy) and colonization tended to decrease over time (Fig. 5), but persistence was relatively stable.

Discussion

To enable more precise occupancy estimates for a critically endangered bird, the Florida Grasshopper Sparrow, we used dynamic occupancy models to investigate the role of prescribed fire on occupancy, while also accounting for the presence of eastern Grasshopper Sparrows. Determining accurate habitat occupancy for an endangered species is vital to monitoring and conservation efforts. Modeling both false negatives and misclassification (false positives) allowed us to determine a probability for detections that reduced biases for modeling occupancy with the Florida Grasshopper Sparrow (Royle and Link 2006). Our study is also the first to use long-term point count data and prescribed burn area comprehensively to test which fire metric (minimum, mean, or maximum) best predicts occupancy dynamics at different spatial scales for the Florida Grasshopper Sparrow.

Our finding that the probability of detecting a Florida Grasshopper Sparrow at a point count station decreased throughout each morning following a peak at civil dawn showed the same pattern as results from prior studies with Florida Grasshopper Sparrows (Hochachka et al. 2009, Delany et al. 2013). These results suggest that point count surveys closer to civil dawn would provide the highest chance of detecting Florida Grasshopper Sparrows, thereby improving population estimates. We also found that detection probability decreased over the duration of our data set, corresponding to a decrease in abundance of this subspecies over time. As abundance decreases and a species becomes rarer, the chance of detection at a point count station also decreases unless the number of point count visits or the size of the grid are increased (Sliwinski et al. 2016). At many of the sites where the Florida Grasshopper Sparrow is currently found it is not always logistically feasible to survey more frequently, especially at Avon Park which is actively used for military training.

The presence of false positives in the data can lead to bias in occupancy estimates but can be adjusted to correct for this bias by determining the misclassification probability (Miller et al. 2013, Ruiz-Gutierrez et al. 2016, Berigan et al. 2019). We found a peak in the probability of misclassification (0.05) and a low probability for certainty (0.0) in April, which corresponds to an increase in migratory movement of eastern Grasshopper Sparrows in Florida (Vickery 1996). Miller et al. (2011) demonstrated using data from surveys with pickerel frogs (*Lithobates palustris*) that even a misclassification probability of 0.027 resulted in occupancy estimates 2.15 times greater than models that did not account for misclassification detections. Misclassification probability decreases and certainty increases by May, after our data showed that a majority of eastern Grasshopper Sparrows have left Florida. The eastern Grasshopper Sparrow is also found in the dry prairie habitat in Florida during the winter and they may begin singing on their wintering grounds prior to migration. It is difficult for observers to distinguish eastern Grasshopper Sparrows and Florida Grasshopper Sparrows by song or visually in the field, so the eastern Grasshopper Sparrow could easily be mistaken for the Florida subspecies prior to their departure in late April. Point count surveys for the Florida Grasshopper Sparrow generally start in late March, which coincides with the beginning of territory establishment. Males sing more frequently during territory establishment and at the start of each breeding cycle (which lasts approximately one month, unless nests are depredated), and decrease in singing frequency once eggs hatch (Lohr et al. 2013). After this first breeding cycle, nesting across the population becomes less synchronous as some nests are depredated, and individual pairs begin new breeding attempts shortly after nest failure (Lohr et al. 2013). Point count surveys conducted after the eastern Grasshopper Sparrows leave in May have a higher certainty of detection but may also be less likely to detect Florida Grasshopper Sparrows given lower levels of nesting synchrony at that point in the breeding season (Delany et al. 2013). Explicitly modeling certainty of detections and misclassifications allows for surveys to be completed at the most likely time to detect Florida Grasshopper Sparrow while also accounting for the presence of the eastern Grasshopper Sparrow.

Fire maintains the Florida dry prairie in an early successional stage and prevents trees and tall shrubs from encroaching on the habitat and clears dead grasses (Platt et al. 2006). Prior studies show that Florida Grasshopper Sparrows prefer recently burned dry prairie and occasionally grazed pasture (Delany et al. 1985, Walsh et al. 1995). Our model used misclassification probability to improve occupancy estimates for Florida Grasshopper Sparrows from point counts with prescribed fire metrics summarized for all the 5 m pixels within each spatial buffer. We found that Florida Grasshopper Sparrow persistence at the same point count station between years was dependent on the maximum years since fire (but not the mean or minimum year since fire) for all the 5 m pixels within the buffer. The probability of a point count station remaining occupied from one year to the next was 0.93 in freshly burned habitat (zero years since fire), which comports with previous research that shows a preference for recently burned habitat (Walsh et al. 1995). Delany et al. (1995) found that marked Florida Grasshopper Sparrows tended to stay in the same breeding territory for 2 – 4 successive years. We did not find a significant relationship between fire and colonization, which is the likelihood of detecting a

Florida Grasshopper Sparrow one year at a previously unoccupied point count station. Florida Grasshopper Sparrows at Avon Park experienced a dramatic decrease in population from approximately 298 individuals in 1997 to 17 in 2003 (Tucker and Bowman 2006). The colonization probability and site occupancy both declined over the years we analyzed (1996-2011), but persistence probability remained relatively stable (Fig. 5). This result suggests that the same point count stations are more likely to remain occupied between successive years than for unoccupied areas to be colonized. The lack of a relationship between fire and colonization was likely a consequence of Florida Grasshopper Sparrows being unavailable to move into unoccupied areas due to an annual reduction in population and site fidelity.

The probability of Florida Grasshopper Sparrows persisting at a point count location between years was influenced by the maximum time since fire at the larger (400 m) spatial scale. This result suggests that larger fires may be more beneficial for retaining Florida Grasshopper Sparrows. The maximum time since fire was 35 years over the time period we sampled, which implies that at least part of the 400 m radius buffer circle included areas that did not regularly burn, such as depression marshes, cypress domes, or military installations. Between 1996 and 2009 the mean fire return interval in dry prairie at Avon Park was generally 2.3 years (Rolek, Schrott, and Bowman 2009), with some areas burned more frequently due to military exercises, but other areas burned less frequently than every 3 years. Perkins et al. (2003) found that Florida Grasshopper Sparrow habitat > 400 m from an edge was a source, and that larger prairie fragments (> 4,000 ha) were better for providing adequate source habitat. Our result confirms that Florida Grasshopper Sparrow persist in larger areas (at least 400 m in radius) that were recently burned.

The influence of fire seasonality on Florida Grasshopper Sparrow nesting and territory density has been the focus of many studies attempting to determine the most effective burning season for management practices that optimize survival and reproduction (Shriver et al. 1996, Shriver and Vickery 2001, Hewett Ragheb et al. 2019). The timing of prescribed fires was originally split into two discrete seasons based on either rainfall or temperature; the summer (growing) season or winter (dormant) season. By increasing the number of weather variables for the south Florida region, a three season fire model was later developed (Platt et al. 2015). The fire transition season burning regime is theorized to more accurately mimic the natural wildfire regime at the end of the dry season before the summer rains begin and saturate the vegetation (Platt et al. 2015). We did not find a significant relationship between fire seasonality and persistence or colonization for Avon Park. The majority of prescribed fires that occurred during 1997-2009 were burned during the winter (dormant season), except for natural lightning wildfires and those started accidentally by military exercises (Delany et al. 1999, Platt et al. 2015). The lack of variation in burn season at Avon Park may have contributed to the lack of a significant result with any of the occupancy metrics. Hewett Ragheb et al. (2019) found no difference in measures of reproductive indices (i.e. number of fledglings produced, clutch size) between different fire treatments at Three Lakes Wildlife Management Area, but the nests were found primarily in current dormant season or previous growing season burn treatments. Shriver et al. (2001) found that Florida Grasshopper Sparrows had higher territory densities in habitat burned during the current dormant season, but higher density does not always translate to higher quality habitat (Van Horne 1983). Shriver et al. (1996, 1999) concluded that summer (growing) season fires extended the breeding season into September and recommended a switch from winter to summer fires, but Hewett Ragheb et al. (2019) found Florida Grasshopper Sparrow nests into August for all fire treatments based on a 4-year demographic study at Three Lakes Wildlife Management Area.

Conclusion

Decreasing bias in occupancy models is vital for accurately estimating the population dynamics of endangered species for the purposes of determining their status and improving monitoring efforts (McClintock et al. 2010, Miller et al. 2015). We used a misclassification probability in our model to reduce biases and improve occupancy estimates for determining the influence that prescribed fire management has on Florida Grasshopper Sparrows. If we had not adjusted occupancy based on certainty of detection and misclassification our results may have led to incorrect conclusions about habitat use of prescribed fires. Our results show that the time of day with the highest probability of detecting a Florida Grasshopper Sparrow is civil dawn, and surveys completed at that time are likely to be the most accurate. Furthermore, while fire is important in maintaining habitat, burn season does not seem to influence colonization and persistence. We caution against drawing definitive conclusions regarding occupancy and colonization because our study uses populations at only one site, Avon Park, so broader implications may be limited. However, Avon Park had the most reliable and complete fire data available, and the time period we analyzed also encompassed a decline in population at all three sites, so our results remain important for continuing work with the Florida Grasshopper Sparrow. For future studies with the Florida Grasshopper Sparrow or other endangered species it is important to standardize and archive data metrics for abiotic factors such as fires, especially when multiple sites are involved. Long-term data is critical to understanding trends that can contribute to population changes over time (Lindenmayer and Likens 2009).

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Table 3.1. Parameter estimates for the global detection model from a dynamic occupancy model that accounted for detection probability and misclassification of subspecies at Avon Park Air Force Range, FL, USA from 1991–2011.

Response variable	Parameter	Covariate	Mean	95% LCI	95% UCI	85% LCI	85% UCI
Detection	β_0	Intercept	-0.27	-0.35	-0.2	-0.33	-0.22
Detection	β_1	DATE	0.51	-0.11	1.13	0.04	0.96
Detection	β_2	DATE2	-0.56	-1.22	0.1	-1.04	-0.06
Detection	β_3	HOUR	-0.55	-0.78	-0.3	-0.72	-0.37
Detection	β_4	HOUR2	0.04	-0.22	0.27	-0.14	0.2
Certainty	α_0	Intercept	13.62	11.85	15.6	12.27	15.1
Certainty	α_1	DATE	-71.36	-82.6	-60.9	-80	-63.1
Certainty	α_2	DATE2	55.94	23.98	89.28	31.76	81.5
Certainty	α_3	DATE3	40.92	12.8	74.3	18.93	64.32
Misclassification	δ_0	Intercept	-6.76	-7.76	-5.96	-7.48	-6.14
Misclassification	δ_1	DATE	9.47	5.99	14.3	6.75	13.49
Misclassification	δ_2	DATE2	-13.72	-19.7	-9.44	-18.6	-10.4

Table 3.2. Results from Bayesian latent indicator scale selection (BLISS) for variable reduction to compare correlated covariates within a dynamic occupancy model that accounted for detection probability and misclassification of subspecies. Covariates receiving the greatest support (probability) in each BLISS set were retained for subsequent analysis. Retained covariates are indicated in bold font.

Response variable	BLISS set	Covariate	Probability
Persistence	1	mean YSF 100m	0.00
Persistence	1	min YSF 100m	0.00
Persistence	1	max YSF 100m	0.00
Persistence	1	mean YSF 400m	0.01
Persistence	1	min YSF 400m	0.00
Persistence	1	**max YSF 400m**	0.86
Persistence	1	mean YSF 100m^2	0.00
Persistence	1	min YSF 100m^2	0.00
Persistence	1	max YSF 100m^2	0.00
Persistence	1	mean YSF 400m^2	0.00
Persistence	1	min YSF 400m^2	0.00
Persistence	1	max YSF 400m^2	0.13
Persistence	2	**SEAS 100m**	1.00
Persistence	2	SEAS 400m	0.00
Colonization	3	mean YSF 100m	0.08
Colonization	3	min YSF 100m	0.09
Colonization	3	max YSF 100m	0.11
Colonization	3	mean YSF 400m	0.15
Colonization	3	**min YSF 400m**	0.16
Colonization	3	max YSF 400m	0.09
Colonization	3	mean YSF 100m^2	0.10
Colonization	3	min YSF 100m^2	0.02
Colonization	3	max YSF 100m^2	0.08
Colonization	3	mean YSF 400m^2	0.09

Colonization	3	min YSF 400m^2	0.03
Colonization	3	max YSF 400m^2	0.01
Colonization	4	**SEAS 100m**	0.81
Colonization	4	SEAS 400m	0.19

Table 3.3. Parameter estimates from occupancy models that account for misclassification and detection probability applied to point count survey data from 1996–2011 at Avon Park Air Force Range, FL, USA.

Response variable	Parameter	Covariate	Mean	SE	95% LCI	95% UCI	Prob. of inclusion
Persistence	ρ_0	Intercept	1.07	0.48	0.10	2.07	1
Persistence	ρ_1	YSF	-0.75	0.16	-1.09	-0.45	1
Persistence	ρ_2	YSF2	-4.97	3.65	-12.27	2.02	0
Persistence	ρ_3	SEAS	2.87	0.87	1.17	4.58	0.04
Persistence	ρ_4	SEAS	0.53	0.55	-0.52	1.62	0.04
Persistence	ρ_5	SEAS*YSF	-3.53	4.47	-12.23	5.21	0
Persistence	ρ_6	SEAS*YSF	-3.29	2.15	-7.48	0.87	0
Persistence	ρ_7	SEAS*YSF2	5.24	5.10	-4.55	15.40	0
Persistence	ρ_8	SEAS*YSF2	4.75	2.75	-0.52	10.22	0
Colonization	ω_0	Intercept	-3.51	0.76	-5.21	-2.05	1
Colonization	ω_1	YSF	0.11	3.98	-7.54	7.98	0.01
Colonization	ω_2	YSF2	-4.49	11.69	-26.11	19.35	0
Colonization	ω_3	SEAS	-1.21	2.76	-6.60	4.30	0
Colonization	ω_4	SEAS	0.94	1.15	-1.30	3.20	0
Colonization	ω_5	SEAS*YSF	4.05	7.39	-10.21	18.45	0
Colonization	ω_6	SEAS*YSF	-5.15	2.94	-10.95	0.66	0
Colonization	ω_7	SEAS*YSF2	-2.90	15.22	-27.97	26.49	0
Colonization	ω_8	SEAS*YSF2	12.04	9.09	-6.50	27.65	0
Detection	β_0	Intercept	-0.80	0.24	-1.30	-0.36	NA
Detection	β_3	HOUR	-0.43	0.06	-0.55	-0.31	NA
Certainty	α_0	Intercept	9.32	1.12	7.12	11.52	NA
Certainty	α_1	DATE	-53.86	8.14	-69.97	-37.37	NA
Certainty	α_2	DATE2	34.65	24.16	-8.17	84.57	NA
Certainty	α_3	DATE3	35.44	23.10	-15.37	77.25	NA
Misclassification	δ_0	Intercept	-8.28	0.94	-10.28	-6.56	NA
Misclassification	δ_1	DATE	20.37	4.91	11.24	30.57	NA
Misclassification	δ_2	DATE2	-26.40	5.95	-38.82	-15.46	NA

Figure 3.1. Probability of detection in response to survey time specified as hours after civil twighlight from a dynamic occupancy model that accounted for detection probability and misclassification and was applied to point count data during the breeding season from Avon Park Air Force Range, FL, USA from 1996–2011. Solid lines depict modeled means and gray polygons depict 95% credible intervals.

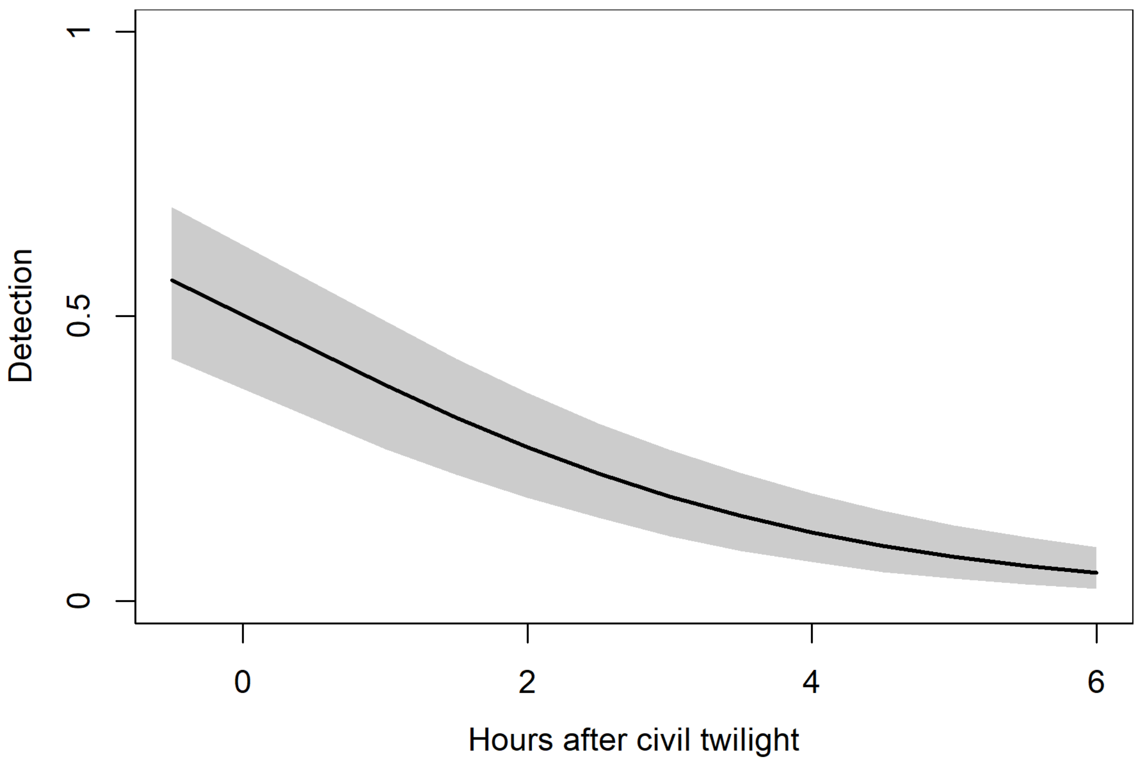


Figure 3.2. Probabilities of detection and misclassification of Florida Grasshopper Sparrows each year during 1996–2011 from a dynamic occupancy model that accounted for detection probability and misclassification and was applied to point count data during the breeding season at Avon Park Air Force Range, FL, USA. Solid lines depict modeled means and gray polygons depict 95% credible intervals.

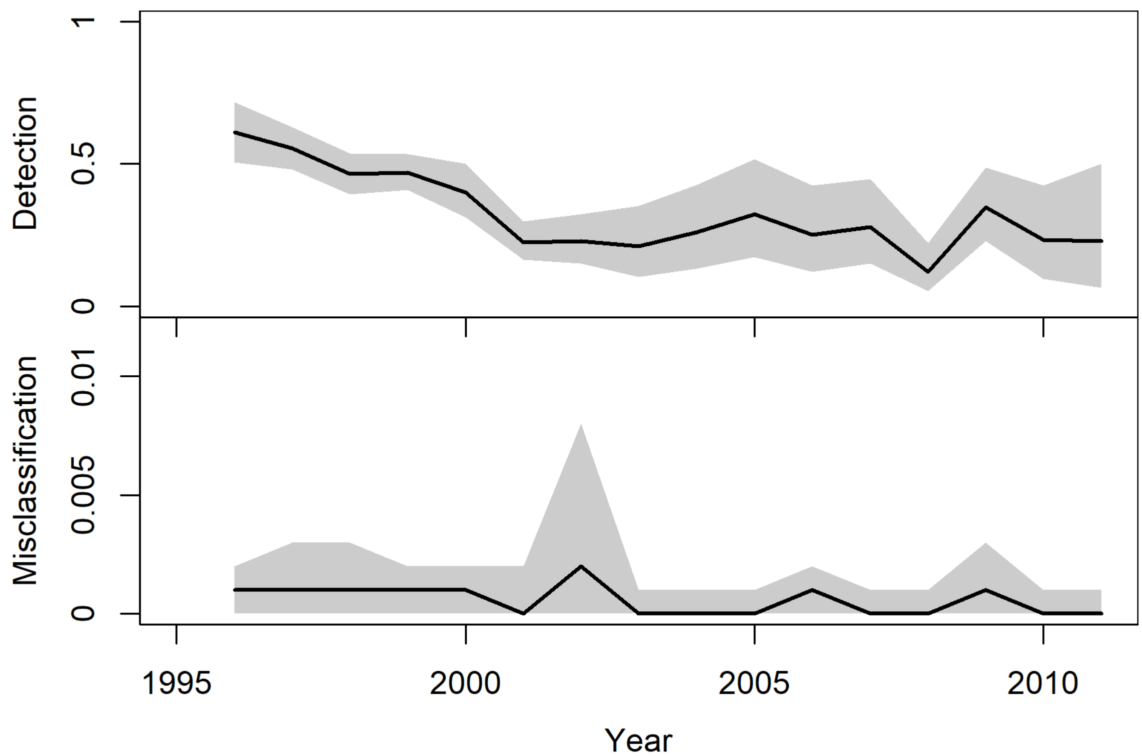


Figure 3.3. Probability of misclassification and certainty of detections in response to DATE (days after 1 March) during the breeding season from a dynamic occupancy model that accounted for detection probability and misclassification and was applied to point count data at Avon Park Air Force Range, FL, USA during 1996–2011. Certainty had a cubic response, and misclassification had a quadratic response to ordinal date. Solid lines depict modeled means and gray polygons depict 95% credible intervals.

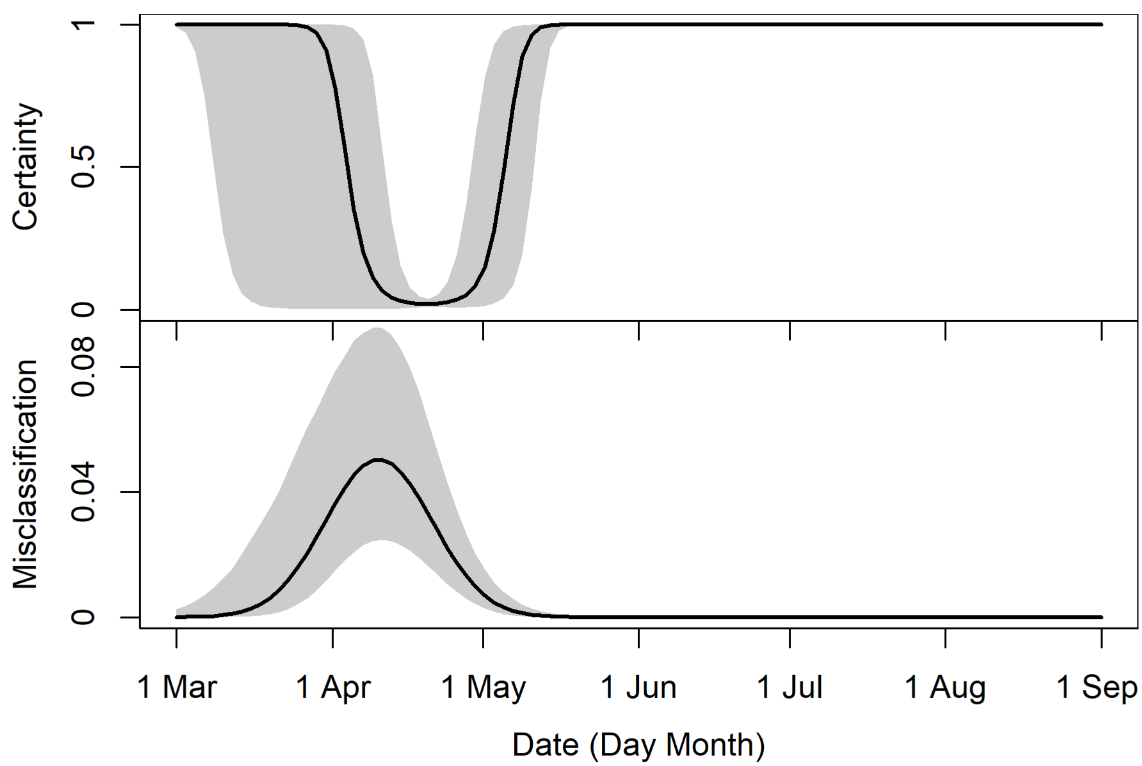


Figure 3.4. Site persistence of Florida Grasshopper Sparrow and maximum years-since-fire within a 400m buffer of the point count center from a dynamic occupancy model that accounted for detection probability and misclassification and was applied to point count data during 1991–2011 at Avon Park Air Force Range, FL, USA. Solid lines depict modeled means and gray polygons depict 95% credible intervals.

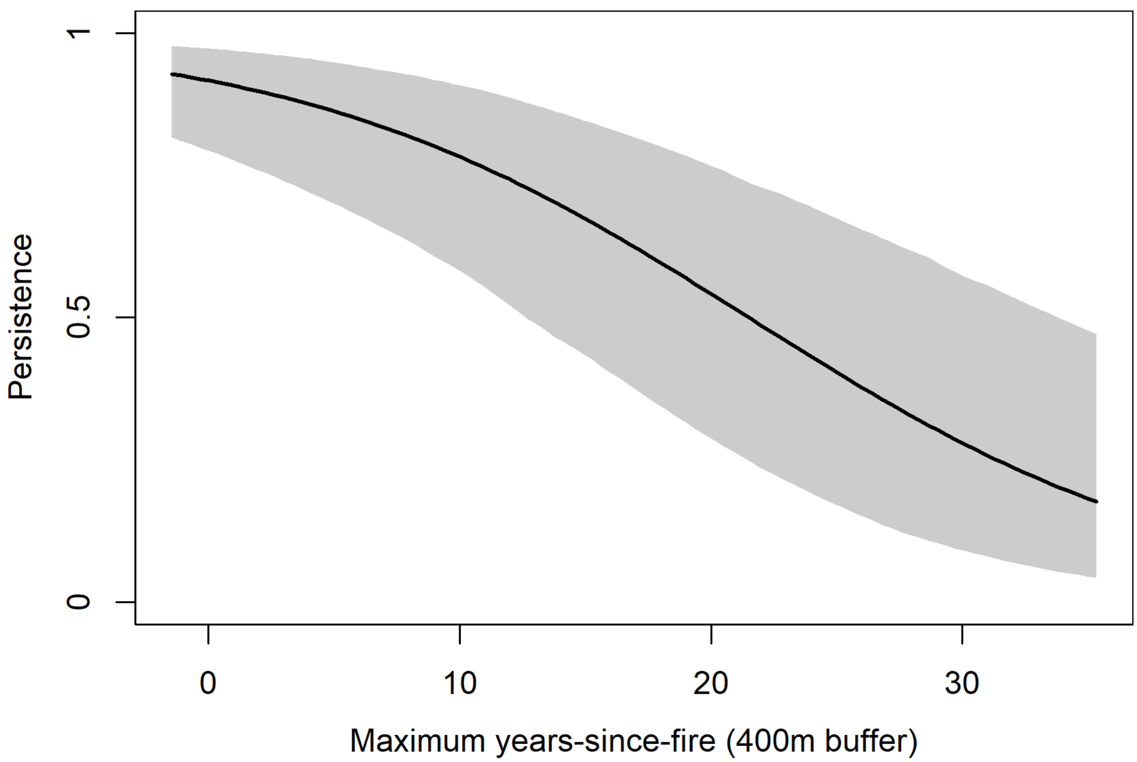
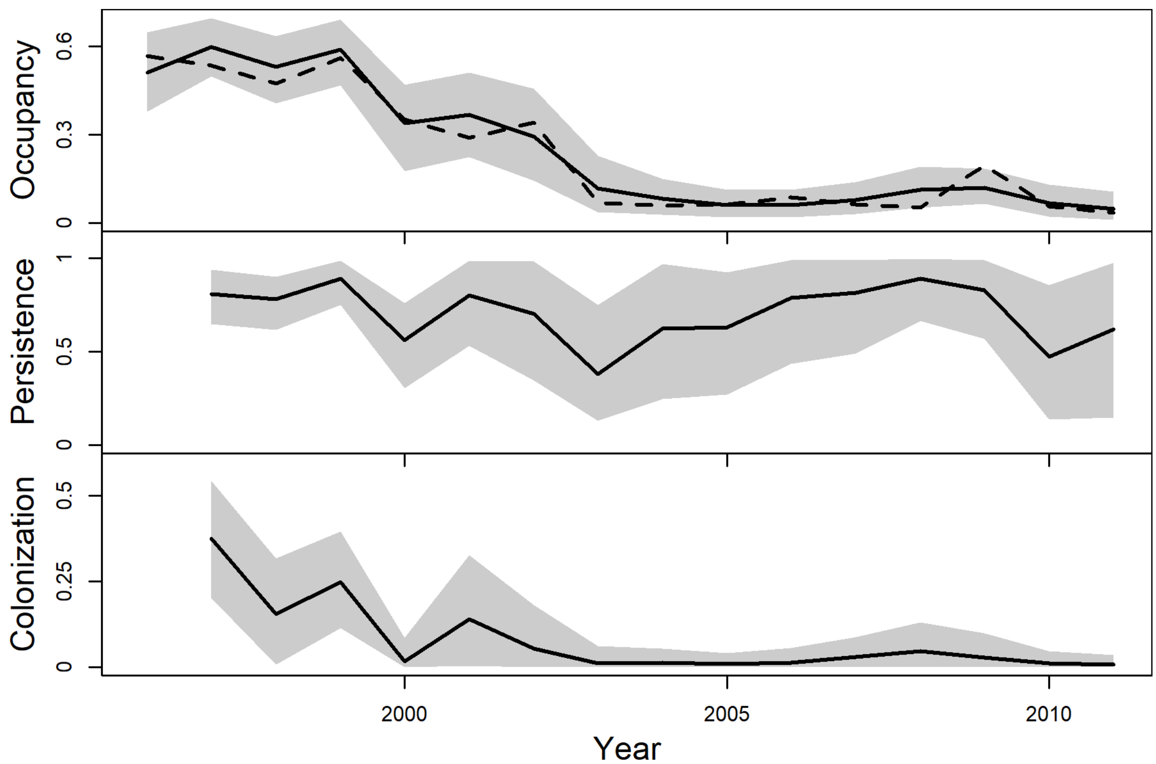
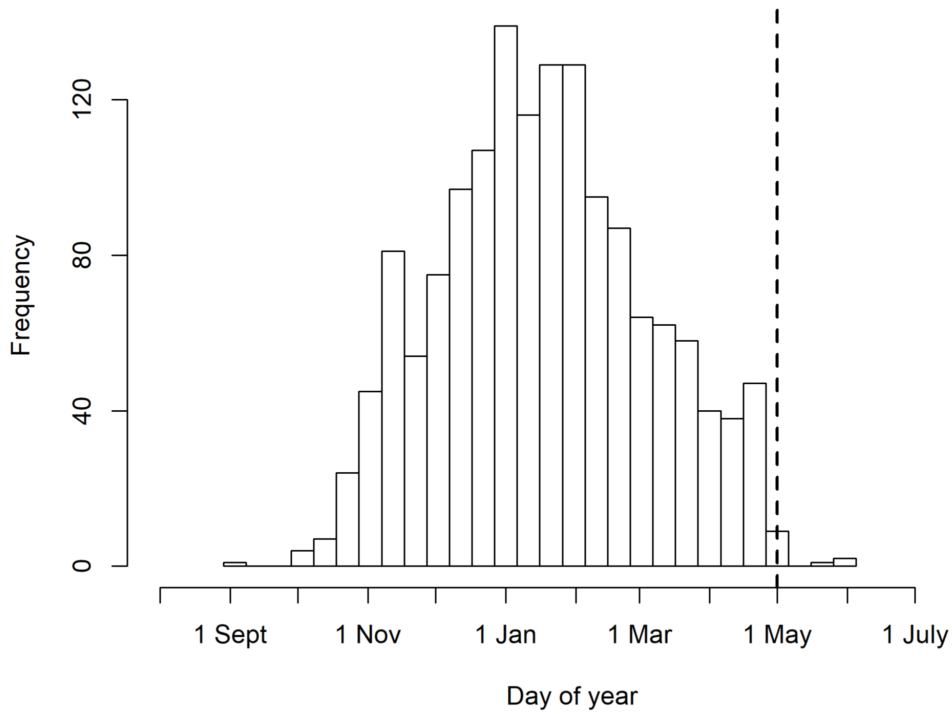


Figure 3.5. Site use (occupancy), site persistence, and site colonization each year of Florida Grasshopper Sparrows during the breeding seasons from 1996–2011 from a dynamic occupancy

model that accounted for detection probability and misclassification and was applied to point count data at Avon Park Air Force Range, FL, USA. Solid lines depict modeled means and gray polygons depict 95% credible intervals. The dashed line depicts mean naïve occupancy.



Appendix 3.A. A histogram of Grasshopper Sparrow detections in Florida using eBird data from 1995-2012 used to determine a threshold (dashed line on 1 May) when we considered Florida Grasshopper Sparrow to be detected with certainty. We excluded data from Highlands, Okeechobee, Osceola, and Polk counties, where breeding populations of Florida Grasshopper Sparrow were known to exist.



Chapter 4: Florida Grasshopper Sparrow nests are oriented northeast

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Abstract

Nest microclimate can be affected by wind and solar radiation, which can influence offspring survival. The endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) constructs a dome style nest on the ground in dry prairie and pasture habitat. We measured the nest opening orientation for Florida Grasshopper Sparrow nests during 2014-2016 at two sites with different habitats to determine if nest opening orientation was directional and the potential factors that influence the orientation. We found that Florida Grasshopper Sparrow nest openings were primarily oriented to the northeast (pooled mean= 30.6°, *n*= 116), with no statistically significant difference between nests at the different sites or between successful and unsuccessful nests. The northeasterly direction of nest openings suggests Florida Grasshopper Sparrows may orient nests to avoid wind-blown rain from summer storms and adverse solar radiation during the hottest part of the day in the breeding season.

Introduction

Nest microclimate can influence nest productivity and many birds have evolved mechanisms for optimizing microclimate characteristics (Collias 1964). Different nest types (e.g. open cup, cavity, domed) provide protection from predators and the environment and help maintain a suitable temperature for development (Collias 1997). For cavity and domed nests, the orientation of the nest opening can affect nest microclimate, and the opening can be oriented in response to solar radiation (Burton 2007), wind (With and Webb 1993; Burton 2006; Long et al. 2009), or vegetation (Delany and Linda 1998a, Hoekman et al. 2002). The orientation of the nest opening can be constructed for optimizing the interior nest temperature, since eggs and nestlings generally require a certain temperature range for proper growth and development (Conway and Martin 2000). In northern latitudes some birds orient their nest openings more to the south or east which would allow solar radiation to warm the interior of a nest in the morning, whereas birds tend to exhibit a more northern orientation with decreasing latitude (Burton 2007). Prevailing winds also may provide relief from increasing internal nest temperatures if a nest opening is oriented in a direction to face the wind (Austin 1974).

Birds nesting in grassland habitats are exposed to high levels of wind and solar radiation because limited amounts of vegetation are available to block wind or provide shade (With and Webb 1993; Long et al. 2009). Solar radiation and wind can change the internal nest temperature, and thus parental behavior, in response. For example, adult Chestnut-collared Longspurs (*Calcarius ornatus*) spend less time feeding and more time shading their nestlings in nests that are facing southeast, resulting in slower growth of nestlings (Lloyd and Martin 2004). Nests placed on the ground, such as those built by Florida Grasshopper Sparrows (*Ammodramus savannarum floridanus*), are susceptible to both wind and solar radiation in the treeless prairie habitat of central Florida (Delany and Linda 1998a). Nests of Florida Grasshopper Sparrows are domed, with an opening situated on the side oriented outward in a particular direction. A prior study of Florida Grasshopper Sparrow nests showed no consistent orientation (Delany and Linda 1998a, *n* = 20), but we investigated this question with an increased sample size, given that many other grassland birds show non-random orientation (Ruth and Skagen 2017; Long et al. 2009).

To answer questions about nest orientation in Florida Grasshopper Sparrows we proposed the following specific questions: 1) Does nest opening orientation show a random or non-random distribution? And 2) Does the orientation of the nest opening vary between different sites, and between successful and unsuccessful nests? If Florida Grasshopper Sparrows follow the pattern reported in other grassland birds, we predicted *a priori* that nest openings would be oriented toward the north or northeast (Ruth and Skagen, 2017; Long et al., 2009; Haggerty, 1995; With and Webb, 1993). By including a comparison between two sites with different habitats, we can also address whether orientation might be influenced more by vegetation or climate.

Methods

We measured Florida Grasshopper Sparrow nest opening orientation during April to August of 2014-2016 at two study sites: Three Lakes Wildlife Management Area (hereafter, Three Lakes) and a private cattle ranch (hereafter, the Ranch) both in Osceola County, Florida. The study area at Three Lakes was the Route 60 Unit near Kenansville, Florida (27.876°, -80.988°) and constituted a mix of wet and dry prairie habitat interspersed with depression ponds approximately 3,000 ha in size, which included a 1,728 ha area of relic dry prairie. Dry prairie in Florida is flat, treeless habitat containing a mix of pyrogenic grasses (e.g., wiregrass [*Aristida stricta*]), shrubs (e.g., saw palmetto [*Serenoa repens*]), and numerous forbs (e.g., narrowleaf silkgrass [*Pityopsis graminifolia*]; Florida Natural Areas Inventory 2010). The study area at the Ranch was 1,012 ha in size and consisted of semi-improved cattle pasture, which was previously a monoculture of bahiagrass (*Paspalum notatum)* that recolonized with some native dry prairie plants.

We searched for and found nests during all stages of the breeding cycle by observing adult behavioral cues and using songs to determine male breeding status (Lohr et al. 2013), or opportunistically flushing females off of nests when walking in the habitat. At both sites all male territories had been mapped using handheld GPS units (Garmin 72H; Olathe, KS) to identify locations of male singing posts. Territories were visited repeatedly every 1-4 days until a nest was located. Nests were monitored at both sites by carefully checking nest contents every 2-3 days until nestlings were 5 days old, then daily until nests fledged or failed. Empty nests were considered fledged if fledglings were sighted or if nestlings were fledging age and parents were seen carrying food or heard producing alarm calls nearby.

We determined the nest opening orientation by using a handheld compass positioned at ground level in the entrance of the nest (we did not measure orientation for 10 destroyed nests). We pooled data from all three years (2014-2016) for this analysis. We performed a Rayleigh's test for circular data to determine if nests were randomly or non-randomly oriented (Zar 1999). We used the Watson-Wheeler test (similar to a t-test for circular data) (Mardia and Jupp 2000) to compare the orientation of successful versus unsuccessful nests, and to compare orientation between Three Lakes and the Ranch. All circular statistics were completed using R package *circular* (Agostinelli and Lund 2017) in RStudio version 1.1.456 (RStudio Team 2016). For the comparison between successful and unsuccessful nests we only used nests from 2014 and the first half of 2015 at Three Lakes, as nests in the second half of 2015 and 2016 were protected by predator exclosure fences that were part of another study (Hewett Ragheb et al. 2019), and nest success at the Ranch was too low to yield statistically meaningful results.

Results

We measured the orientation of 82 Florida Grasshopper Sparrow nest openings at Three Lakes and 34 at the Ranch. Florida Grasshopper Sparrow nest openings were not randomly oriented at either site (Three Lakes: Rayleigh test, $z = 0.3537$, $P < 0.001$, $n = 82$; the Ranch: $z = 0.4967$, $P < 0.001$, $n = 34$) and were generally oriented towards the northeast. Mean nest orientation for Florida Grasshopper Sparrows at Three Lakes was 44.6° (0° = north) (95% CI low= 7.97°, high= 265.37°), and for the Ranch was 6.6° (95% CI low= 335.63°, high= 226.52°) (Fig. 1). Despite differences in dominant vegetation at the two sites there was no detectable difference between the orientation of nest openings at the sites ($W = 1.68$, $P = 0.43$) and the pooled mean was 30.6°. At Three Lakes, 15 out of a total of 42 nests included in our analysis were successful and we found no detectable difference between the orientation of nest openings ($W = 1.39$, $P = 0.50$).

Discussion

Florida Grasshopper Sparrows at both sites primarily oriented their nest openings to the northeast. There was no detectable difference in orientation between the sites or between successful or unsuccessful nests at Three Lakes. These results suggest that nest orientation is consistent in this subspecies across habitat types despite marked differences in vegetation between the two sites. The lack of difference in orientation between successful and unsuccessful nests further suggests that orientation is climate related since nest success appears unrelated to orientation. Having nest openings oriented northeasterly may facilitate the maintenance of a relatively stable nest microclimate by avoiding windblown rain from storms and more direct solar radiation from the south. In central Florida, where rain and storms are common in the summer, most thunderstorms result from convection drawing in moisture from the surrounding warm ocean, with the strongest convective winds and storms coming from the west (Wilson and Megenhardt 1997). A number of other species with domed nests also appear to orient their nest openings in directions opposite of the prevailing winds or sun (With and Webb 1993; Haggerty 1995; Long et al. 2009; Ruth 2017). Our results align with those of most other studies of grassland birds having domed nests, that also show an orientation to the north or northeast (Ruth 2017, Long et al. 2009, Haggerty 1995, With and Webb 1993).

Nest opening orientation is one mechanism by which birds may influence the microclimate inside the nest. In some cavity nesters for example, cavity openings face south or southwest (Inouye 1976) possibly to help ventilate and warm the nest. Similarly, Tree Swallows (*Tachycineta bicolor*) selected nest boxes with a preferred orientation to regulate the temperature of their nest, particularly in the early part of the breeding season (Ardia et al. 2006). In cavity or box nesters sunlight would likely not fall directly on eggs or nestlings because of the height of the opening. In open-cup or domed nests, however, sunlight may fall directly on eggs or nestlings and, as the sun reaches a higher azimuth in the sky, nest openings oriented in a northerly direction may avoid the most intense solar radiation reaching the interior of the nest (With and Webb 1993). Nests on the ground in an open grassland, where less shade is available, may be more susceptible to adverse high temperatures, which can slow nestling development (Rodriguez and Barba 2016). Nests oriented to avoid direct solar radiation during the hottest part of the day or breeding season have been shown to improve hatching success in some species, such as Tree Pipits (*Anthus trivialis*), which alter the orientation of their open-cup ground nests from south to north through the breeding season, as temperatures increase (Burton 2006).

Prevailing winds and adverse weather conditions can also impact nest microclimate. For example, Cactus Wrens (*Campylorhynchus brunneicapillus*) orient their nest openings in the direction of winds to ventilate their nests during the hottest part of the breeding season, which has a positive impact on nesting success (Austin 1974; Facemire et al. 1990). On the other hand, winds can also result in adverse conditions for nests. Eastern Meadowlarks (*Sturnella magna*) and Grasshopper Sparrows (*Ammodramus savannarum*) in the tallgrass prairies in Kansas, for example, have been shown to orient their nest openings opposite prevailing wind direction and even changing the orientation seasonally (Long et al. 2009). Rain and storms can decrease nestling survival due to nestling exposure (Martin et al. 2017).

Finally, variation in nest orientation for some ground nesting birds may be influenced by the location of shrubs or other vegetation in the environment (Hoekman et al. 2002), but we found no evidence for association with habitat type in Florida Grasshopper Sparrow nests. Habitat differences between our two sites in vegetation types and the physical structure and patterning of vegetation on the landscape, did not result in differences in nest opening orientation at the two sites. Further research could help determine if variation in orientation within sites was affected by vegetation near the nest as Delany and Linda (1998b) noted a preference for nest openings to face patches of bare ground to facilitate adult escape. Future studies might also examine whether temperature of the nest interior depends on its placement within vegetation of different types, and on the orientation of the nest.

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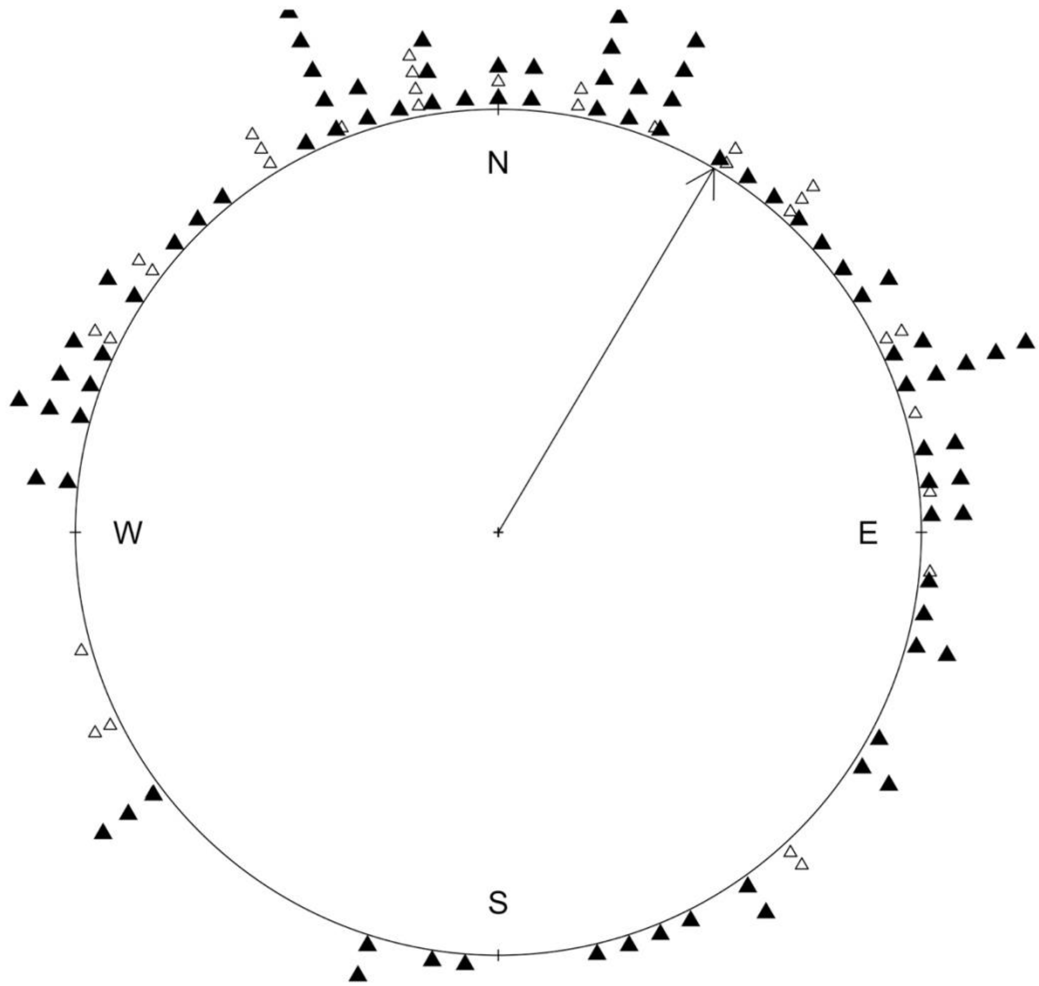
Figure 4.1. Nest orientation for Florida Grasshopper Sparrow nest openings (2014-2016) at Three Lakes, FL (Filled triangles, n = 82) and at the Ranch, FL (Open triangles, n = 34). Arrow depicts pooled mean of 30.6°.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Summary and Conclusions

Habitat selection is the result of decision-making behaviors by an organism whereby certain characteristics of an area are preferentially selected (Jones 2001). The selection process is often dependent on multiple factors depending on the intended use of the habitat, such as breeding, foraging, or cover from predators. The cues used to select a certain habitat and the results of the selection process can be difficult to determine in species exhibiting low population densities, in which high-quality habitat may not be occupied mainly due to a lack of individuals (Greene and Stamps 2001). By using long-term data and incorporating fitness from demographic studies, I attempt to parse out any potential conflicts between habitat quality and selection.

In my dissertation I explored habitat selection for several different functions, including nesting habitat, territory occupancy based on resource availability, and habitat occupancy based on prescribed fire area and timing. The Florida Grasshopper Sparrow is critically endangered and information from this dissertation can help elucidate several fundamental questions regarding important parts of their life for habitat management and for future monitoring of the sparrows. Specifically, I looked at the nesting habitat at the two sites containing the largest remaining populations of the sparrows and was not able to determine any microhabitat characteristics that contributed to nest success, which suggests that other factors are impacting nest success (Ch. 1). I also compared the habitat around nests at these two different sites, dry prairie and cattle pasture, and determined the range of microhabitat characteristics that the sparrow can tolerate and what their selection criteria might be in the different habitats.

I also examined another critical aspect of territory settlement decision-making process, that of food availability to see how the Florida Grasshopper Sparrows respond to differences in food availability (Ch. 2). The habitat is burned by prescribed fires on a periodic basis, but it was not known how or if the timing of prescribed fires affects arthropod abundance in the habitat. I found that there is a significant difference in the number of arthropods in the different burn treatments and this may be one reason that the Florida Grasshopper Sparrows choose to settle in recently burned habitats. The number of arthropods also differed between the habitat types, with more present on the grazed site than the dry prairie, which may help to explain why Florida Grasshopper Sparrows are attracted to the site and they choose to remain there.

The entire population of Florida Grasshopper Sparrows has experienced a large decline since the 1990's, which is more pronounced at some sites, such as Avon Park Air Force Range (96% decline), and less severe at Three Lakes Wildlife Management Area (65% decline; Florida Grasshopper Sparrow Working Group, unpublished data). Since they were federally listed as endangered in 1986, management goals were established to burn the dry prairie habitat where the sparrows are found on a 2-3 year rotation (Delany et al. 1985). I looked at long-term point count data from one of the sites, Avon Park Air Force Range, in addition to prescribed fire extent data to determine past patterns of occupancy and colonization (Ch. 3). We found a relationship with the likelihood that the Florida Grasshopper Sparrows would persist at a point count station between years with the maximum time since the last fire at the larger spatial scale. We did not find a relationship with colonization or with seasonality of the prescribed fires, which may be in part due to the dramatically declining population at the site over the time period. The misclassification model that we developed for the statistical analysis of this chapter can also be used in other studies, in particular, those involving endangered or threatened species where accuracy of occupancy is important.

Currently the Florida Grasshopper Sparrow population is very low and may already be susceptible to Allee effects or other problems that occur in small populations (Courchamp et al.

1999). In spring of 2019 reintroductions of captive bred individuals to supplement the current breeding population were started in an effort to avoid extinction. Information from my chapters on nesting habitat and arthropod availability may help to determine suitable management strategies to ensure that preferred habitat and food resources are maintained for this vulnerable sparrow and may be useful for other declining organisms as well.

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