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Research Paper

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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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 seven of eight 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 because of the more homogenous habitat at that site. We did not find a vegetative component of nest success, which suggests that other nonvegetative 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.

Le microhabitat influe sur la sélection du site de nidification dans les prairies sèches, mais pas dans les pâturages, chez le Bruant sauterelle de Floride (*Ammodramus savannarum floridanus*), espèce en voie de disparition

RÉSUMÉ. Les caractéristiques de la végétation peuvent influer sur la sélection du site de nidification et la survie du nid des oiseaux. Le Bruant sauterelle de Floride (*Ammodramus savannarum floridanus*), un oiseau de prairie endémique du centre de la Floride qui niche au sol, est en voie de disparition critique. Présentement, les deux populations restantes les plus grandes se trouvent à des endroits dont l'habitat est aménagé différemment. Le premier endroit fait l'objet de brûlages réguliers afin d'y maintenir l'habitat naturel de prairie sèche, tandis que le second est un pâturage qui est fauché et brûlé pour optimiser le broutement du bétail. L'effet de la végétation sur la sélection du site de nidification et le succès de nidification du Bruant sauterelle de Floride dans ces différents milieux est mal connu. Nous avons mesuré les caractéristiques du microhabitat (pourcentage de la couverture de végétation et hauteur de l'herbe) autour des nids de bruants et avons appareillé aléatoirement des parcelles aux deux endroits durant trois saisons de nidification (2014-2016). Le pourcentage de la couverture différait significativement entre les sites pour sept des huit types de végétation; le pâturage était principalement caractérisé par des herbes, et la prairie sèche, par une végétation naturelle plus diversifiée. Malgré ces différences en matière de végétation, la hauteur des herbes était la même aux deux endroits, ce qui laisse croire que la hauteur des plantes, plutôt que l'assemblage d'espèces végétales, pourrait être plus importante dans la sélection du site du nid chez cet oiseau. Le microhabitat autour des nids dans la prairie sèche comportait 31 % moins de sol nu et 32 % plus d'herbes que les parcelles sans nid. Aucune variable n'a prédit le positionnement des nids dans le pâturage de bétail, peut-être à cause de la plus grande homogénéité de l'habitat à cet endroit. Nous n'avons pas trouvé de composante végétale associée au succès de nidification, laissant planer que d'autres facteurs non liés à la végétation pourraient influer sur la prédation des nids. La compréhension des caractéristiques végétales associées aux nids de Bruant sauterelle de Floride contribuera à guider les stratégies d'aménagement d'habitat destinées à maintenir la hauteur de la végétation aux sites de nidification de cette espèce en voie de disparition critique.

Key Words: *Ammodramus savannarum; conservation; dry prairie; endangered species management; Florida Grasshopper Sparrow; nest site selection; vegetation structure*

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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. 2005*a*). 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. 2019*a*), 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 because 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 because 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 because 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 because of 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). Although some studies show a relationship between nest success and microhabitat vegetation variables (Taylor et al. 1999, Winter et al. 2005*b*), others show no relationship (Vickery et al. 1992*a*, Rodewald et al. 2001, Winter et al. 2005*b*). It is unlikely that a single vegetation component influences nesting success and may be a combination of different vegetation variables. Grasshopper Sparrows 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 because of rapid declines and a dramatic loss of habitat (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 (Hewett Ragheb et al. 2019*b*). 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 1998*a*). 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. 2019*b*).

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? (3) Does microhabitat predict nesting success? We aim 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 1998*a, b*). 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 (16–21 m) 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 3000 ha in size, which included a 1728 ha area of relic dry prairie (Fig. 1). The Florida Fish and Wildlife Conservation Commission manages Three Lakes for Florida Grasshopper Sparrows and other wildlife by frequent prescribed burning (~2-year interval), mechanical roller chopping to reduce shrub density (prior to burning), and tree removal when necessary (Hewett Ragheb et al. 2019*a*). The dry prairie habitat at Three Lakes was characterized by low shrubs, pyrogenic grasses, and herbaceous forbs with small patches of bare ground (FNAI 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 (FNAI 2010).

Fig. 1. Dry prairie habitat at Three Lakes Wildlife Management Area, Osceola County, Florida.

The study area at the Ranch was 1012 ha in size and consisted of semi-improved pasture interspersed with small ponds and hammocks (Fig. 2). The Ranch had been privately managed for cattle grazing for at least 12 years by mowing every two to three 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 (Willcox et al. 2010; G. Hendricks, Florida Eco Enterprises, LLC, *unpublished data*). 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*).

Fig. 2. Cattle pasture habitat at the Ranch, Osceola County, Florida.

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. 2019*a, b*). 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 two to three days until nestlings were five days old, then daily until nestlings fledged at seven to eight 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 two 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 nonoak 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 four meters from the nest viewing from a height of one 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 renesting nearby. We acknowledge that grassland birds often have one side of the nest that is less obstructed to provide an escape to facilitate antipredator displays (Delany and Linda 1998*b*). 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 nonoak shrubs. Most of these categories were identified as important to nesting in previous studies with Florida Grasshopper Sparrows (Delany and Linda 1998*b*, Fisher and Davis 2010), however, we added the categories of prostrate saw palmetto trunks and separated dwarf oak from nonoak 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 0º and 359º for the paired non-nest plot. If the random point was in a nongrassland 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 because 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 ($\alpha = 0.005$) to examine the differences in vegetation variables (8% 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 8% 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 overparameterization. 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 two AICc units of the top model were considered to be parsimonious and carried over to the next stage unless an examination of the 95% 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 nonoak 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 ($\alpha = 0.05$; *ResourceSelection* package in RStudio; RStudio Team 2016, 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 pseudoreplication 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. 2019*b*). We used the 8% 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 overparameterization. For Stage 1, we compared the null model with a model containing only a fixed-effect covariate for site (Three Lakes, Ranch), and univariate and additive multivariate combinations of 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 because 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, respectively. 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 renesting 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.

Table 1. Total number of Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) nests found at both sites, Three Lakes Wildlife Management Area 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)

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%), nonoak 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 95% 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 the 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 three models within two AICc values of the top model, but we concluded that none of the variables were informative because the 95% 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. 3) and increasing grass cover (odds ratio: 9.274; Fig. 4). 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 -0.831, 1.024), -2.514 (CI -4.165, -0.642), and 2.227 (CI 0.437, 3.543), respectively.

Table 2. All but two microhabitat variables at nest and non-nest plots in Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) territories differed between Three Lakes Wildlife Management Area (n = 182) and the Ranch (n = 64) in Osceola County, Florida during 2014–2016. Mann-Whitney U-test α = 0.005, * P < 0.005.

		Three Lakes	Ranch
Variable	U	Mean (SD)	Mean (SD)
Bare Ground (%)	946.5	34.0 (19.1) *	7.6 (11.9) *
Litter (%)	2818.5	14.5 (14.0) *	5.8 (3.9) *
Saw palmetto trunks (%)	4087.5	4.1 (7.2) *	0.5 (2.6) *
Saw palmetto leaves (%)	2381	12.0 (15.0) *	1.8 (7.5) *
Grass (%)	10906.5	36.4 (21.1) *	84.0 (20.7) *
Forbs (%)	6222	8.7 (8.8)	9.0 (9.3)
Dwarf oak (%)	1082.5	23.7 (20.1) *	1.1 (3.9) *
Nonoak shrubs (%)	3161.5	9.8 (15.6) *	0.9 (2.2) *
Grass height (cm)	6241.5	56.1 (18.1)	59.8 (21.9)
Visual obstruction (cm)	4166	32.9 (11.9)	39.1 (16.9)

Fig. 3. Modeled estimates of the relative probability that a plot at Three Lakes Wildlife Management Area, Osceola County, Florida would be selected for Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) nest placement based on the percent cover of bare ground. Dotted lines are upper and lower 95% confidence intervals.

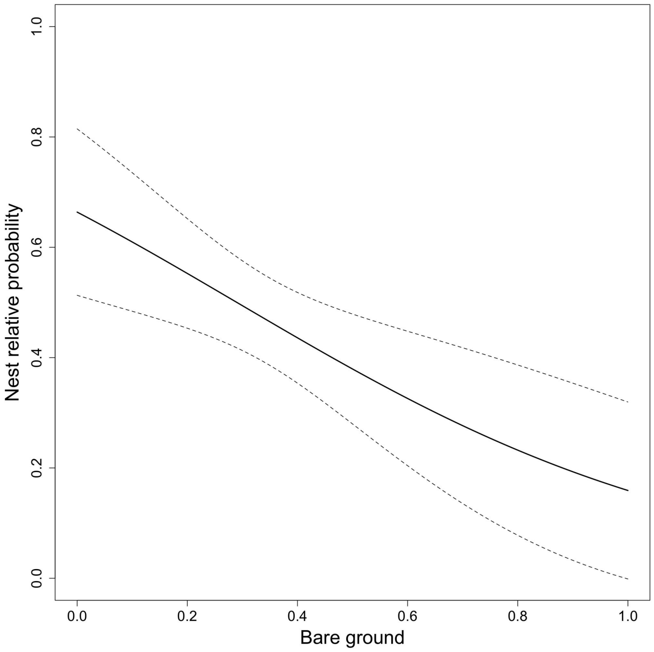
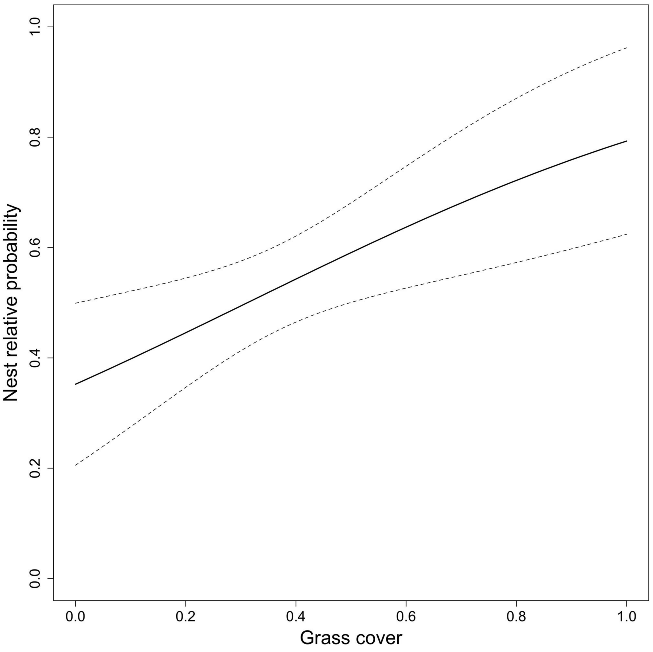


Fig. 4. Modeled estimates of the relative probability that a plot at Three Lakes Wildlife Management Area, Osceola County, Florida would be selected for Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) nest placement based on the percent cover of grasses. Dotted lines are upper and lower 95% confidence intervals.



For the Ranch, no microhabitat variables predicted nest site selection because 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 95% confidence interval for the grass height parameter estimate (0.016) contained zero (-0.007, 0.040) 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 four 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

Table 3. Model selection table for generalized linear models representing the influence of vegetation on Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) nest site selection at Three Lakes Wildlife Management Area (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 ≤ 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 + nonoak 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 + nonoak 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

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 two 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. 2005*a*). Although bare ground in front of a nest entrance may facilitate antipredator distraction displays (Delany and Linda 1998*b*), too much would leave a nest without enough concealment for the adults to hide from predators. In contrast to our results, Delany and Linda (1998*b*) 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 1998*b*).

The entire nesting cycle for Florida Grasshopper Sparrows lasts ~21 days (Vickery 1996). It is unclear how long the female takes to determine a suitable nesting site, but renesting 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 two weeks after nest completion (the average time between nest completion and data collection was 8.6 days). Although 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.

Table 4. Model selection table for generalized linear models representing the influence of vegetation on Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) 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 variable				
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+ dwarf oak+ nonoak 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

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 because 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 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 are 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 two 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. (2019*b*). Although our nest success data did not show a site effect, evidence from Hewett Ragheb et al. (2019*b*) 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. 2019*b*), and rate of decline in the population as a whole (Florida Grasshopper Sparrow Working Group, *unpublished data*) suggest it might not persist there.

Table 5. Model selection table for Shaffer logistic exposure models representing the influence of vegetation on Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) nest success at Three Lakes Wildlife Management Area 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
Nonoak 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 + nonoak shrubs	3	1.49	0.057	-98.987
Palmetto leaves + nonoak 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
Nonoak 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

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 because of depredation by mammals and snakes, while nests at the cattle pasture were primarily depredated by fire ants (*Solenopsis invicta*; Hewett Ragheb et al. 2019*b*). 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. 2005*b*, 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. 1992*b*).

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. Because 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.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1558

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