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RESEARCH ARTICLE

# Nest-site selection and nest survival of Bachman's Sparrows in two longleaf pine communities

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## ABSTRACT

Longleaf pine (*Pinus palustris*) ecosystems of the southeastern United States have experienced high rates of habitat loss and fragmentation, coinciding with dramatic population declines of a variety of taxa that inhabit the system. The Bachman's Sparrow (*Peucaea aestivalis*), a species closely associated with fire-maintained longleaf pine communities, is listed as a species of conservation concern across its entire range. Bachman's Sparrow breeding biology may provide valuable insights into population declines and inform restoration and management of remnant longleaf pine forest, but the species' secretive nesting habits have received little attention. We located 132 Bachman's Sparrow nests in the Coastal Plain and Sandhills physiographic regions of North Carolina, USA, during 2014–2015, and modeled nest-site selection and nest survival as a function of vegetation characteristics, burn history, temporal factors, and landscape-level habitat amount. There were distinct differences in nest-site selection between regions, with Bachman's Sparrows in the Coastal Plain region selecting greater woody vegetation density and lower grass density at nest sites than at non-nest locations. In contrast, sparrows selected nest sites with intermediate grass density and higher tree basal area in the Sandhills region. Despite clear patterns of nest-site selection, we detected no predictors of nest survival in the Sandhills, and nest survival varied only with date in the Coastal Plain. Daily survival rates were similar between regions, and were consistent with published studies from the species' core range where declines are less severe. Overall, our results indicate that creating and maintaining community-specific vegetation characteristics through the application of frequent prescribed fire should increase the amount of nesting cover for Bachman's Sparrows.

*Keywords:* Bachman's Sparrow, fire, landscape, longleaf pine, nest survival, nest-site selection, *Peucaea aestivalis*, physiographic region

## Selección del sitio de anidación y supervivencia de los nidos de *Peucaea aestivalis* en dos comunidades de pinos de hoja larga

## RESUMEN

Las comunidades de pinos de hoja larga (*Pinus palustris*) del sudeste de Estados Unidos han experimentado altas tasas de pérdida de hábitat y fragmentación, coincidiendo con la disminución poblacional drástica de una variedad de taxa que habitan el sistema. *Peucaea aestivalis*, una especie muy asociada con los ecosistemas de pino de hoja larga mantenidos por fuego, está listada como de preocupación para la conservación a lo largo de todo su rango. La biología reproductiva de *P. aestivalis* podría brindar información importante sobre las disminuciones poblacionales y contribuir con las acciones de restauración y manejo de los bosques remanentes de pino de hoja larga, pero los hábitos reservados de anidación de la especie han sido poco estudiados. Localizamos 132 nidos de *P. aestivalis* en las regiones fisiográficas de la Llanura Costera y las Colinas de Arena de Carolina del Norte durante 2014 y 2015, y modelamos la selección de los sitios de anidación y la supervivencia de los nidos como una función de las características de la vegetación, la historia de incendios, los factores temporales y la cantidad de hábitat a escala de paisaje. Hubo diferencias distintivas en la selección del sitio de anidación entre regiones. *P. aestivalis* eligió mayor densidad de vegetación leñosa y menor densidad de pastos en los sitios de anidación que en las localizaciones sin nidos en la región de la Llanura Costera. Por el contrario, *P. aestivalis* eligió sitios de anidación con una densidad intermedia de pastos y mayor área basal de árboles en las Colinas de Arena. A pesar de estos patrones claros de selección del sitio de anidación, no detectamos predictores de la supervivencia del nido en las Colinas de Arena, y la supervivencia del nido solo varió con la fecha en la Llanura Costera. Las tasas de supervivencia diaria fueron similares entre regiones y fueron consistentes con los estudios publicados provenientes del rango central de la especie, donde las disminuciones son menos severas. En general, nuestros resultados indican que la creación y el mantenimiento de

características comunitarias específicas de la vegetación a través de prescripciones frecuentes de fuego deberían aumentar la cantidad de hábitat de anidación para *P. aestivalis*.

*Palabras clave:* fuego, paisaje, *Peucaea aestivalis*, pino de hoja larga, región fisiográfica, selección del sitio de anidación, supervivencia del nido

## INTRODUCTION

Habitat selection theory assumes that birds are under selective pressures to choose nest sites that maximize reproductive success and fitness (Jaenike and Holt 1991). Predation is the primary cause of nest failure for a wide range of species (Ricklefs 1969, Martin 1995), and nest success has direct consequences on fitness (Martin 1998). Thus, when selecting nest sites, birds should attempt to minimize the likelihood of nest failure by selecting sites that reduce the risk of predation (Martin 1998). Birds can inhibit the search efficiency of predators by choosing vegetation characteristics that increase nest concealment or by selecting nest sites that are surrounded by many potential nest substrates (Martin 1993, Moorman et al. 2002). Such nest-site selection behaviors are likely to change in response to variation in resource availability, climatic conditions, predation risk, brood parasitism, or competition stemming from broad environmental gradients or disparate geographic areas that a species may occupy across its range (Flesch and Steidl 2010, Boves et al. 2013).

Although theory predicts that nest-site selection should be adaptive, empirical studies often demonstrate a lack of congruence between factors important for nest-site selection and nest survival (Chalfoun and Schmidt 2012). For example, anthropogenic habitat change may lead to a decoupling of previously adaptive nest-site selection and nest survival in the form of ecological traps (Misenhelter and Rotenberry 2000, but see Meyer et al. 2015). Diverse predator communities and nest-searching behaviors could also preclude birds from choosing nest sites that are safe from all predators simultaneously (Filliater et al. 1994). Further, landscape context (Thompson et al. 2002, Shake et al. 2011), proximity to habitat edges (Chalfoun et al. 2002, Shake et al. 2011), variation in weather conditions (McFarland et al. 2017), nest initiation date or year (Grant et al. 2005), and nest age (Davis 2005, Grant et al. 2005) can all have a greater influence on nest survival than vegetation characteristics at the nest site. Therefore, gaining insight into the factors that are important for nest-site selection, and their effects on nest survival, is not always straightforward. Nevertheless, understanding the relationship between nest-site selection and nest survival can be critical for guiding management strategies for declining species, and this information may need to be gathered across a wide range of environmental conditions when species have a broad geographic distribution.

The Bachman's Sparrow (*Peucaea aestivalis*) is a species of conservation concern that is strongly associated with the imperiled and fire-dependent longleaf pine (*Pinus palustris*) ecosystem in the southeastern U.S. (Dunning 2006). As a ground-nesting species, the Bachman's Sparrow relies on a diverse groundcover of grasses, forbs, and low shrubs, typically maintained by prescribed fire (Dunning and Watts 1990, Plentovich et al. 1998). Preferred vegetation conditions are ephemeral; sparrows regularly abandon sites in the absence of frequent fire (>3-yr interval) or mechanical disturbance that prevents the development of tall shrubs that outcompete herbaceous vegetation (Engstrom et al. 1984, Glitzenstein et al. 2003) and dense grass that can impede movement on the ground (Dunning 2006, Brooks and Stouffer 2010, Jones et al. 2013, Taillie et al. 2015). Throughout their range, Bachman's Sparrows use forests dominated by longleaf pine that are strikingly variable and diverse depending on geographic location, climate, soil, topography, and fire frequency (Peet 2006). Due to extensive habitat loss from forest conversion and fire suppression, the longleaf pine ecosystem has been reduced to 3–5% of its historical range (Frost 2006), and much of the remaining habitat exists as scattered and degraded remnant patches (Van Lear et al. 2005). Consequently, the Bachman's Sparrow population has steadily declined across its range (−3.43% since 1966; Sauer et al. 2017), and this trend, along with its recent status as an indicator species for longleaf pine forests, has spurred renewed interest in its study (Dunning 2006, Hannah et al. 2017).

Although knowledge of demographic rates, such as reproductive success, is potentially important to reversing population declines, published data on the breeding biology of Bachman's Sparrows are limited due to the difficulty of finding the species' well-hidden nests (Dunning 2006). Several studies have estimated daily nest survival rates (Haggerty 1988, Stober and Krementz 2000, Perkins et al. 2003, Tucker et al. 2006, Jones et al. 2013), but few have attempted to identify which vegetation features are important for nest-site selection or to link nest success to nest-site characteristics (Haggerty 1988, 1995, Jones et al. 2013). Three studies included temporal covariates (e.g., nest stage, time within breeding season, and year) in their analyses (Haggerty 1995, Stober and Krementz 2000, Tucker et al. 2006), and Stober and Krementz (2000) showed that nest survival varied significantly by year and declined later in the breeding season. Previous research was based on samples comprising <50
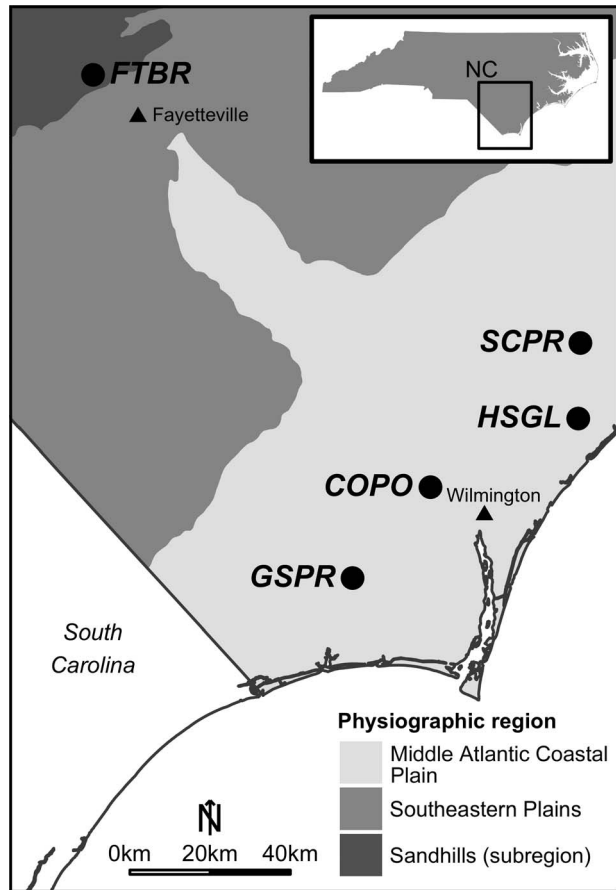
**FIGURE 1.** Study sites and physiographic regions in North Carolina (NC), USA, where nest-site selection and nest survival data for Bachman's Sparrows were collected in 2014–2015. Physiographic region designation is adapted from USEPA level III classifications, except for the Sandhills which is a level IV subregion of the Southeastern Plains (https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states). Study sites are indicated with 4-letter abbreviations. From west to east: FTBR = Fort Bragg Military Installation (*n* = 85 nests), GSPR = Green Swamp Preserve (*n* = 3 nests), COPO = Compass Pointe (*n* = 1 nest), HSGL = Holly Shelter Game Land (*n* = 42 nests), and SCPR = Shaken Creek Preserve (*n* = 1 nest).

nests, was restricted to single sites, and did not address the effects of landscape-scale factors on nest survival. Given the lack of nesting information and the variability of longleaf pine communities across the species' range, research examining community-specific nest-site selection and nest survival is needed to guide conservation efforts and to provide further insights into Bachman's Sparrow population declines.

Here, we investigate spatial variation in the nesting ecology of Bachman's Sparrows in longleaf pine communities in the Middle Atlantic Coastal Plain and Sandhills physiographic regions of south-central North Carolina, USA. Specifically, the objectives of our study were to (1) identify important vegetation features selected for nest

sites; and (2) evaluate the influence of temporal, local-, and landscape-scale covariates on nest survival within each region.

## METHODS

### Study Area

In 2014 and 2015, we located and monitored nests of Bachman's Sparrows at 5 sites within the Middle Atlantic Coastal Plain (hereafter, Coastal Plain) and Sandhills physiographic regions in North Carolina, USA (Figure 1). The Coastal Plain consisted of flat terrain with little topographic variability (elevation: 0–30 m), and mean annual precipitation was 160 cm (Palmquist et al. 2015). Four study sites in the Coastal Plain ranged in size from 552 to 25,695 ha, and were managed by the North Carolina Wildlife Resources Commission (NCWRC), The Nature Conservancy, and one private landowner. Study plots (*n* = 22, size range = ~2–161 ha) were primarily composed of mesic longleaf pine savannas bordered by pocosin wetlands. Wet pine savannas were characterized by seasonally saturated soils, an open canopy of longleaf pine, and a diverse understory of threeawn (*Aristida* spp.), bluestem (*Andropogon* spp.), cinnamon fern (*Osmunda cinnamomea*), western brackenfern (*Pteridium aquilinum*), inkberry (*Ilex glabra*), blue huckleberry (*Gaylussacia frondosa*), blueberry (*Vaccinium* spp.), swamp bay (*Persea palustris*), coastal sweetpepperbush (*Clethra alnifolia*), switchcane (*Arundinaria tecta*), and insectivorous plants, depending on soil moisture (Figure 2). Prescribed fire typically was applied in the dormant and early growing seasons at a 1–5 yr return interval, but time since fire exceeded 10 yr at a site owned by a resort community (Compass Pointe; Table 1). Study sites in the Coastal Plain were imbedded in a matrix of urban and rural residential development, row crop agriculture, and loblolly pine (*Pinus taeda*) plantations.

In contrast, the Sandhills physiographic region, located in central North Carolina, was characterized by rolling, hilly terrain (elevation: 43–176 m) interspersed with hillside seeps feeding numerous blackwater streams (Sorrie et al. 2006). Mean annual precipitation was 120 cm (Sorrie et al. 2006). We focused our work in the Sandhills in a single site, Fort Bragg Military Installation (hereafter, Ft. Bragg), which occupied 73,469 ha in parts of Cumberland, Harnett, Hoke, and Moore counties. At Ft. Bragg, our study was restricted to 28 plots ranging in size from ~8 to 74 ha, which were part of larger areas chosen to represent high- and low-intensity military training levels (intensity of military training did not affect Bachman's Sparrow abundance or nest survival; Fish 2017). Ft. Bragg and other adjacent areas in the Sandhills comprised the largest contiguous remnant of the longleaf pine ecosystem in North Carolina (Sorrie et al. 2006). Uplands in this region

**FIGURE 2.** Examples of typical longleaf pine community understory in the Coastal Plain (left) and Sandhills (right) physiographic regions in North Carolina, USA. Note the greater diversity and abundance of low shrubs and forbs in the Coastal Plain region. Both photographs show locations that had been burned in the preceding year.

were xeric and characterized by well-drained, sandy soils (Sorrie et al. 2006). Longleaf pine was the dominant tree species, with an understory of sparse vegetation, including threeawn, dwarf huckleberry (*Gaylussacia dumosa*), turkey oak (*Quercus laevis*), and blackjack oak (*Quercus marilandica*), that was less diverse than the Coastal Plain understory community (Figure 2). Ft. Bragg was divided into >1,300 burn units, which were managed with prescribed fire at a 3-yr return interval, with burns usually occurring between January and September (Table 1).

### Nest Searching and Monitoring

Female Bachman's Sparrows construct exceptionally well-concealed nests (Dunning 2006, Tucker et al. 2006), and finding nests by extensively searching nesting cover was logistically unfeasible. Therefore, we generally relied on

**TABLE 1.** Time since fire (yr) averaged across study plots surveyed for Bachman's Sparrow nests by physiographic region and study site in North Carolina, USA, 2014–2015. 'NA' indicates that a site was not surveyed in the corresponding year. See Figure 1 for study site and physiographic region locations.

| Physiographic region | Site | Time since fire (yr) | |
|---|---|---|---|
| | | 2014 | 2015 |
| Coastal Plain | Compass Pointe | >10.0 [a] | NA |
| Coastal Plain | Green Swamp Preserve | NA | 3.3 |
| Coastal Plain | Holly Shelter Game Land | 2.1 | 1.6 |
| Coastal Plain | Shaken Creek Preserve | 2.0 | NA |
| Sandhills | Fort Bragg Military Installation | 2.1 | 2.1 |

[a] No data available for time since fire, but it had been at least 10 yr.

observing the breeding behaviors of adult sparrows to find nests. At the beginning of each breeding season, we used mist nets and recorded vocalizations of Bachman's Sparrows to capture most of the focal males, which were banded with a U.S. Geological Survey (USGS) metal band and a unique combination of colored leg bands. We then collected behavioral data on individual male sparrows (Coastal Plain: $n = 84$; Sandhills: $n = 68$) at 1-week intervals, during which an observer spent 60 min in a male's territory recording reproductive behaviors and mapping territory boundaries (Vickery et al. 1992, Tucker et al. 2006). Nests were typically located by observing the following behavioral cues: (1) females carrying nesting material; (2) adults carrying food to nestlings or removing fecal sacs from nests; and (3) sparrows flushing from a nest or performing distraction displays. Prior to the onset of breeding, we trained field crews on these key behavioral cues and potential nest substrates based on the literature. Field crews in each region consisted of 1–2 crew leaders with experience searching for ground nests, and 2–3 technicians with no previous experience searching for passerine nests.

Nests were also found by radio-tagging and tracking a subset of color-banded male (Coastal Plain: $n = 37$) or female (Sandhills: $n = 24$) sparrows to nests for concurrent telemetry studies. We attached a 0.64-g (~3.5% of body mass) radio-transmitter (Blackburn Transmitters, Nacogdoches, Texas, USA) using a modified figure-eight leg-loop harness (Streby et al. 2015) to track males and females to nests. Following discovery by either nest-searching method, nests were flagged 5–10 m away and monitored every 1–4 days using standard nest-monitoring methods that minimized nest-site disturbance (Martin and Geupel 1993). We considered a nest successful if at least 1 Bachman's Sparrow young fledged, and confirmed fledging

by observing parental behavior (i.e. alarm calling and carrying food) near the nest during checks and weekly behavioral surveys.

Because of differences in nest-searching methods, nests in the Coastal Plain region were typically located by observing adults attending nests; this resulted in nests being found mostly during the nestling stage (73% of nests). Conversely, nests in the Sandhills were located mainly by following radio-tagged females, and 59% of nests found were in the nest-building or incubation stage.

### Nest-site Vegetation Measurements

Groundcover vegetation structure was measured at 1-m increments along 2 perpendicular 10-m transects centered on the nest site. At each transect point, vegetation structure was quantified by recording the number of 'hits' (i.e. contacts) of each vegetation category on a 1.5-m vertical pole. Vegetation categories included grass, woody vine–shrub (hereafter 'woody vegetation'), and forb–fern following Taillie et al. (2015). Using this sampling protocol, we obtained 3 indices of density and height for each vegetation category: (1) vertical density, which included the number of vegetation hits along the entire length of the pole; (2) groundcover density, calculated using the number of hits on the first 0.1-m section of the pole only (Wiens and Rotenberry 1981); and (3) maximum height, recorded as the tallest 0.1-m section of the pole with a vegetation contact (Wiens and Rotenberry 1981, Moorman and Guynn 2001, Taillie et al. 2015). Groundcover vegetation structure measurements were then averaged across the 21 sampling points for each plot. Finally, we estimated the total basal area of pines surrounding each nest from the plot center with a 10-factor prism.

We repeated these measurements at a reference plot (i.e. a non-nest location) 50 m away from the nest in a random direction and within the same longleaf pine stand. We selected this distance to eliminate overlap between nest and reference points while constraining reference locations to within a bird's home range (mean ± SD: 7.92 ± 4.05 ha; Winiarski 2016). Vegetation sampling for nests and paired reference plots was completed within 14.6 ± 11.4 days (range = 0–69 days) of a nest fledging or failing.

### Landscape Data

Distance to the nearest edge for each nest was calculated using the gDistance function in the rgeos package (Bivand and Rundel 2015) in R (R Core Team 2015). Our definition of edge included abrupt changes in vegetation type (i.e. pocosin edges), fire breaks, roads, and power line corridors, and we digitized these features from aerial images or Geographic Information System data layers provided by agency personnel at Ft. Bragg and the NCWRC. We also obtained landscape-scale habitat amount surrounding each nest site using a Bachman's Sparrow species distribution model (SDM; Pickens et al. 2017) converted to a binary habitat model (i.e. probability of occurrence ≥0.5 classified as habitat, and values <0.5 classified as nonhabitat). The SDM was built using Bachman's Sparrow occurrence (i.e. point counts conducted in North Carolina from 2006 to 2013), fire, and land-cover data, and had high predictive ability (area under the curve value = 0.88; Pickens et al. 2017). We used the spatialEco package (Evans 2016) in R (R Core Team 2015) and the binary SDM to derive the proportion of Bachman's Sparrow habitat within a 1-km buffer around each nest. We chose this metric because it offered a simple yet comprehensive index of patch size and isolation (Fahrig 2013) and has been shown to be an important predictor of Bachman's Sparrow occupancy (Taillie et al. 2015).

### Statistical Analyses

**Summary statistics.** We conducted all statistical analyses using R (R Core Team 2015). We used Mann-Whitney $U$ tests to compare nest-site vegetation variables between the Coastal Plain and the Sandhills. For all descriptive statistics of vegetation variables we present means ± SD, and we considered $U$ tests significant at $P \leq 0.05$.

**Nest-site selection.** We modeled nest-site selection using mixed-effects logistic regression models with the lme4 package (Bates et al. 2015). Because of strong regional variation in vegetation composition and structure, we developed separate model sets for each physiographic region. Prior to analysis, we tested for correlations ($r > |0.60|$) between all combinations of vegetation variables (Table 2). We used a manual forward-selection approach for model building (Burnham and Anderson 2002), in which we built univariate models separately and then sequentially added variables that lowered the value of Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002). In addition to a single linear effect of grass, we considered a quadratic effect of vertical grass density because dense grass can restrict Bachman's Sparrow movements on the ground in the absence of fire (Brooks and Stouffer 2010, Taillie et al. 2015). For all models, we included 'plot pair ID' as a random effect to account for nonindependence between each nest and its paired reference plot.

Because longleaf pine communities in the Coastal Plain and Sandhills are distinct, we expected different patterns of nest-site selection in each region. However, this expectation could potentially be confounded by variation in fire return intervals between physiographic regions rather than by regional differences in groundcover composition and structure. Therefore, we ran additional post hoc models to account for the effect of time since fire on nest-site characteristics in the Coastal Plain and Sandhills separate-

**TABLE 2.** Description of variables considered (indicated with an 'x') for examining nest-site selection and nest survival of Bachman's Sparrows in North Carolina, USA, 2014–2015.

| Variable | Description | Nest-site selection | Nest survival |
|---|---|:---:|:---:|
| GrdFB | Forb groundcover density (hits) | x | x |
| GrdGR | Grass groundcover density (hits) | x [a,b] | x [a,b] |
| GrdWD | Woody groundcover density (hits) | x [a] | x [a] |
| MaxFB | Forb maximum height (m) | x [a] | x [a] |
| MaxGR | Grass maximum height (m) | x | x |
| MaxWD | Woody vegetation maximum height (m) | x | x |
| VerFB | Forb vertical density (hits) | x | x |
| VerGR [c] | Grass vertical density (hits) | x | x |
| VerWD | Woody vegetation vertical density (hits) | x | x |
| PineBA | Pine basal area ($m^2$ $ha^{-1}$) | x | x |
| Date [c] | Ordinal date | | x |
| Edge | Distance to nearest edge (m) | | x |
| Fire | Time since fire (yr) | x | x |
| Habitat | Habitat amount within 1 km of the nest site (%) | | x |
| Year | Study year (2014 or 2015) | | x |

[a] Variables that were omitted in final analyses because of correlations with other variables (Coastal Plain). Vertical density measurements were chosen instead of groundcover density measurements based on lower $AIC_c$ values in preliminary analyses.
[b] Variables that were omitted in final analyses because of correlations with other variables (Sandhills). Vertical density measurements were chosen instead of groundcover density measurements based on lower $AIC_c$ values in preliminary analyses.
[c] Linear and quadratic relationships were tested.

ly. We analyzed individual nest-site characteristics (response variables) in relation to time since fire (predictor variable) for each physiographic region using generalized linear mixed models with the lme4 package (Bates et al. 2015). Response variables were fit to Poisson distributions by rounding vegetation data to the nearest whole number value. We included a random effect in each model to account for variation among study plots.

**Nest survival.** We included only depredated nests in the nest survival analysis and excluded abandoned nests, several of which we believed were related to researcher activity. We analyzed daily nest survival using the logistic-exposure method (Shaffer 2004). The logistic-exposure method is a generalized linear model with a binomial error distribution (0 = nest failed, 1 = nest survived) and a modified logit link function that adjusts for variable exposure length for each nest (i.e. the number of days between subsequent nest visits; Shaffer 2004). We applied the same manual forward-selection approach to building nest survival models for each region using the variables presented in Table 2. We included within-year (linear and quadratic relationships) and between-year effects because nest survival may be driven by temporal variation in weather patterns, predator abundance, and prey availability (Rotenberry and Wiens 1989, Grant et al. 2005). We included vegetation characteristics selected by Bachman's Sparrows at nest sites because we expected that they were adaptive and increased nest survival. We tested the effect of time since fire because it can alter predator communities in longleaf pine systems (Jones et al. 2004) and has been shown to limit reproductive performance of Bachman's

Sparrows when it exceeds 3 yr (Tucker et al. 2006). Finally, we included habitat amount and distance to edge to determine the influence of landscape-scale factors on nest survival. Daily nest survival estimates were used to derive percent nest success for each region by exponentiating the daily survival rate to the 22-day nesting period (Haggerty 1988, Tucker et al. 2006).

**Model selection.** We ranked the top nest-site selection and nest survival models according to their $AIC_c$ values using the MuMIn package (Bartoń 2016), and models were considered to be competitive if $\Delta AIC_c \leq 2$ (Burnham and Anderson 2002). For both analyses, we considered variables to be important if the 95% confidence intervals of the β estimates did not overlap zero.

## RESULTS

### Nest-site Characteristics between Regions

We located 132 Bachman's Sparrow nests (Coastal Plain: $n = 47$; Sandhills: $n = 85$) between 2014 and 2015. In the Coastal Plain, nests were primarily found in a single site, Holly Shelter Game Land ($n = 42$), with fewer nests found in the Green Swamp Preserve ($n = 3$), Compass Pointe ($n = 1$), and Shaken Creek Preserve ($n = 1$) sites. Across sites and years, time since fire averaged 1.4 yr in the Coastal Plain and 1.8 yr in the Sandhills. We used 130 nests in the nest-site selection analysis because 2 nests were destroyed by prescribed fire and could not be measured for vegetation characteristics. Several nest-site selection variables differed between physiographic regions: maximum height of forbs ($U = 2506.0$, $P < 0.02$), woody vegetation

**TABLE 3.** Summary statistics (mean ± SD) for Bachman's Sparrow nest site and reference plot vegetation variables, and Mann-Whitney $U$ statistics comparing nest-site vegetation between the Coastal Plain and Sandhills physiographic regions in North Carolina, USA, 2014–2015.

| Variable [a] | Coastal Plain | | Sandhills | | |
| --- | --- | --- | --- | --- | --- |
| | Nest site | Reference | Nest site | Reference | $U$ |
| GrdFB | 0.12 ± 0.12 | 0.07 ± 0.12 | 0.12 ± 0.20 | 0.18 ± 0.35 | 2106.0 |
| GrdGR | 1.40 ± 0.90 | 1.94 ± 1.04 | 1.48 ± 0.75 | 1.18 ± 0.85 | 1775.0 |
| GrdWD | 1.33 ± 0.64 | 1.00 ± 0.65 | 0.18 ± 0.17 | 0.18 ± 0.20 | 3802.0 [b] |
| MaxFB | 0.27 ± 0.11 | 0.25 ± 0.12 | 0.18 ± 0.15 | 0.19 ± 0.15 | 2056.0 [b] |
| MaxGR | 0.37 ± 0.11 | 0.42 ± 0.13 | 0.39 ± 0.11 | 0.39 ± 0.17 | 1724.0 |
| MaxWD | 0.24 ± 0.09 | 0.23 ± 0.10 | 0.37 ± 0.15 | 0.43 ± 0.26 | 842.0 [b] |
| VerFB | 0.65 ± 0.86 | 0.35 ± 0.53 | 0.52 ± 0.77 | 0.63 ± 0.83 | 2167.0 |
| VerGR | 5.61 ± 3.47 | 7.90 ± 4.57 | 5.29 ± 2.45 | 4.08 ± 2.88 | 1922.0 |
| VerWD | 2.90 ± 1.34 | 2.11 ± 1.12 | 1.11 ± 0.62 | 1.12 ± 1.00 | 3429.0 [b] |
| PineBA | 11.78 ± 6.90 | 11.36 ± 5.76 | 13.39 ± 5.12 | 11.43 ± 5.57 | 1539.5 |

[a] Variable abbreviations: GrdFB = forb groundcover density, GrdGR = grass groundcover density, GrdWD = woody vegetation groundcover density, MaxFB = forb maximum height, MaxGR = grass maximum height, MaxWD = woody vegetation maximum height, VerFB = forb vertical density, VerGR = grass vertical density, VerWD = woody vegetation vertical density, and PineBA = pine basal area.
[b] $P \leq 0.05$.

vertical density ($U = 3429.0$, $P < 0.001$) and groundcover density ($U = 3802.0$, $P < 0.001$) were greater at nest sites in the Coastal Plain, while woody vegetation maximum height ($U = 842.0$, $P < 0.001$) was greater at nest sites in the Sandhills (Table 3).

## Nest-site Selection
The top mixed-effects logistic regression models for Bachman Sparrow nest-site selection differed between physiographic regions (Table 4). Nest sites had lower grass vertical density and greater vertical density of

woody vegetation than reference locations in the Coastal Plain (Table 5, Figure 3). In the Sandhills, sparrows selected nest sites with intermediate vertical grass densities and greater tree basal area compared with reference locations (Table 5, Figure 3). There were no differences in nest-site characteristics (grass vertical density, woody vegetation vertical density, and pine basal area) across different fire return intervals in either the Coastal Plain or the Sandhills (Table 6), suggesting that Bachman's Sparrows consistently selected specific vegetation features regardless of time since fire.

**TABLE 4.** Number of parameters ($K$), Akaike's Information Criterion corrected for small sample size (AIC$_c$), difference in AIC$_c$ value ($\Delta$AIC$_c$), model weight ($w_i$), and negative log likelihood (−LogLike) for mixed-effects logistic regression models of nest-site selection by Bachman's Sparrows in the Coastal Plain and Sandhills physiographic regions of North Carolina, USA, 2014–2015. Paired plot ID was used as a random effect in all models.

| Model [a] | $K$ | $\Delta$AIC$_c$ [b] | $w_i$ | −LogLike |
| --- | --- | --- | --- | --- |
| **Coastal Plain** | | | | |
| VerWD + VerGR + GrdFB | 5 | 0.00 | 0.64 | −54.22 |
| VerWD + VerGR | 4 | 1.40 | 0.32 | −56.04 |
| VerWD | 3 | 5.81 | 0.04 | −59.34 |
| Null | 2 | 12.54 | 0.00 | −63.77 |
| **Sandhills** | | | | |
| MaxWD + PineBA + VerGR + VerGR$^2$ | 6 | 0.00 | 0.65 | −101.06 |
| PineBA + VerGR + VerGR$^2$ | 5 | 1.50 | 0.31 | −102.88 |
| MaxWD + VerGR + VerGR$^2$ | 5 | 7.45 | 0.02 | −105.86 |
| MaxWD + PineBA + VerGR | 5 | 8.50 | 0.01 | −106.38 |
| VerGR + VerGR$^2$ | 4 | 9.23 | 0.01 | −107.81 |
| PineBA + VerGR | 4 | 10.11 | 0.00 | −108.25 |
| MaxWD + VerGR | 4 | 13.89 | 0.00 | −110.14 |
| VerGR | 3 | 15.89 | 0.00 | −112.19 |
| Null | 2 | 22.34 | 0.00 | −116.45 |

[a] Variable abbreviations: VerWD = woody vegetation vertical density, VerGR = grass vertical density, GrdFB = forb groundcover density, MaxWD = woody vegetation maximum height, PineBA = pine basal area, VerGR$^2$ = grass vertical density squared, GrdFB = forb groundcover density, MaxGR = grass maximum height, and MaxWD = woody vegetation maximum height.
[b] AIC$_c$ values for the top-ranked models for the Coastal Plain and Sandhills regions were 119.14 and 214.63, respectively.

**TABLE 5.** Parameter estimates for the top Bachman's Sparrow nest-site selection models (Table 4) for the Coastal Plain and Sandhills physiographic regions of North Carolina, USA, 2014–2015.

| Parameter [a] | β | Lower 95% CL | Upper 95% CL |
|---|---|---|---|
| Coastal Plain | | | |
| GrdFB | 3.68 | −0.10 | 7.95 |
| VerGR | −0.14 | −0.27 | −0.04 |
| VerWD | 0.55 | 0.17 | 0.96 |
| Sandhills | | | |
| MaxWD | −1.68 | −3.52 | 0.04 |
| PineBA | 0.10 | 0.04 | 0.17 |
| VerGR | 0.91 | 0.47 | 1.41 |
| VerGR$^2$ | −0.06 | −0.10 | −0.02 |

[a] Parameter abbreviations: GrdFB = forb groundcover density, VerGR = grass vertical density, VerWD = woody vegetation vertical density, MaxWD = woody vegetation maximum height, PineBA = pine basal area, and VerGR$^2$ = grass vertical density squared.

**TABLE 6.** Generalized linear mixed model test statistics for analyses examining the effect of time since fire on important vegetation variables for Bachman's Sparrow nest-site selection for the Coastal Plain and Sandhills physiographic regions of North Carolina, USA, 2014–2015. Study plot ID was used as a random effect in all models.

| Variable | Z | P |
|---|---|---|
| Coastal Plain | | |
| Grass vertical density | 1.58 | 0.12 |
| Pine basal area | −1.76 | 0.08 |
| Woody vegetation vertical density | 0.38 | 0.71 |
| Sandhills | | |
| Grass vertical density | −0.97 | 0.33 |
| Pine basal area | −1.02 | 0.31 |
| Woody vegetation vertical density | −0.85 | 0.40 |

### Nest Survival

Of our total sample of 132 nests, we included 70 from the Sandhills and 43 from the Coastal Plain in the nest survival analysis, representing an effective sample size of 939 exposure days (Coastal Plain: $n = 285$; Sandhills: $n = 654$).

We excluded 2 nests destroyed by prescribed fire, 4 nests discovered the same day the nest fledged, 3 nests with unknown fates, and 9 nests considered abandoned by adults. Reasons for abandonment may have included finding nests during the building or egg-laying stages, attaching radio-tags to breeding females, or natural causes of abandonment that we were unable to separate from research activities. We also omitted an additional nest from the Coastal Plain as it represented an extreme outlier (i.e.
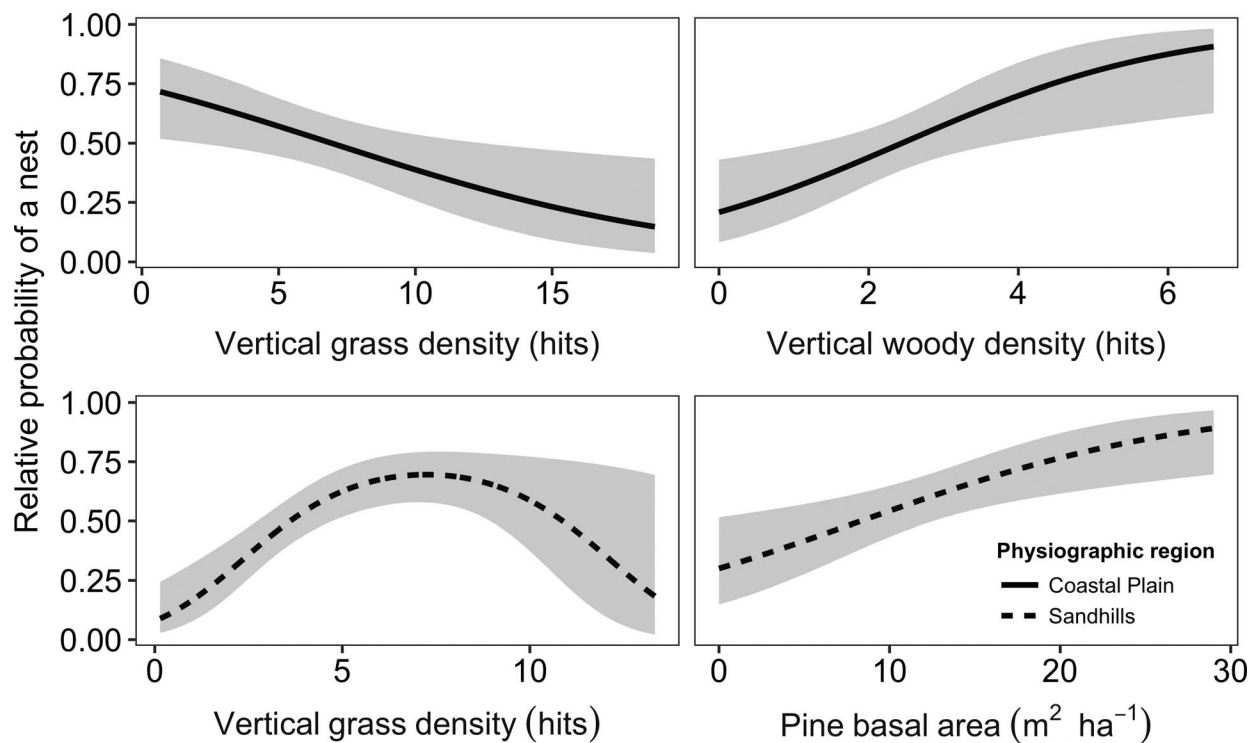


**FIGURE 3.** Predicted probability of selection of a nesting site by Bachman's Sparrows by physiographic region in North Carolina, USA, in 2014–2015. 'Hits' refers to the total number of vegetation contacts on a 1.5-m vertical pole averaged across a plot; each plot consisted of 2 perpendicular 10-m transects centered on a nest site and hits were measured at 1-m increments. Top left and bottom left plots show a linear and quadratic relationship, respectively, with vertical grass density. Shaded regions indicate 95% confidence intervals.
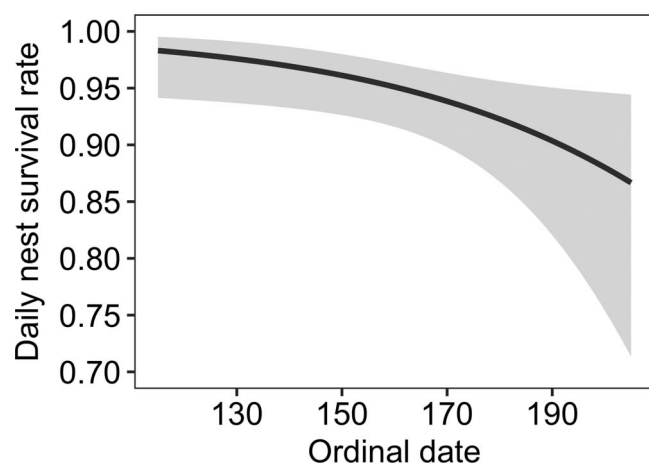
**FIGURE 4.** Predicted probability of Bachman's Sparrow daily nest survival rate in relation to ordinal date (day 130 = May 10 and day 190 = July 9) for the Coastal Plain of North Carolina, USA, in 2014–2015. Shaded region indicates 95% confidence interval.

**TABLE 7.** Number of parameters ($K$), Akaike's Information Criterion corrected for small sample size ($AIC_c$), difference in $AIC_c$ value ($\Delta AIC_c$), model weight ($w_i$), and negative log likelihood (−LogLike) for the final Bachman's Sparrow nest survival models following the forward selection procedure for the Coastal Plain and Sandhills physiographic regions of North Carolina, USA, 2014–2015. The top 5 models only are listed for the Sandhills region.

| Model [a] | $K$ | $\Delta AIC_c$ [b] | $w_i$ | −LogLike |
|---|---|---|---|---|
| Coastal Plain | | | | |
| Date | 2 | 0.00 | 0.42 | −42.45 |
| Date + Habitat | 3 | 1.74 | 0.18 | −42.27 |
| Date + Date² | 3 | 2.00 | 0.16 | −42.40 |
| Habitat | 2 | 2.10 | 0.15 | −43.50 |
| Null | 1 | 2.96 | 0.10 | −44.97 |
| Sandhills | | | | |
| Null | 1 | 0.00 | 0.12 | −92.91 |
| Year | 2 | 0.07 | 0.12 | −91.92 |
| Habitat | 2 | 1.14 | 0.07 | −92.46 |
| Edge | 2 | 1.15 | 0.07 | −94.46 |
| MaxWD | 2 | 1.21 | 0.07 | −92.49 |

[a] Variable abbreviations: Date = ordinal date, Date² = ordinal date squared, Habitat = percent habitat within 1 km of the nest site, Year = study year, Edge = distance to the nearest edge, and MaxWD = woody vegetation maximum height.
[b] $AIC_c$ values for the top-ranked models for the Coastal Plain and Sandhills regions were 89.01 and 187.84, respectively.

time since fire exceeded 120 mo) in the analysis. The best-fitting model for nest survival in the Coastal Plain included a negative linear relationship between increasing ordinal date and daily survival rate (DSR; β = −0.020; 95% CL: −0.047, −0.003; Figure 4). The 2 next-best models differed from the top model only by the addition of habitat amount and a quadratic term for ordinal date (Table 7), but the 95% confidence intervals around the parameter estimates for these models overlapped zero. In the Sandhills, there were no predictors of daily survival rate (all predictor variables had 95% confidence intervals that overlapped zero), and the null model was the top-ranked model (Table 7). The estimated daily survival rate was 0.951 (95% CI: 0.916–0.972) from the top Coastal Plain model and 0.939 (95% CI: 0.918–0.956) from the null Sandhills model. Nest success derived from these estimates was 33% (95% CI: 15–54%) for the Coastal Plain, and 25% (95% CI: 15–36%) for the Sandhills. Nest survival did not differ between physiographic regions ($Z = 0.02$, $P = 0.98$).

## DISCUSSION

Bachman's Sparrow nest sites were characterized by vegetation structure that varied by physiographic region. Although these differences could potentially have been attributed to differences in fire frequency between each region, mean time since fire was similar for nests located in the Coastal Plain and in the Sandhills. Nest-site characteristics also did not change across different burn histories within the Coastal Plain and the Sandhills, providing further evidence that vegetation composition and structure—rather than varying fire return intervals—likely drove differential nest-site selection in these regions.

However, it is important to note that these vegetation characteristics typically become less common as time since fire increases. Interestingly, nest-site features did not influence nest survival; instead, nest survival in the Coastal Plain region varied with date within the breeding season, whereas results from the Sandhills seemed to suggest that predation was opportunistic. Nevertheless, our results emphasize the importance of examining nest-site selection in different environments across a species' range, and highlight the need for managers to account for local conditions when developing conservation strategies for Bachman's Sparrows.

### Nest-site Selection
Bachman's Sparrows selected nest sites with a higher density of woody vegetation (Coastal Plain) and low or intermediate grass densities (Coastal Plain and Sandhills, respectively), but it remains unclear why these nest-site characteristics were important. One explanation could be that these vegetation features improved access to nests. Consistent with Haggerty (1995), adult sparrows in our Coastal Plain study sites often used woody shrubs as perches before approaching their nests (J. Winiarski personal observation). Also, woody shrubs may constitute important escape cover for Bachman's Sparrows and other sparrow species (Pulliam and Mills 1977, Dunning 2006). We also observed adults moving to nests on the ground after landing a few meters away, and that nest entrances

were open and characterized by little or no grass cover (J. Winiarski and A. Fish personal observations). Our observations and those of other researchers suggest that dense grass may restrict movement on the ground (Brooks and Stouffer 2010, Taillie et al. 2015) and consequently may hinder provisioning of nestlings (Haggerty 1988, Jones et al. 2013).

Microclimatic conditions could affect several components of nest success and productivity that we did not assess. For example, dense woody foliage could provide shelter from solar radiation and reduce thermal stress (Haggerty 1988, With and Webb 1993, Jones et al. 2013). Conversely, dense grass may negatively affect microclimate by holding more moisture from rain and dew compared with more sparse grasses (Jones et al. 2013). Adverse microclimatic conditions could affect several components of reproductive success (e.g., length of the nesting season, nest abandonment rate, and nestling growth; Dawson et al. 2005, Guthery et al. 2005), but we did not examine these components in our study. We observed signs of black foot disease (e.g., swollen, scaly, or lost digits) in 3 adults and in nestlings from 9 nests across the 2 regions (A. Fish and J. Winiarski personal observations); disease risk could be another factor exacerbated by moist conditions (J. Cox personal communication). Because Bachman's Sparrows in North Carolina and elsewhere are likely to experience intense solar radiation and heavy rainfall events during the breeding season, the importance of microclimate in relation to nest-site vegetation characteristics and nest success deserves further investigation.

Bachman's Sparrows in the Sandhills selected locations with higher pine basal area than reference sites, but the role of this nest-site characteristic is not well understood. Longleaf pine canopy cover, which is highly correlated with basal area, affects small-scale variability in fire intensity (Thaxton and Platt 2006). In frequently burned savannas, canopy trees regularly shed highly flammable needles (Landers 1991), which represent a primary fuel source in these ecosystems (Hiers et al. 2009). The local accumulation of these fuels near canopy trees can increase fire continuity and lead to higher-intensity fire capable of killing shrubs and encouraging the establishment of herbaceous groundcover (Thaxton and Platt 2006), including grass that was important for nest sites in the Sandhills. However, the closed canopies associated with some high basal area pine forests can prevent sunlight from reaching the ground and thereby reduce the development of an appropriate herbaceous layer (Harrington and Edwards 1999).

The observed variation in nest-site selection between physiographic regions likely can be attributed to the understory plant community that was available to nesting sparrows. One of the most notable differences between the Coastal Plain and the Sandhills was the composition and abundance of understory plant species, which were shaped by distinct soil characteristics and fire return intervals. Mesic soils in the Coastal Plain are relatively nutrient-rich compared with most soil types associated with longleaf pine forests, and support a diverse plant community (Peet 2006). Conversely, the soil productivity of xeric longleaf pine uplands at Ft. Bragg and other Sandhills locations is relatively low (Perry and Amecher 2009, Lashley et al. 2015). Low soil productivity, combined with the long-term and uniform application of prescribed fire (i.e. fire prescriptions with little variability in frequency, season, application method, and weather conditions) in upland areas of Ft. Bragg has resulted in a groundcover layer composed primarily of grasses and relatively few woody stems (Lashley et al. 2014, Just et al. 2015).

Understory composition and abundance is likely to be reflected in the differences in vegetation structure that we found for each physiographic region, which might help to explain the distinct patterns of nest-site selection observed in this study. Although data were not collected at the species level, we observed that woody vegetation at Ft. Bragg was dominated by resprouting oaks (*Quercus* spp.) which did not share the dense coverage of shrubs such as inkberry, huckleberry, blueberry, and swamp bay that were frequently used as nesting cover in the Coastal Plain (A. Fish and J. Winiarski personal observations). Indeed, woody vegetation vertical density and groundcover density at Ft. Bragg were approximately 2.5 and 7 times lower, respectively, than in the Coastal Plain. Woody vegetation height was also greater in Ft. Bragg reference plots compared with those in the Coastal Plain, and tall shrubs were less likely to be used for nest sites (Jones et al. 2013).

## Nest Survival

Habitat selection theory suggests that birds should select locations for nesting that optimize their fitness (Jaenike and Holt 1991). Yet, the vegetation characteristics that predicted nest-site selection in our study did not influence nest survival. However, this is not an uncommon finding in nest survival studies (e.g., Filliater et al. 1994, Davis 2005, Bulluck and Buehler 2008), and is consistent with past research examining the nesting biology of Bachman's Sparrows (Haggerty 1988, 1995, Jones et al. 2013). Birds cannot select sites that avert all possible sources of nest loss because of random patterns of nest predation (Filliater et al. 1994) and the varied search behaviors of diverse predators (Davis 2005). Rather, important vegetation features for Bachman's Sparrow nest-site selection in the present study may have been related to factors that we did not examine, such as nest access, microclimate, or fledgling survival.

We showed that nest survival in the Coastal Plain declined significantly later in the breeding season. This pattern was consistent with Bachman's Sparrow nest

survival in the Coastal Plain of South Carolina, USA (Stober and Krementz 2000), and may have corresponded to changes in predator abundance and activity (Grant et al. 2005). Although we did not focus on nest predators here, snakes were a significant cause of fledgling mortality in a concurrent telemetry study at Ft. Bragg (A. Fish personal observation), and fluctuations in snake activity can drive seasonal variation in nest survival (Sperry et al. 2008). However, the impact of snakes and other predators on Bachman's Sparrow nest survival is unknown and cannot reliably be inferred without video cameras (Staller et al. 2005). Differences in the abundance and diversity of predators or alternative prey species may be a possible explanation for seasonal variation in nest survival (Staller et al. 2005) and for the observed differences in nest predation between the 2 studied physiographic regions.

Increasing time since fire did not influence nest survival, which was unexpected given the importance of frequent fire (≤3-yr interval) for increasing the density (Tucker et al. 2004) and breeding success of Bachman's Sparrows as estimated from weekly behavioral observations of individual males (Tucker et al. 2006). However, Tucker et al. (2006) similarly showed no effect of time since fire when examining daily nest survival with fewer nests ($n = 28$) than in this study. Moreover, it is important to note that all nests in our nest survival analysis were located in stands managed for presumed optimal breeding conditions (i.e. last burned ≤3 yr ago), effectively excluding longer fire return intervals from analyses. For a single nest found on land owned by a resort community in the Coastal Plain, an extreme absence of fire (i.e. >10-yr interval) did not result in nest failure, but groundcover conditions were maintained instead through periodic mowing at the site (J. Winiarski personal observation).

Based on general patterns of reproductive success for other songbirds in fragmented systems, we also expected nest survival to increase farther from edges and with increasing habitat amount in the surrounding landscape. Landscape-level habitat amount and connectivity appear to play an important role in determining the abundance and distribution of Bachman's Sparrows (Dunning et al. 1995, Taillie et al. 2015), but the demographic mechanisms underlying these patterns are not well understood. We documented no difference in nest survival rates between the Coastal Plain and the Sandhills, despite the relatively continuous landscape of Ft. Bragg and its status as the largest tract of longleaf pine ecosystem remaining in North Carolina (Sorrie et al. 2006). However, in the present study we located few nests ($n = 5$) in more fragmented landscapes in the Coastal Plain, and several isolated sites that were part of broader-scale research on Bachman's Sparrow reproductive success in this physiographic region apparently contained no nests (Winiarski 2016).

Bachman's Sparrow populations are declining throughout the species' range, with the greatest declines occurring at the shrinking range margins (e.g., −6.79% in North Carolina; Sauer et al. 2017). Nonetheless, we estimated daily nest survival rates (Coastal Plain: DSR = 0.951; Sandhills: DSR = 0.939) that were consistent with estimates from Bachman's Sparrow populations studied in Arkansas pine plantations (0.919–0.965; Haggerty 1988), the Coastal Plain of South Carolina (0.952; Stober and Krementz 2000), Florida dry prairie (0.899–0.960; Perkins et al. 2003), and old-growth longleaf pine forest in Georgia, USA (0.960; Jones et al. 2013). However, an important caveat when interpreting our results is that the species is generally not well sampled by the Breeding Bird Survey (BBS; Dunning 2006, Sauer et al. 2017), and the overall negative BBS trend for the species in North Carolina may not reflect the true trajectory of the local populations that we studied. Although information regarding population trends specific to our study area is lacking, Taillie et al. (2016) showed that Bachman's Sparrows were restricted mainly to large, fire-maintained landholdings in the Coastal Plain and Sandhills (e.g., Green Swamp Preserve, Holly Shelter Game Land, and Ft. Bragg) where we found the majority of nests. Future studies combining site-specific population counts with nest survival data could help to provide a more complete picture of the influence of nest success on Bachman's Sparrow population ecology.

Nevertheless, our results and those from core Bachman's Sparrow populations suggest that reduced nest survival may not pose the most significant threat to this declining species at its current northern extent. It remains uncertain which demographic parameters may be underlying Bachman's Sparrow population declines, although previous work has suggested that adult survival is the primary vital rate influencing population growth rates in this species (Cox and Jones 2010). Other potential contributing factors, including low pairing success, which has been observed for male Bachman's Sparrows in highly isolated longleaf pine patches in the Coastal Plain (Winiarski 2016), and fledgling survival rates, also deserve further investigation. On the other hand, perhaps the most plausible explanation is that regional Bachman's Sparrow declines simply stem from the outright loss of longleaf pine communities, rather than demographic processes within remaining habitat patches.

## Research and Management Implications

Although Bachman's Sparrows in this study exhibited clear patterns of nest-site selection, nest survival appeared to be high regardless of vegetation characteristics at the nest site. This outcome raises an important set of hypotheses and variables to test in future studies of Bachman's Sparrow nesting ecology. First, fledgling survival may be prioritized over nest survival when birds select nest sites,

such that habitat characteristics associated with increased fledgling survival may differ from those that lead to increased nest success (Streby et al. 2014a). Therefore, researchers should determine the adaptive nature of nest-site selection using a more comprehensive measure of reproductive success (i.e. nest success and fledgling survival; Streby et al. 2014b). Second, we may not have measured all of the variables that can affect Bachman's Sparrow nest survival, or examined nest-site selection and nest survival across the full spectrum of habitat conditions. Future studies could improve our knowledge of Bachman's Sparrow breeding ecology by studying nest-site selection and survival in locations with a wider range of fire return intervals and varying population densities. Under such a scenario, researchers may observe pronounced differences in nest-site selection and could determine whether differential nest-site selection and survival are correlated with low population densities and site abandonment.

Overall, our results indicate that habitat management and restoration activities that approximate historical fire regimes in longleaf pine ecosystems should continue to be promoted as essential tools for Bachman's Sparrow conservation. Although alternative methods are available to manage and improve groundcover vegetation (e.g., hardwood removal via mechanical and herbicide treatments), frequent prescribed fire (i.e. ≤3-yr cycle) alone is the most cost-effective and practical approach to restoring and maintaining habitat for Bachman's Sparrows and other longleaf pine specialist birds (Steen et al. 2013). Most importantly, prescribed fire can be used to create and maintain important vegetation characteristics for nesting, including low to intermediate grass density (Coastal Plain and Sandhills) and low-statured woody vegetation (Coastal Plain; Glitzenstein et al. 2003). When such features are available for breeding Bachman's Sparrows, managers are likely to ensure nest survival rates that are relatively high.

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