HABITAT SELECTION AND BREEDING ECOLOGY OF BACHMAN'S SPARROW (*PEUCAEA AESTIVALIS*) IN A WIREGRASS-FREE ECOSYSTEM

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ABSTRACT

Through much of its range, Bachman's Sparrow (*Peucaea aestivalis*) uses the wiregrass (*Aristida spp.*) dominant understory typical of longleaf pine (*Pinus palustris*) forest. The central South Carolina Coastal Plain, however, lies within the "wiregrass gap" where longleaf pine understories are absent of wiregrass and instead are dominated by bluestem grasses (*Schizachyrium spp.* and *Andropogon spp.*), bracken fern (*Pteridium aquilinum*), and shrubs. Habitat use of Bachman's Sparrow in this region has yet to be studied and declining Bachman's Sparrow populations necessitate a better understanding of habitat selection processes and population dynamics across regional habitat types. The goal of this study was to describe breeding season habitat selection and breeding ecology of Bachman's Sparrow in the unique wiregrass-free longleaf pine ecosystem of Tom Yawkey Wildlife Center, Santee Coastal Reserve, and Washo Reserve, South Carolina to inform best management practices for Bachman's Sparrow. I conducted repeated visit point count surveys at 95 sites and used open *N*-mixture models to estimate the effects of habitat management and forest stand characteristics (e.g. prescribed burns, basal area, stem density, pine species, canopy closure) on Bachman's Sparrow abundance, apparent survival probability, and recruitment rates during the 2020 and 2021 breeding seasons. I also located nests to identify vegetation composition and structure characteristics that Bachman's Sparrows select for nest-sites. To determine if habitat selection in the study population was adaptive, I monitored nests and related nest-site selection to nest survival rates by comparing habitat characteristics related to selection with those related to survival. Across the nine primary sampling periods, I estimated the abundance of male

Bachman's Sparrows within the study area to be between 23 and 49 individuals. Initial abundance and recruitment rate were strongly predicted by the proportion of longleaf pine to other pine species within the sample area, with abundance and recruitment rate increasing with longleaf pine dominance. Apparent survival probability decreased as the density of stems between 10 and 25 cm DBH increased. Nest-site selection in the study population was non-adaptive. Bachman's Sparrows selected nest-sites that had intermediate groundcover densities compared to available nest-sites; however, nest survival rates decreased at intermediate groundcover densities. The results of this study can be used to inform region-specific management plans and restoration of degraded habitats, which often lack typical understory species like wiregrass, to increase Bachman's Sparrow abundance and reproductive success.

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CHAPTER ONE

BACKGROUND

Longleaf pine (*Pinus palustris*) forest currently exists at less than 3% of its historic range in the Southeast United States due to a history of habitat degradation, land-use change, and fire suppression (Frost 1993, 2006, Outcalt and Sheffield 1996). The vast reduction in longleaf pine habitat has resulted in the decline of longleaf pine obligate species (Van Lear et al. 2005, Means 2006) and a renewed interest to conserve and restore this unique ecosystem (Landers et al. 1995, Noss et al. 1995, McIntyre 2018, ALRI 2019). Current management practices for longleaf pine forest are geared towards improving ecosystem functioning through prescribed burning, midstory removal, and restoration of understory vegetation (Brockway and Lewis 1997, Brockway et al. 2005, Walker and Silletti 2006, Johnston and Gjerstad 2006). Management for avian use has historically been focused on recovery of the federally endangered Red-cockaded Woodpecker (*Dryobates borealis*). Through intensive research on its habitat selection, population dynamics, and applied management, the Red-cockaded Woodpecker has become a conservation success story, as many populations are now stable or growing (USFWS 2003, 2019). However, much remains unknown about the unique habitat use of other longleaf pine avifauna, such as Bachman's Sparrow (*Peucaea aestivalis*), which are similarly of conservation concern due to habitat loss and degradation. While forest management for Red-cockaded Woodpecker generally improves habitat for Bachman's Sparrow (Plentovich et al. 1998, Conner et al. 2002), it may not encompass all of

Bachman’s Sparrow habitat needs (Liu et al. 1995, Plentovich et al. 1998, Krementz and Christie 1999). For example, prescribed burning and stand thinning often are not specifically implemented to optimize understory structure and composition for Bachman’s Sparrow recruitment, survival, and reproductive success (Plentovich et al. 1998). The widespread decline of Bachman’s Sparrow and other longleaf pine obligate species suggest the need to supplement holistic ecosystem management with specific management plans for the species at greatest risk (Van Lear et al. 2005, Goble et al. 2012).

Bachman’s Sparrow is a small, secretive passerine that inhabits pine-grass woodlands, especially longleaf pine forest, and other open habitats in the Southeastern United States. The species currently occurs from North Carolina to Florida on its eastern extent and from southern Missouri to East Texas on its western extent (Dunning et al. 2018). Aside from some short-distance migratory populations at the northern range periphery (Eifrig 1915, Brooks 1938, Weston 1968), Bachman’s Sparrows are year-round residents. They are ground nesters and foragers and thus rely on frequent fire or other disturbance to maintain appropriate understory conditions. In general, Bachman’s Sparrow habitat is characterized by short, dense understory growth abundant in grasses, forbs, some small shrubs, and patches of bare ground (Dunning and Watts 1990, Haggerty 2000, Brooks and Stouffer 2010, Jones et al. 2013, Taillie et al. 2015, Winiarski et al. 2017a). Selected habitat characteristics are ephemeral and Bachman’s Sparrows disperse when habitat conditions are no longer suitable (Cox and Jones 2007, Jones et al. 2014, Cerame et al. 2014).

Bachman’s Sparrow received little research attention until the mid-1980’s. The species experienced a range expansion in the early 1900s due to wide-scale agricultural abandonment and clearcutting (Eifrig 1915, Brooks 1938). However, Bachman’s Sparrow populations have since declined and their range retracted after this early-successional habitat was lost (Sauer 2017). Conversion of mature longleaf forest into plantations of faster-growing pines further reduced habitat availability in the Southeast (Frost 2006), as plantation forestry practices often inhibit understory growth if groundcover maintenance is not a management objective (Noss 1989, Harrington and Edwards 1999, Harrington et al. 2003). To this day a departure from natural and historic disturbance regimes contributes to habitat loss. In 2000, it was estimated that only half of the remaining longleaf forest was burned on a frequent basis (i.e. five year burn rotation; Outcalt 2000). Over the past three centuries, the Southeast has drastically shifted from a landscape of vast, open longleaf pine forest to fire suppressed loblolly pine (*Pinus taeda*) stands (Frost 2006). Although the total amount of pine landcover has not been drastically reduced (Frost 2006), species that rely on frequently burned open pine forest, such as Bachman’s Sparrow, have been limited to fragmented patches of remaining pine-grasslands (Simberloff 1993, Van Lear et al. 2005). Consequently, populations have declined and Bachman’s Sparrow has been listed as a species of conservation concern in all states across its range. A growing interest in conserving this lesser-known longleaf pine specialist has motivated research on habitat relationships and sources of population declines in order to conserve the species on remaining managed lands.

Management techniques and resulting forest stand characteristics can impact habitat occupancy by Bachman's Sparrow. Burn frequency influences Bachman's Sparrow occupancy as frequent burns maintain suitable understory conditions (Engstrom et al. 1984, Tucker et al. 2004, Cox and Jones 2009). Bachman's Sparrow density peaks around two years post-burn and declines after three years since burn (Tucker et al. 2004). Bachman's Sparrows typically do not occupy stands that have not been burned in over five years (Engstrom et al. 1984). Preferred understory habitat rich in grasses and forbs can also be maintained by increasing light availability (Harrington and Edwards 1999, Platt et al. 2006). Thus, treatments such as midstory removal, stand thinning, and prescribed burning can be useful tools for managing Bachman's Sparrow habitat (Brockway and Lewis 1997, Harrington and Edwards 1999, Meyer 2006, USFWS n.d.). By identifying habitat treatments and measuring vegetation characteristics that Bachman's Sparrows select, best management practices for Bachman's Sparrow can be refined.

Although habitat use by Bachman's Sparrow can be generalized across the species' range, there are regional differences (Dunning and Watts 1990, Haggerty 2000, Winiarski et al. 2017b). For example, Bachman's Sparrows in the North Carolina Sandhills select nest-sites with intermediate vertical grass density and greater pine basal area, while individuals in the Coastal Plain select nest-sites with lower vertical grass density and greater vertical shrub density (Winiarski et al. 2017b). Often, differences in resource use in a species with a wide geographic range, such as Bachman's Sparrow, occur because the geographic range of a resource is smaller than that of the species (Fox and Morrow 1981, Haggerty 2000). Resource use is driven by resource availability (Johnson 1980), and thus regional differences in availability lead to different patterns in selection as long as the species' basic requirements for survival and reproduction are met (Grinnell 1917, James et al. 1984, Haggerty 2000). Despite the variation in habitat composition over geographic space, wide-ranging species – even those, like Bachman's Sparrow, that are considered to be habitat specialists – occur across resource gradients (Fox and Morrow 1981, Lawton et al. 2012). Thus, range-wide, habitat selection is more likely to be dictated by broad structural characteristics rather than specific vegetation associations. In local populations, habitat selection patterns may be region specific and reflect resource availability.

Through much of Southeast, Bachman's Sparrow uses the dense wiregrass (*Aristida spp.*) understory typical of longleaf pine forest. However, central South Carolina lies between the ranges of *Aristida stricta* to the north and *Aristida beyrichiana* to the south (Figure 1, Peet 1993, 2006), resulting in understories absent of wiregrass and with greater shrub density. Habitat use of Bachman's Sparrow in this unique wiregrass-free longleaf pine ecosystem has not received much research attention. The South Carolina State Wildlife Action Plan (SCDNR 2015) lists Bachman's Sparrow as a species of highest priority for conservation, and thus there is interest in increasing statewide populations. Understanding the drivers of Bachman's Sparrow habitat selection and survival in the unique longleaf pine ecosystem of the central South Carolina Coastal Plain can inform the development of region-specific management plans for species persistence in the current habitat. In addition to improving existing habitat for Bachman's Sparrow, studying how the wiregrass gap population uses the unique ecosystem can guide restoration of degraded habitats, which often have unsuccessful or slow wiregrass regeneration, and ultimately encourage Bachman's Sparrow recruitment.

The goal of this study was to describe the drivers of Bachman's Sparrow habitat selection in the wiregrass gap in order to inform targeted management for the species. In chapter two, I determine how stand-scale habitat metrics and management treatments (i.e. prescribed burning, stand thinning, midstory removal) influence abundance of Bachman's Sparrow. In chapter three, I describe nest-site selection in Bachman's Sparrow, focusing on vegetation structure and composition. I also quantify nest survival rates and relate drivers of nest survival to nest-site selection to determine if selection is adaptive. This research expands the current understanding of Bachman's Sparrow habitat selection to a new region and has implications for restoration of longleaf pine ecosystems where wiregrass has not been established.

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FIGURES

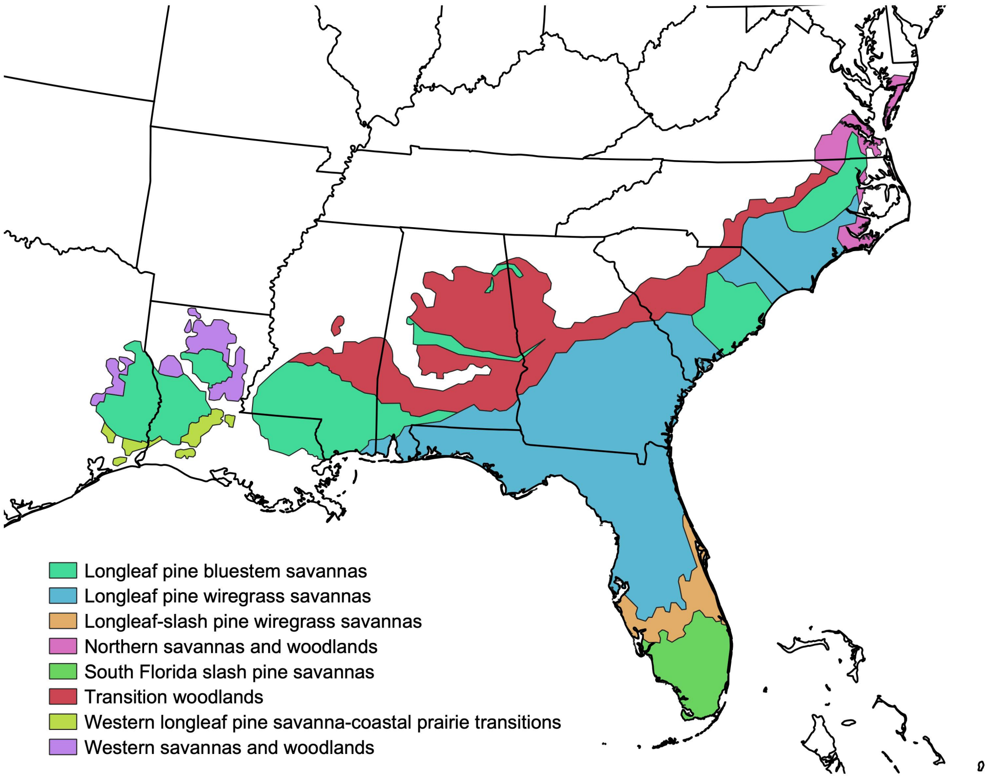

Figure 1. Pine-grass woodlands and savannas of the Southeast United States.
Data: Costanza et al. 2018, CC BY 4.0

CHAPTER TWO

BREEDING HABITAT SELECTION OF BACHMAN'S SPARROW IN A WIREGRASS-FREE ECOSYSTEM

INTRODUCTION

Bachman's Sparrow (*Peucaea aestivalis*) is a small passerine native to the southeastern United States that typically associates with frequently burned open pine-grasslands, particularly longleaf pine (*Pinus palustris*) forest. Due to a history of habitat degradation, deforestation, and fire suppression, longleaf pine forest currently exists at less than 3% of its historic extent in the southeast United States (Frost 1993, 2006, Outcalt and Sheffield 1996). Despite efforts to manage and restore longleaf pine habitat, resident avifauna remains at risk (Van Lear et al. 2005, SECAS 2020). Current population trends of Bachman's Sparrow suggest the need for a better understanding of regional habitat selection processes and abundance in order to inform management decisions (Sauer 2017). Although best management practices for other longleaf pine obligate species such as the Red-cockaded Woodpecker (*Dryobates borealis*) generally support Bachman's Sparrow (Plentovich et al. 1998, Conner et al. 2002), these species-focused management actions typically are not sufficient for maintaining the specific understory structure that Bachman's Sparrow selects for foraging and nesting (Liu et al. 1995, Plentovich et al. 1998, Krementz and Christie 1999). If forest management goals include increasing Bachman's Sparrow abundance, recruitment rates, and survival rates, prescribed treatments may be more effective if they are species and region specific.

While habitat use by Bachman's Sparrow is somewhat varied among sites due to local availability, populations share general selection patterns. Although largely considered to be a longleaf pine specialist, Bachman's Sparrow will use loblolly (*Pinus taeda*), slash (*Pinus elliotii*), shortleaf (*Pinus echinata*), and other mixed-pine forest with frequently burned or disturbed understory and an open canopy (Dunning and Watts 1990, Haggerty 1998). In addition to frequently burned pine forest, Bachman's Sparrow also uses other early successional habitat including grasslands such as dry prairie (Perkins et al. 2003), clearcuts (Dunning and Watts 1990), utility rights-of way, and abandoned agricultural fields (Brooks 1938). Bachman's Sparrow habitat typically has a dense grass and forb understory, patches of exposed ground, shorter woody growth, and an open midstory (Dunning and Watts 1990, Haggerty 1998, Plentovich et al. 1998, Cox and Jones 2009, Brooks and Stouffer 2010, Taillie et al. 2015, Winiarski et al. 2017a). Bachman's Sparrow is a ground foraging and nesting species, and thus depends on appropriate understory structure for survival and reproduction. Selected habitat characteristics are ephemeral as southeastern pine-grass woodlands were historically disturbed by fire on average every three to four years (range = 1 – 10 years, Fryer and Luensmann 2012).

Forest management treatments including prescribed burning, stand thinning, and midstory removal can be employed to mimic the historic disturbance regimes that shape the species composition and structure of longleaf pine forest (Brockway and Lewis 1997, Harrington and Edwards 1999, Walker and Silletti 2006). Thus, proper forest management can increase the probability of use by Bachman's Sparrow, particularly when understory maintenance is prioritized. Burn frequency influences Bachman's Sparrow habitat occupancy, as frequent burns prevent midstory encroachment and understory overgrowth which may inhibit foraging and movement (Engstrom et al. 1984, Tucker et al. 2004, Cox and Jones 2009). Bachman's Sparrow density peaks around two years post-burn and declines after three years since burn (Tucker et al. 2004), and Bachman's Sparrows typically do not occupy areas after five years since the last burn (Engstrom et al. 1984). Additionally, reducing basal area and removing midstory increases light availability to the understory which promotes the growth of grasses and forbs (Harrington and Edwards 1999, Platt et al. 2006). Management treatments are thus useful tools for modifying groundcover; however, prescriptions may need to be tailored to biotic and abiotic site characteristics in order to achieve desired outcomes.

In South Carolina, Bachman's Sparrow is considered a species of highest priority for conservation (SCDNR 2015), and thus there is motivation to understand Bachman's Sparrow habitat use across the state and refine best management practices for the species. Through much of the southeastern USA, Bachman's Sparrow uses the dense wiregrass (*Aristida spp.*) understory typical of longleaf pine forest. Central South Carolina, however, lies between the ranges of *Aristida stricta* to the north and *Aristida beyrichiana* to the south (Peet 1993, 2006), resulting in understories that are dominated by bluestem grasses (*Schizachyrium spp. and Andropogon spp.*) and have higher shrub density than regions outside of the Coastal Plain. Habitat use of Bachman's Sparrow within this unique "wiregrass gap" has been little studied. Understanding how Bachman's Sparrow uses the unique longleaf pine ecosystem of the central South Carolina Coastal Plain can aid in the development of region-specific management plans to avoid further range contraction. Additionally, it can inform the restoration of degraded habitats, which may also lack wiregrass, to encourage Bachman's Sparrow recruitment. Lastly, by examining how species use diverse habitats, we can better assess a species' adaptive capacity and potential for range expansion.

The objective of this study was to understand how current habitat management and forest stand characteristics affect Bachman's Sparrow abundance within the wiregrass gap of central South Carolina. I conducted repeated visit point count surveys and used open *N*-mixture models to estimate the abundance, recruitment rate, and apparent survival probability of Bachman's Sparrows within the wiregrass gap. I hypothesized that Bachman's Sparrow abundance, recruitment rate, and apparent survival probability would be highest in forest that was burned the previous year, had low basal area and stem density, and had low-intermediate canopy closure as Bachman's Sparrows rely on understories shaped by frequent fire and high light availability for foraging and nesting.

METHODS

Study Area

The study sites, Tom Yawkey Wildlife Center Heritage Preserve (YWC), Georgetown County, South Carolina and Santee Coastal Reserve Wildlife Management Area (SCR), Charleston County, South Carolina, are coastal properties managed by South Carolina Department of Natural Resources (SCDNR) and lie within the Coastal Plain ecoregion. YWC and SCR are both approximately 97 km^2 and contain diverse habitat including upland pine, maritime forest, marsh, and freshwater wetlands. Upland ridges with sandy marine soils are intersected by hardwood slough and pocosin, creating a patchy habitat structure. YWC is comprised of Cat, North, and South Islands and is separated from the mainland by the Intracoastal Waterway. The Washo Reserve (WR), a property owned by the Nature Conservancy and co-managed with SCDNR, lies within SCR. Upland areas of WR were included in SCR sampling. Thus, WR will not be discussed independent of SCR.

Study areas were dominated by longleaf and loblolly pine as well as mixed pine and hardwood forest. The understory vegetation composition of YWC and SCR is unique because the sites fall between the *Aristida stricta* and *Aristida beyrichiana* ranges and thus are free of wiregrass. Instead, understories are composed of predominantly bluestem grasses, bracken fern (*Pteridium aquilinum*), and short-statured shrubs (e.g. *Ilex glabra*, *Gaylussacia dumosa*, *Gaylussacia frondosa*, *Vaccinium spp*., *Lyonia lucida*). Switchcane (*Arundinaria tecta*) was common in areas, particularly those bordering hardwood slough. Longleaf, mixed pine, and mixed pine and hardwood stands at both sites are managed through dormant season prescribed burning, primarily in January through early April. Stands at YWC and SCR are typically burned every one to five years (YWC: mean = 1.33, SD = 2.67; SCR: mean = 2.11, SD = 1.38).

Point Count Surveys

I randomly selected 50 locations for point count surveys (hereafter sites) from portions of the study area classified as upland pine and mixed hardwood and pine stands routinely treated with prescribed fire based on delineations by SCDNR (Figures 1-2). Three sites at YWC and two sites at SCR were not surveyed due to inaccessibility, leaving 95 sites that I surveyed. To maintain independence between sampling units, I placed sites a minimum of 500 m away from each other. Observers conducted four rounds of point count surveys at each site between 16 April and 04 July 2020. Observers conducted five rounds of point count surveys at each site between 28 March and 06 July 2021.

Observers conducted surveys between 30 min before sunrise and four hours after sunrise. After arriving at a site, the observer waited quietly for two minutes before beginning the observation period to allow the birds to settle. After the waiting period, the observer passively listened for Bachman's Sparrows for three minutes (Period 1). After three minutes, the observer played a 30 s recording of Bachman's Sparrow song and agitated chips (Stokes et al. 1997). Following the playback, the observer passively listened for another two minutes (Period 2) before playing the 30 s recording a second time. The observer listened for another two minutes (Period 3) before ending the 10-minute survey period. The number of unique vocalizing male Bachman's Sparrows within the 200 m radius of the site was recorded during each of the three sampling periods (Period 1: 0:00 – 2:59, Period 2: 3:00 – 5:59, Period 3: 6:00-7:59). Additional data on time of day and weather, which could affect detection, were recorded. Ambient temperature was recorded after each survey using a thermometer. Cloud cover and precipitation was scored as 0: clear to mostly clear, 1: partly to mostly cloudy, 2: cloudy or overcast, or 3: fog. Wind speed was recorded using the Beaufort scale. Observers did not conduct surveys if it was raining, fog was limiting visibility, or if wind was ≥ 4 on the Beaufort scale.

Forest Characterization at Sites

I calculated the surveyed area of each site by subtracting the area of unsuitable and unsurveyed habitat (i.e., water, wetland, hardwood stands) from the total 125,664 m^2 site area (i.e., the 200 m radius observation area around the point count location). I used the 2016 National Landcover Database (Dewitz 2019) to quantify the percent of each site that is classified as evergreen. Sites often spanned across management units with different burn histories. Thus, the unit-scale habitat variable "years since burn" assigned to each point was the weighted average of all management units within each site. For example, if 25% of a site was within a management unit burned the previous year and 75% of a site was within a management unit burned three years ago, the years since burn for the site would average 2.5 years.

To quantify all other forest characteristics at each site, I randomly selected five 0.04 ha circular plots within each site. I spaced plot center points at least 60 m apart because I estimated basal area using variable radius plots and doing so prevented plot overlap. Some sites were comprised of > 60% unsuitable or inaccessible habitat so only three (n = 2) or four (n = 3) of the five points within the sites were sampled. At each plot center, I measured basal area of pine stems using a 10-factor prism. I measured canopy closure using a spherical densiometer. To quantify small stem density, I counted the number of pine, nonpine, and dead stems with a diameter at breast height (DBH) ≥ 10 cm and < 25 cm within the plot. To quantify large stem density, I counted the number of pine, nonpine, and dead stems with a DBH ≥ 25 cm within the plot. I calculated the percent of all stems ≥ 10 cm DBH that were pine species. I also calculated the proportion of longleaf pine stems to all pine species stems. I averaged basal area, canopy closure, and percent pine stems, and proportion longleaf measurements for each point count location. I summed the stem counts of pines, hardwoods, and dead trees to calculate the total number of small (≥ 10 cm and < 25 cm DBH) and large (≥ 25 cm DBH) trees per hectare.

Statistical Analysis

I used open *N*-mixture models (Dail and Madsen 2011) to estimate the effects of habitat management and forest characteristics on site-specific initial abundance, recruitment rate, apparent survival probability, and detection probability of adult male Bachman's Sparrows. *N*-mixture models are suitable for estimating abundance in unmarked populations because they simultaneously model the ecological processes affecting abundance while accounting for imperfect detection using spatially and temporally replicated count data (Royle 2004). Open *N*-mixture models are a generalized form of the Royle (2004) model that explicitly model population dynamic parameters (e.g. initial abundance, recruitment rate, and apparent survival probability under constant population dynamics) to account for migration, births, and deaths when estimating abundance. I used open *N*-mixture models with a short time interval robust design (Figure 3; Pollock 1982, Betts et al. 2008) because resighting of a limited number of color-banded individuals at the study sites (Appendix) suggested some males moved within the breeding season, violating the population closure assumption of *N*-mixture models (Royle

2004). Under the robust design, observations are temporally replicated over primary and secondary sampling periods. Site closure is not assumed between primary periods. I conducted point count surveys over nine three-week primary periods during the 2020 and 2021 breeding seasons. All sites were visited once during each primary period. Initial abundance, recruitment rate, and apparent survival probability were estimated over the nine primary sampling periods. Detections during each primary period, along with changes in the number of detections between each primary period, were used to estimate initial abundance, recruitment rate, and apparent survival probability of adult male Bachman's Sparrows. Site-specific abundance was modeled under constant population dynamics. Initial abundance is the estimated site-specific abundance during the first primary period (16 Apr – 06 May 2020). Recruitment rate is the estimated rate of new adult males arriving at a site through immigration since the previous primary period. Apparent survival probability is the estimated probability that adult males will be lost to death or emigration at each site since the previous primary period. The eight minutes of active survey were divided into three sequential secondary periods over which detection probability was estimated. Site closure was assumed over the eight minutes of active survey time. Candidate models (Table 1) were fitted and analyzed using the pcountOpen function in package unmarked (Fiske and Chandler 2011) in R 4.0.3 (R Core Team 2020) using detection data collected from point count surveys and covariate data collected from forest surveys.

I built four *a priori* candidate sets of models that represented the hypothesized effects of habitat management and forest characteristics on initial abundance, recruitment rate, and apparent survival probability as well as the hypothesized effects of timing, weather, and different observers on detection probability (Table 1). Covariates that I used to explain state processes of initial abundance, recruitment rate, and apparent survival probability included the percent of each survey area that was classified as evergreen, average number of years since the last prescribed burn, canopy closure, average pine basal area, proportion of longleaf pine to other pine species, percent of all stems > 10 cm DBH that were pine species, total small (≥ 10 cm and < 25 cm DBH) stem density, and total large (≥ 25 cm DBH) stem density. To explain the detection process, I included the covariates secondary period, ordinal date, minutes elapsed since sunrise, observer, temperature, sky code, and wind speed. I included secondary period as a covariate in all detection probability models because each secondary period was a different duration and was influenced by the use of playback in previous periods. I was not able to consider random effects such as study site because random effects currently cannot be estimated in unmarked for open *N*-mixture models. I screened for collinearity between all state covariates and between all detection process covariates by calculating Pearson's correlation coefficients for all covariate pairs. When $|r| > 0.6$, I removed the variable with less hypothesized ecological significance.

Because open *N*-mixture models model multiple ecological processes, I used a six-step model selection process to compare the effects of covariates on detection probability, initial abundance, recruitment rate, and apparent survival probability separately (Table 1). I used Akaike's Information Criterion to rank and compare among models and I retained a confidence set of models that held 95% of the Akaike weight (Burnham and Anderson

2002). *N*-mixture models can be fitted through Poisson, zero-inflated Poisson, or negative binomial regression. In the first step in model selection, I compared null models using a Poisson and zero-inflated Poisson distribution. I did not consider the negative binomial distribution because it has been found to have problems with parameter identifiability (Kéry 2018). When using a null model, the zero-inflated Poisson distribution best fit the data; however, the Poisson distribution was within 0.79 ΔAIC of the zero-inflated Poisson distribution (Table 1). I proceeded with model selection using the top-ranked zero-inflated Poisson distribution. In the second step, I ranked and compared models in my detection probability candidate model set. In the third step, I used the top-ranked detection probability model in addition to the initial abundance candidate model set to rank and compare models estimating initial abundance. I included an offset parameter in all initial abundance models to account for differences in site area. I continued this process of selecting the top-ranked model for the remaining parts of the model formula (recruitment rate and apparent survival probability) in steps four and five to obtain the most parsimonious model. In the final model selection step, I again compared distributions with the fully parameterized model. The Poisson distribution best fit the data (Table 1). I used a Pearson's Chi-squared goodness-of-fit test on 1000 bootstrapped samples to estimate c-hat, identify overdispersion, and test if the data violated distributional assumptions ($\alpha = 0.05$). In addition, I evaluated variables not included in the top model at each stage of the selection process by examining 85% confidence intervals around beta coefficient estimates (Arnold 2010).

Using the complete top-ranked model, I estimated abundance of males across all sites during each primary period using the ranef function in unmarked. The ranef function estimates the posterior distributions of the latent abundance at each site using empirical Bayes methods. I summed the estimated abundance at all sites and divided the sum by the total area of all sites to estimate the density of male Bachman's Sparrows at the study sites. I used area expansion to estimate the total abundance of males within the 26.589 km^2 sample area at the study sites.

RESULTS

I detected adult male Bachman's Sparrows at 27 of 95 sites in 2020 and 2021 (Figures 1-2). A maximum of two adult male Bachman's Sparrows were detected during any site visit (mean = 0.113, SD = 0.356). Although less supported than the top models, I report second-ranked models as variables were often important and likely had biological significance. When interpreting models that included covariates that were not in the final top model, I report below estimated beta coefficients from the stage of the model selection process in which that model was considered.

Model Selection

Detection Probability

The top-ranked model included minutes elapsed since sunrise and the secondary period as covariates (Table 1). The second and third ranked models were both within 2 ΔAIC of the top model (Table 1); however, the second and third ranked models only differed from the top model by the addition of covariates that did not aid in prediction.

The second ranked model included ordinal day as a covariate in addition to minutes elapsed since sunrise and secondary period, but 85% confidence intervals of the beta coefficient overlapped zero (β_{DAY}= 0.204, 85% CI = -0.013 – 0.422). The third ranked model included ordinal day as well as linear and quadratic terms for temperature as covariates in addition to minutes elapsed since sunrise and secondary period, but 85% confidence intervals of the beta coefficients also overlapped zero (β_{DAY}= 0.063, 85% CI = -0.234 – 0.360; β_{TEM}= 0.441, 85% CI = 0.026 – 0.856; $\beta_{TEM}{}^2$= 0.192, 85% CI = -0.010 – 0.395). Therefore, I used the top model to estimate detection probability. Detection probability decreased as time since sunrise progressed and increased with each subsequent secondary period (Figure 4, Table 2).

Initial Abundance

The top model indicated that the proportion of longleaf pine to all pine species within the site best explained initial abundance (Table 1, w_i = 0.99). According to the top model, initial abundance increased as the proportion of longleaf pine increased (Figure 5, Table 2). The second-best model included the quadratic form for canopy closure. Although this model only carried 0.98% of the Akaike weight and standard errors were large, confidence intervals for the beta coefficients did not overlap zero (β_{CLO}= -5.961, 85% CI = -9.964– -1.958; $\beta_{CLO}{}^2$= -5.373, 85% CI = -9.426 – -1.320). Initial abundance was highest at approximately 40% canopy closure.

Recruitment Rate

The top model indicated that the proportion of longleaf pine to all pine species within the site best explained recruitment rate (Table 1, w_i = 1.00). According to the top model, recruitment rate increased as the proportion of longleaf pine increased (Figure 6, Table 2). The second-best model included the effect of the percent of stems that were pine species, with recruitment rate increasing as the percentage of pine stems increased. Although this model only carried 0.0000054% of the Akaike weight, confidence intervals for the beta coefficients did not overlap zero (β_{PSD}= 1.192, 85% CI = 0.789 – 1.594).

Apparent Survival Probability

The top model indicated that the density of small (10 – 25 cm DBH) stems within the site best explained apparent survival probability (Table 1, w_i = 0.56). The apparent survival probability model that included a covariate for small stem density was 4.2 times more likely to be the best predicting model than the second ranked model. The second ranked model included the number of years since the last burn as a covariate and confidence intervals of the beta coefficient did not overlap zero (β_{YSB}= -2.287, 85% CI = -4.091 – -0.483). The small stem density and years since last burn models were the only two models to rank higher than the null model. According to the top model, apparent survival probability increased as the density of small stems decreased (Figure 6, Table 2).

Goodness-of-fit

I failed to reject the null hypothesis that the top model at the completion of the selection process provided a good fit to the data, thus concluding that the data did not violate distributional assumptions. The bootstrapped *p*-value for the Pearson's Chi-square goodness-of-fit test on the top model (n sims = 1000) was 0.48. There was no evidence of overdispersion (c-hat = 0.8).

Parameter and Abundance Estimates

Each population dynamic parameter was modeled by the combinations of covariates that were best supported in each separate step of our modeling procedure. I estimated each parameter using average covariate values (Table 3). Across the nine primary periods, estimated density of adult male Bachman's Sparrow at YWC and SCR ranged from 0.85 – 1.70 birds/km^2 (85% CI: 0.76 – 1.85 birds/km^2, Figure 8). Bachman's Sparrow density decreased in 2021 (85% CI: 0.76 – 1.30 birds/km^2) compared to 2020 estimates (85% CI: 1.30 – 1.85 birds/km^2, Figure 8). Over the 26.589 km^2 area of upland habitat that was sampled, estimated abundance of adult male Bachman's Sparrows was between 23 (Primary Period: 20 Jun – 10 Jul 2021) and 49 individuals (Primary Period: 07 – 27 May 2020).

DISCUSSION

In this study, I examined the effects of habitat management and stand-level forest characteristics on changes in Bachman's Sparrow abundance and population parameters. While previous studies have described how habitat features impact Bachman's Sparrow occupancy on multiple spatial scales (e.g. Taillie et al. 2015), this study provides novel information on how the habitat selection process differs throughout the breeding season. In this study, different forest characteristics drove site selection and dispersal. I found that the proportion of longleaf pine to other pine species best predicted initial abundance and recruitment while small stem density best predicted apparent survival probability. These results suggest that initial site selection after a dispersal may be driven by overstory composition. On the contrary, once an individual is established at a site, the decision of whether to stay at a territory or disperse may be driven by structural habitat attributes, like small stem density, which impact nesting and foraging success.

Although the association between Bachman's Sparrow and the longleaf pine ecosystem is well established, the fact that Bachman's Sparrow initial abundance and recruitment rate strongly correlated with longleaf pine dominance within a matrix of longleaf and loblolly dominated stands highlights the species' use of longleaf over loblolly forest. At the study sites, differences in long-term management history and in understory composition between longleaf pine dominated stands and stands dominated by other pine species could be driving selection; however, these fine-scale differences were outside of the scope of this study. On a microhabitat level, Bachman's Sparrows select home ranges with short, dense understory growth abundant in grasses, forbs, and some small shrubs (Dunning and Watts 1990, Haggerty 2000, Taillie et al. 2015) as well as patchy bare ground interspersed with vegetation (Brooks and Stouffer 2010, Jones et al. 2013, Taillie et al. 2015, Winiarski et al. 2017b). Bachman's Sparrows generally consume insects and grass seeds from the ground and short-statured vegetation, and thus depend on habitat with short vegetation, particularly grasses, and patches of bare ground to forage (Dunning et al. 2018). These characteristics are common in areas with frequent fire, but are not necessarily dependent on overstory composition. Longleaf is generally selected over other pine types (Brown 2012); however, Bachman's Sparrows inhabit loblolly, slash, and other southeastern pine forests as long as a frequently burned or disturbed understory and an open canopy is maintained (Dunning and Watts 1990, Haggerty 1998). Therefore, it is important to determine if Bachman's Sparrow selection of longleaf dominated stands over other pine dominated stands is due to abiotic conditions which support longleaf pine communities over loblolly, or whether longleaf dominance shapes different understory vegetation communities under the same growing conditions.

Although longleaf and loblolly were often observed growing together at my study sites and have similar environmental requirements, the species do thrive under unique conditions (Boyer 1990a, Baker and Langdon 1990). Variation in abiotic conditions such as fire frequency, soil type, and soil moisture may favor one species over the other (Boyer 1990a, Baker and Langdon 1990, Outcalt 2000, Scott and Burger 2014). Compared to longleaf, loblolly tends to grow in more mesic conditions and is not dependent on fire for regeneration (Baker and Langdon 1990). Loblolly seedlings are more susceptible to fire, and thus longleaf outcompetes loblolly in areas with frequent fire (Wakeley 1935, Frost 1993, Outcalt 2000). Unlike loblolly, longleaf pine is dependent on fire for regeneration as it creates bare mineral earth for seed germination and reduces understory competition (Boyer 1990a). At YWC and SCR, loblolly dominated sites tended to be wetter and supported shrubbier understories. Given that Bachman's Sparrows occupy frequently burned loblolly forests at high densities in other parts of their range (e.g. Dunning and Watts 1990, Haggerty 1998), it is likely that Bachman's Sparrow abundance is lower in stands dominated by loblolly because of a correlation with wetter, shrubbier understories under a longer burn rotation rather than a direct association with the overstory pine species.

In addition to environmental conditions, land-use histories, in particular past and present silviculture, may be driving pine species dominance and understory characteristics. The effects of intensive land-use lead to changes in abiotic and biotic condition, such as soil conditions and species diversity, that last decades to centuries after abandonment and often persist even after areas are restored (Foster et al. 2003, Brudvig et al. 2013, 2021). Bachman's Sparrows may be affected by land use histories affecting understory composition and structure. Areas with loblolly were more likely to be used for silviculture and loblolly was planted frequently within the region to replace longleaf pine because of its fast growth rate and regeneration time (Frost 1993, Outcalt 2000, Kirkman et al. 2007). Historical fire suppression may have allowed loblolly to outcompete longleaf pine. A history of fire suppression can also impact understory species abundance and diversity by reducing grass and herbaceous cover, reducing seen production, and, over time, diminishing the seedbed (Clewell 1989, Streng et al. 1993, Brockway and Lewis 1997, Haywood et al. 2001). Although frequent fires have been restored across all sampled upland areas at YWC and SCR, legacy effects of fire suppression and human use may have altered overstory composition and understory diversity.

Apparent survival probability, or the probability that individuals survive and remain faithful to a site, decreased as small stem density increased. Generally, Bachman's Sparrow use of habitat with open midstory (Dunning and Watts 1990, Haggerty 1998, Hannah et al. 2017). In forest with an open midstory, more light can reach the forest floor. This light availability, paired with frequent fire, supports growth of diverse grasses and forbs (Peet and Allard 1993, Harrington and Edwards 1999, Walker and Silletti 2006), which Bachman's Sparrows select over shrubs (Fish et al. 2018, Hannon et al. 2021). Increasing hardwood stem density decreases occupancy probability of Bachman's Sparrow (Hannon et al. 2021). Similarly, Bachman's Sparrow density decreases with increased tall pine sapling volume, particularly in young-aged stands (Dunning and Watts 1990). I suspect that the relationship between small stem density and apparent survival probability in this study was the result of Bachman's Sparrows dispersing from sites once light penetration was insufficient for the growth of grasses and forbs that they rely on for nesting and foraging. Some evidence suggests that the wiregrass gap may be more susceptible to woody encroachment than sites with wiregrass, thus increasing small stem density and reducing Bachman's Sparrow abundance. For example, in the nearby Francis Marion National Forest (~45 km WSW of YWC and SCR), a plot planted with wiregrass in 1993 experienced little woody encroachment compared to neighboring bluestem plots (Fill et al. 2017). Fill et al. (2017) suggest that the more columnar growth habit of bluestems leaves more bare ground for woody regeneration while the cespitose growth habitat of wiregrass allows it to outcompete woody species.

Bachman's Sparrow density at YWC and SCR (0.0085 – 0.0170 birds/ha) was low compared to density estimates from other parts of the Southeast (e.g. 0.26-0.67 birds/ha across burn treatments in Conecuh National Forest, Alabama and Blackwater River State Forest, Florida [Tucker et al. 2004]; 0.0-0.48 birds/ha across stand ages at Savannah River Site and Francis Marion National Forest, South Carolina [Dunning and Watts 1990]). Areas with longleaf pine and low small stem density at the study sites supported higher abundances of Bachman's Sparrows; however, average density was likely biased low because I included mixed pine and hardwood and other suboptimal upland habitat types in the sampling area. Although Bachman's Sparrows typically use frequently burned, open-midstory pine forest, I sampled across all upland stands with a pine component because I did not want to presume what habitat types are available to Bachman's Sparrow or miss detections in novel habitat by applying conclusions about habitat use in other regions to study sites in the wiregrass gap. Although there were patches of high-quality habitat within unsuitable habitat, patchy structure limits occupancy (Fahrig and Merriam 1985, Pulliam and Danielson 1991, Villard et al. 1999, Betts et al. 2007). At my study sites, strips of upland habitat were often divided by hardwood slough, pocosin, and other wetlands. Bachman's Sparrow occupancy is reduced in patchy habitat, despite habitat quality (Dunning et al. 1995, Taillie et al. 2015). Individuals in fragmented habitat due to land-use change also have lower pairing success (Winiarski et al. 2017b).

Despite the documented relationship between Bachman's Sparrow habitat use and time since burn (Engstrom et al. 1984, Tucker et al. 2004, Cox and Jones 2009), I did not find years since burn to be a primary driver of Bachman's Sparrow abundance at YWC and SCR. This was likely because burn regimes for forest stands at YWC and SCR were almost all between one and five years and the majority of burns occurred before the breeding season began, reducing dispersal triggered by recent burning to only a few weeks (Appendix; Seaman and Krementz 2000, Cox and Jones 2007, Jones et al. 2014). Stands dominated by longleaf pine were generally burned with greater frequency, at least every three years. Bachman's Sparrow density typically declines significantly after three years post-burn (Dunning and Watts 1990, Tucker et al. 2004) and the species typically does not occupy stands that have not been burned in over five years (Engstrom et al. 1984). At YWC and SCR, Bachman's Sparrows were only detected at sites zero to three years post-burn. This could be because population density was fairly low and hence competitive exclusion may not have been an important factor in habitat use (Fretwell and Lucas 1970, Fretwell 1972, Perkins et al. 2003). Alternatively, vegetation composition and growth rates in the mesic outer Coastal Plain may differ from more xeric sites, causing outer Coastal Plain pine understories to become overgrown prior to xeric sites under the same burn regime (Peet 2006, Winiarski et al. 2017a). Lastly, while years since burn was not a covariate in the top model, current and past burn regimes likely impacted forest composition and structure, including pine species composition and small stem density. Regenerating loblolly pines are more susceptible to fire than longleaf, giving longleaf the competitive advantage under frequent burn regimes (Wakeley 1935, Frost 1993, Outcalt 2000). Thus, longleaf pine overstory dominance suggests that stands were frequently burned historically. Frequent burns can also prevent midstory encroachment, particularly of hardwood species, because saplings die back before reaching a size at which they may be tolerant of fire (Boyer 1990b, Glitzenstein et al. 1995, Brockway and Lewis 1997, Jose et al. 2006).

Scale at which selection occurs and habitat perception by the study species is important to consider when designing resource selection studies (Wiens 1973, Johnson 1980, Thomas and Taylor 1990, Orians and Wittenberger 1991, McGarigal et al. 2016).

Although the goal of this study was to identify habitat management treatments that Bachman's Sparrows select for home ranges (second order, Johnson 1980), the selection process, while still second order, was likely occurring based on microhabitat characteristics (Wiens and Rotenberry 1981, Fisher and Davis 2010, Winiarski et al. 2017a, Fish et al. 2018). Vegetation characteristics have a greater effect on Bachman's Sparrow occupancy than habitat type and stand age (Dunning and Watts 1990). Habitat treatments and forest characteristics influence understory characteristics; however, as ground foragers and ground nesters, Bachman's Sparrows are likely selecting home ranges based on understory characteristics rather than overstory composition. Inclusion of finer scale habitat variables, such as grass cover and vegetation density, may clarify patterns of home range selection in Bachman's Sparrow within the wiregrass gap.

In conclusion, Bachman's Sparrow abundance at YWC and SCR was largely driven by the proportion of longleaf pine and small stem densities at sites. YWC and SCR supported small populations of Bachman's Sparrow relative to other sites in the southeastern US, likely due to limited suitable habitat. This study provides an initial description of Bachman's Sparrow habitat selection in the wiregrass gap and demonstrates how intensive management can improve habitat for Bachman's Sparrow and potentially increase abundance. Although forests at YWC and SCR can support Bachman's Sparrow, abiotic conditions and landscape structure may limit management success to small areas that support longleaf pine and its associated understory vegetation. Further research into microhabitat home range selection may benefit direct understory management for Bachman's Sparrow.

Management Implications

Although the stand-scale habitat covariates that I measured are likely confounded with understory characteristics, my findings suggest that a high proportion of longleaf pine to other pine species attracts Bachman's Sparrows to a site, while low stem density supports retention. Thus, it is important to manage the appropriate habitat variables to improve the desired demographic parameter. For example, if a management objective is to initially attract Bachman's Sparrow to a restoration site, planting and maintaining longleaf stands may be a priority. However, if the management goal is to increase site fidelity within an existing population, midstory removal may be a better habitat treatment for meeting that objective regardless of pine overstory composition. This study provides important information about habitat treatments that may increase Bachman's Sparrow abundance in the wiregrass-free ecosystems; however, further research into the microhabitat characteristics that Bachman's Sparrows select within the home range can inform directed understory vegetation management for the species.

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TABLES AND FIGURES

Table 1. Candidate set of *N*-mixture models estimating abundance of adult male Bachman's Sparrows during the 2020 and 2021 breeding seasons. Stepwise model selection schema is outlined along with model selection results. *K* = number of parameters, AIC = Akaike's Information, ΔAIC = the difference between the model AIC value and the top model AIC value, and w_i = Akaike weight.

	nPars	AIC	ΔAIC	w_{i}	$cum.w_{\text{i}}$
1. Distribution					
Zero-inflated Poisson $\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(.)$	5	857.59	0.00	0.59	0.59
Poisson $\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(.)$	4	858.31	0.72	0.41	1.00
2a. Detection Probability					
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(PER)$	6	845.83	0.00	1.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(.)$	4	858.31	12.48	0.00	1.00
2b. Detection Probability					
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	7	834.29	0.00	0.42	0.42
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(DAY + MIN + PER)$	8	834.50	0.21	0.37	0.79
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(TEM + I(TEM^2) + DAY + MIN + PER)$	10	835.79	1.50	0.20	0.99
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(OBS + PER)$	8	842.51	8.22	0.01	0.99
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(DAY + PER)$	7	845.00	10.71	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(PER)$	6	845.83	11.54	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(TEM + PER)$	7	846.66	12.37	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(TEM + I(TEM^2) + PER)$	7	846.66	12.37	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(WIN + PER)$	9	849.51	15.22	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(SKY + PER)$	9	849.97	15.68	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(TEM + I(TEM^2) + WIN + SKY + PER)$	14	855.25	20.96	0.00	1.00
3. Initial Abundance					
$\lambda(PPP)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	826.49	0.00	0.99	0.99
$\lambda(CLO + I(CLO^2))\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	9	835.72	9.23	0.01	1.00
$\lambda(PBA + I(PBA^2) + YSB + I(YSB^2))\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	11	846.13	19.63	0.00	1.00
$\lambda(YSB + I(YSB^2))\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	9	848.92	22.42	0.00	1.00
$\lambda(PSD)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	849.19	22.69	0.00	1.00
$\lambda(PBA + I(PBA^2))\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	9	850.26	23.77	0.00	1.00
$\lambda(EVR)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	851.16	24.66	0.00	1.00
$\lambda(YSB)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	852.16	25.67	0.00	1.00
$\lambda(SSD)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	852.59	26.09	0.00	1.00
$\lambda(CLO)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	852.65	26.15	0.00	1.00
$\lambda(PBA + YSB)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	9	853.31	26.81	0.00	1.00
$\lambda(.)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	7	853.46	26.96	0.00	1.00
$\lambda(PBA)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	854.77	28.28	0.00	1.00
$\lambda(LSD)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	855.17	28.68	0.00	1.00
4. Recruitment Rate					
$\lambda(PPP)\gamma(PPP)\omega(.)[\text{Const.}]p(MIN + PER)$	9	770.86	0.00	1.00	1.00
$\lambda(PPP)\gamma(PSD)\omega(.)[\text{Const.}]p(MIN + PER)$	9	804.31	33.46	0.00	1.00
$\lambda(PPP)\gamma(CLO + I(CLO^2))\omega(.)[\text{Const.}]p(MIN + PER)$	10	811.91	41.05	0.00	1.00
$\lambda(PPP)\gamma(PBA + I(PBA^2) + YSB + I(YSB^2))\omega(.)[\text{Const.}]p(MIN + PER)$	12	819.51	48.65	0.00	1.00
$\lambda(PPP)\gamma(YSB + I(YSB^2))\omega(.)[\text{Const.}]p(MIN + PER)$	10	821.30	50.45	0.00	1.00
$\lambda(PPP)\gamma(SSD)\omega(.)[\text{Const.}]p(MIN + PER)$	9	824.32	53.46	0.00	1.00
$\lambda(PPP)\gamma(CLO)\omega(.)[\text{Const.}]p(MIN + PER)$	9	824.59	53.73	0.00	1.00
$\lambda(PPP)\gamma(YSB)\omega(.)[\text{Const.}]p(MIN + PER)$	9	825.56	54.71	0.00	1.00
$\lambda(PPP)\gamma(PBA + I(PBA^2))\omega(.)[\text{Const.}]p(MIN + PER)$	10	825.63	54.77	0.00	1.00
$\lambda(PPP)\gamma(PBA + YSB)\omega(.)[\text{Const.}]p(MIN + PER)$	10	826.24	55.38	0.00	1.00
$\lambda(PPP)\gamma(EVR)\omega(.)[\text{Const.}]p(MIN + PER)$	9	826.28	55.42	0.00	1.00
$\lambda(PPP)\gamma(.)\omega(.)[\text{Const.}]p(MIN + PER)$	8	826.49	55.64	0.00	1.00
$\lambda(PPP)\gamma(LSD)\omega(.)[\text{Const.}]p(MIN + PER)$	9	827.19	56.33	0.00	1.00
$\lambda(PPP)\gamma(PBA)\omega(.)[\text{Const.}]p(MIN + PER)$	9	827.29	56.43	0.00	1.00

Table 1. (cont.)

	nPars	AIC	ΔAIC	w_{i}	$cum.w_{\mathrm{i}}$
5. Apparent Survival Probability					
$\lambda(PPP)\gamma(PPP)\omega(SSD)[\text{Const.}]p(MIN+PER)$	10	766.19	0.00	0.55	0.55
$\lambda(PPP)\gamma(PPP)\omega(YSB)[\text{Const.}]p(MIN+PER)$	10	769.05	2.86	0.13	0.69
$\lambda(PPP)\gamma(PPP)\omega(.)[\text{Const.}]p(MIN+PER)$	9	770.86	4.67	0.05	0.74
$\lambda(PPP)\gamma(PPP)\omega\left(YSB+I(YSB^2)\right)[\text{Const.}]p(MIN+PER)$	11	770.94	4.76	0.05	0.79
$\lambda(PPP)\gamma(PPP)\omega(PBA+YSB)[\text{Const.}]p(MIN+PER)$	11	771.05	4.86	0.05	0.84
$\lambda(PPP)\gamma(PPP)\omega(EVR)[\text{Const.}]p(MIN+PER)$	10	772.55	6.37	0.02	0.86
$\lambda(PPP)\gamma(PPP)\omega(CLO)[\text{Const.}]p(MIN+PER)$	10	772.83	6.64	0.02	0.88
$\lambda(PPP)\gamma(PPP)\omega(PSD)[\text{Const.}]p(MIN+PER)$	10	772.84	6.65	0.02	0.90
$\lambda(PPP)\gamma(PPP)\omega(PBA)[\text{Const.}]p(MIN+PER)$	10	772.84	6.65	0.02	0.92
$\lambda(PPP)\gamma(PPP)\omega(PPP)[\text{Const.}]p(MIN+PER)$	10	772.85	6.67	0.02	0.94
$\lambda(PPP)\gamma(PPP)\omega(LSD)[\text{Const.}]p(MIN+PER)$	10	772.86	6.67	0.02	0.96
$\lambda(PPP)\gamma(PPP)\omega\left(PBA+I(PBA^2)+YSB+I(YSB^2)\right)[\text{Const.}]p(MIN+PER)$	13	772.99	6.81	0.02	0.98
$\lambda(PPP)\gamma(PPP)\omega\left(PBA+I(PBA^2)\right)[\text{Const.}]p(MIN+PER)$	11	773.78	7.59	0.01	0.99
$\lambda(PPP)\gamma(PPP)\omega\left(CLO+I(CLO^2)\right)[\text{Const.}]p(MIN+PER)$	11	774.56	8.38	0.01	1.00
6. Distribution					
Poisson $\lambda(PPP)\gamma(PPP)\omega(SSD)[\text{Const.}]p(MIN+PER)$	10	766.19	0.00	0.52	0.52
Zero-inflated Poisson $\lambda(PPP)\gamma(PPP)\omega(SSD)[\text{Const.}]p(MIN+PER)$	11	766.34	0.15	0.48	1.00

Table 2. Parameter estimates of the scaled predictors for the top *N*-mixture model with 85% confidence intervals. Covariates in the top model include minutes elapsed since sunrise (MIN), secondary period (PER), proportion of longleaf pine to all pine species (PPP), and 10-25 cm DBH stem density (SSD).

Predictor	**β**	**7.5%**	**92.5%**
Detection Probability (p)			
Intercept	-0.063	-0.367	0.242
MIN	-0.475	-0.696	-0.254
PER_2	0.936	0.503	1.369
PER_3	1.185	0.734	1.636
Initial Abundance (λ)			
Intercept	-2.975	-3.951	-2.000
PPP	1.734	1.053	2.414
Recruitment Rate (γ)			
Intercept	-3.708	-4.155	-3.261
PPP	1.457	1.124	1.789
Apparent Survival Probability (ω)			
Intercept	-0.936	-1.606	-0.265
SSD	-1.319	-2.202	-0.436

Table 3. Parameter estimates for the top *N*-mixture model using average covariate values with 85% confidence intervals. p_{PER1} = detection probability during secondary period 1, p_{PER2} = detection probability during secondary period 2, p_{PER3} = detection probability during secondary period 3, λ = initial abundance (males per site during the first primary period), γ = recruitment rate (additional males per site between primary periods), ω = apparent survival probability (probability of male survival or site-fidelity between primary periods).

Parameter	**Estimate**	**7.5%**	**92.5%**
p_{PER1}	0.484	0.408	0.560
p_{PER2}	0.705	0.632	0.779
p_{PER3}	0.754	0.684	0.825
λ	0.051	0.001	0.101
γ	0.025	0.014	0.035
ω	0.282	0.146	0.417

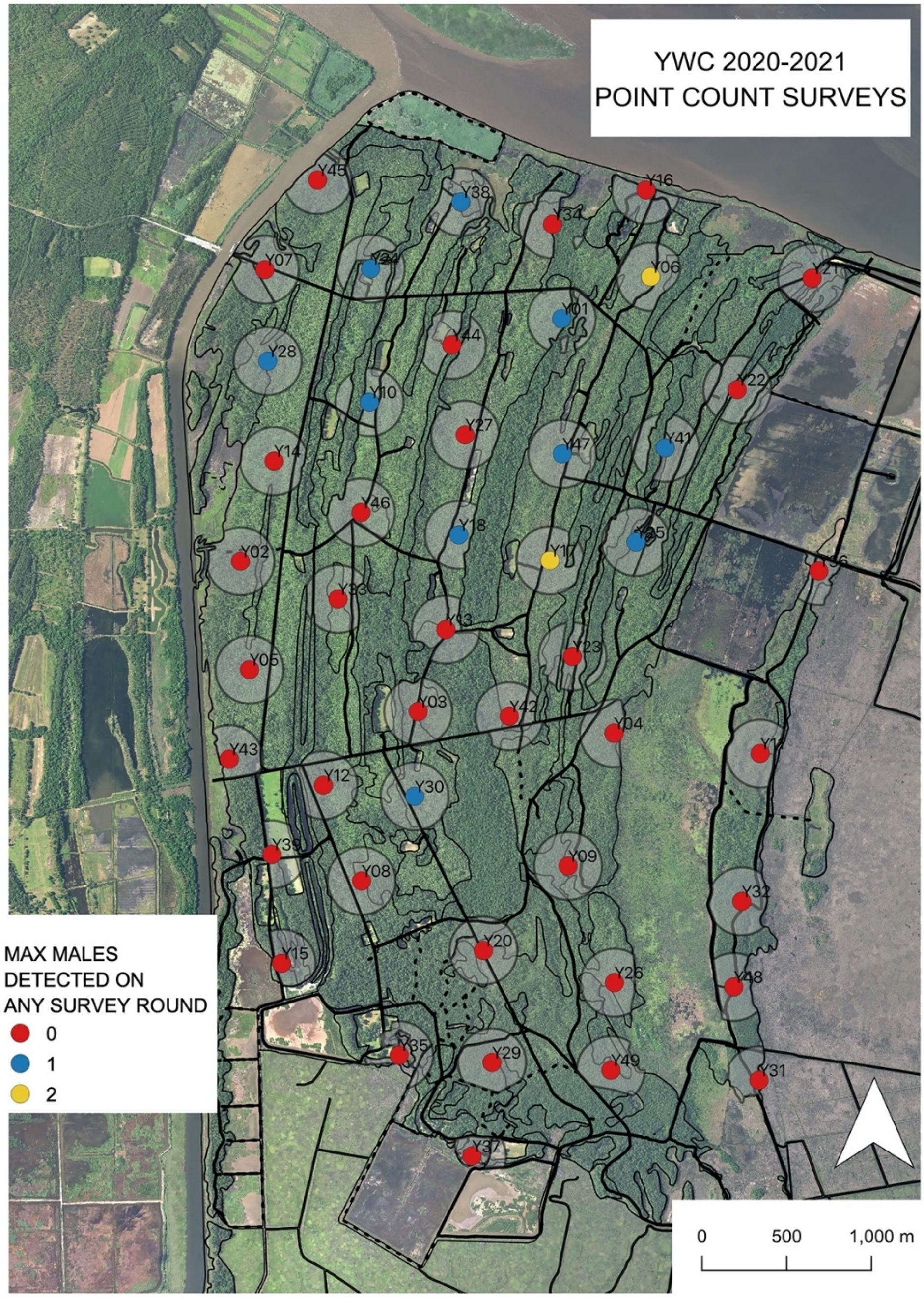

Figure 1. Point count sites with variable areas at Yawkey Wildlife Center. The maximum abundance (red = 0, blue = 1, yellow = 2) during any primary period is presented.

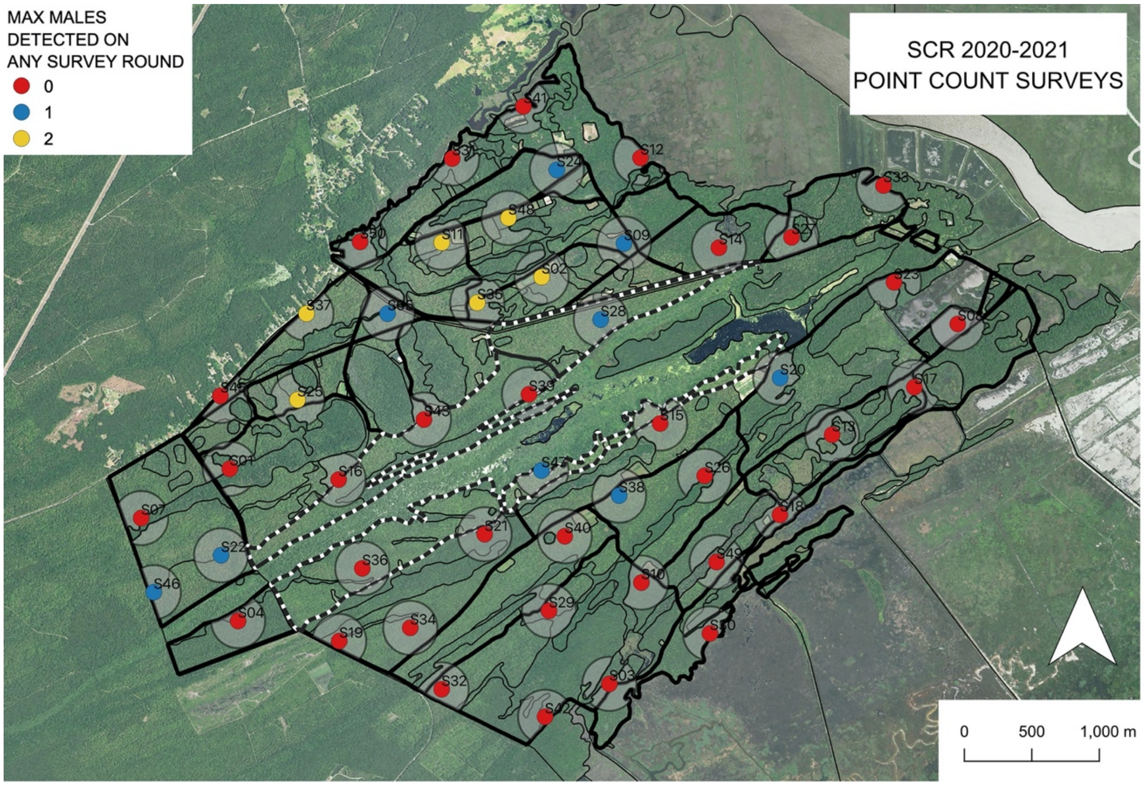

Figure 2. Point count sites with variable areas at Santee Coastal Reserve. The maximum abundance (red = 0, blue = 1, yellow = 2) during any primary period is presented.

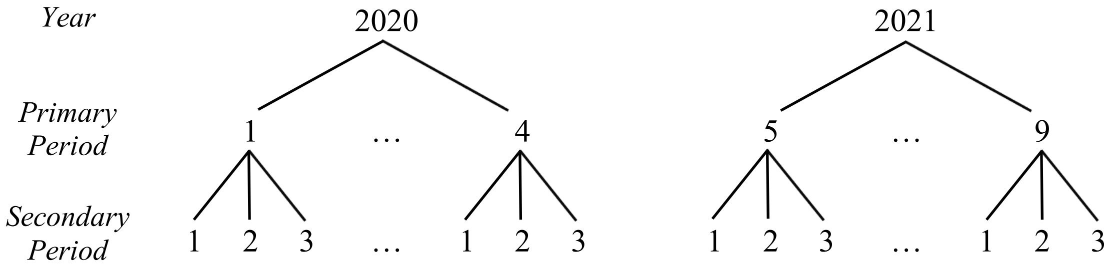

Figure 3. Short time interval robust sampling design in which each primary period is a sequential 3 week period during the breeding season and each secondary period is a sequential section of an 8 minute survey.

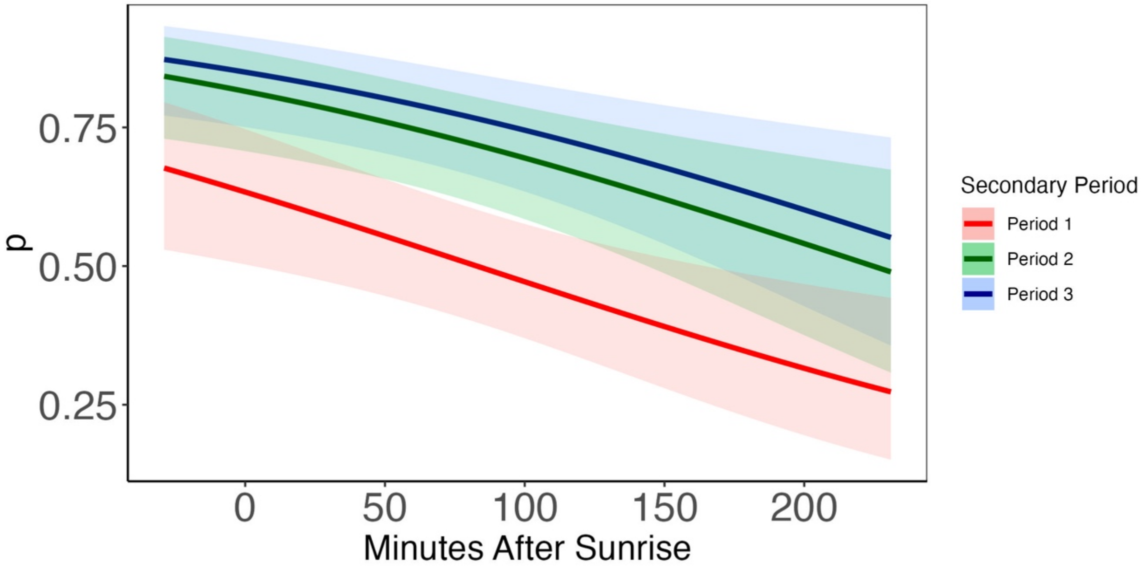

Figure 4. Detection probability (*p*) of adult male Bachman's Sparrows at survey sites as it relates to the minutes elapsed since sunrise and for each secondary period (red = Period 1, green = Period 2, blue = Period 3) during the 2020 and 2021 breeding seasons at YWC and SCR. Respective colored bands represents the 85% confidence intervals around the predictions.

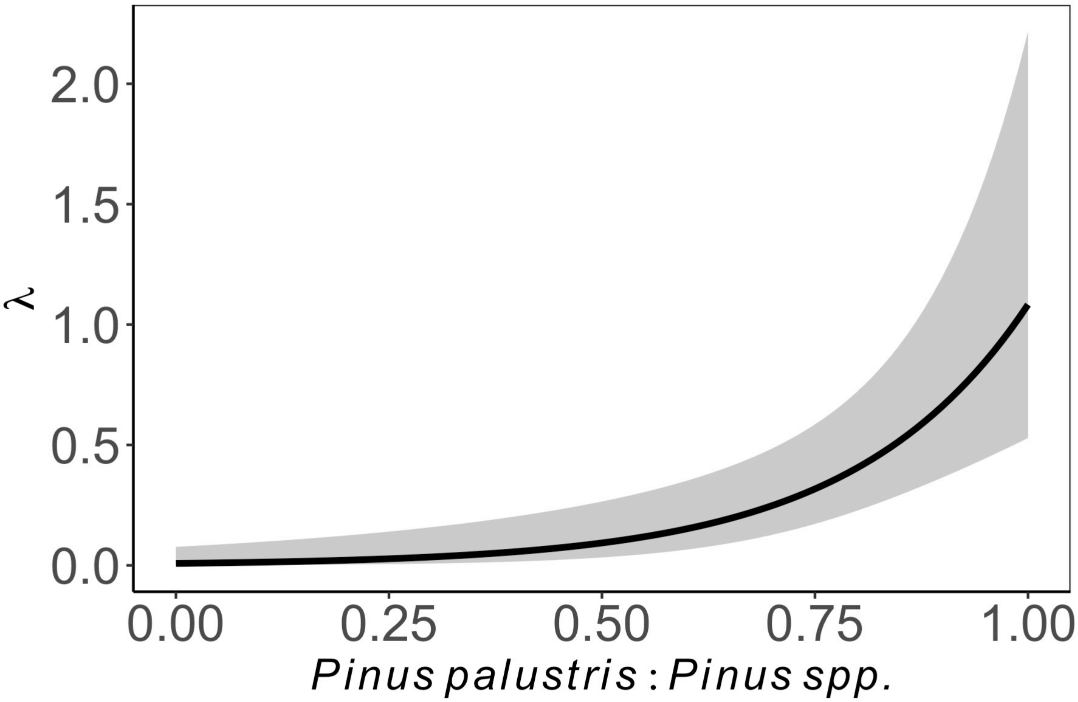

Figure 5. Predicted initial abundance (site-specific abundance during the first primary period, λ) of adult male Bachman's Sparrows at survey sites in response to the proportion of longleaf pine to other pine species during the 2020 breeding season at YWC and SCR. Gray band represents the 85% confidence interval around the prediction.

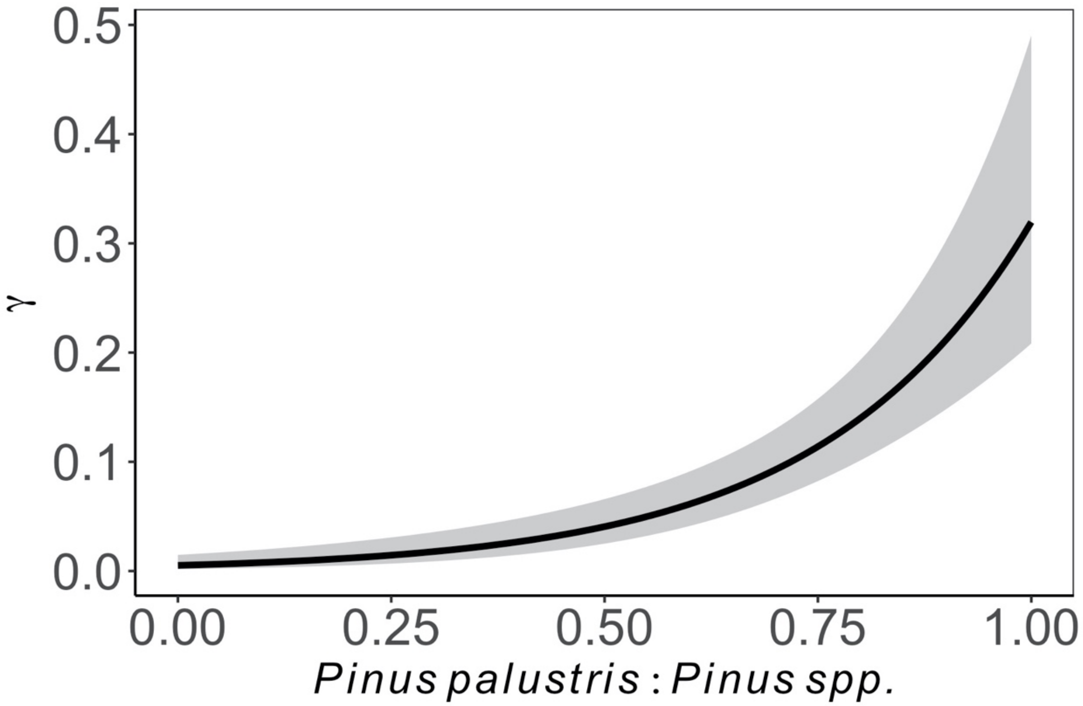

Figure 6. Predicted recruitment rate (gains due to birth or immigration between primary periods, γ) of adult male Bachman's Sparrows at survey sites in response to the proportion of longleaf pine to other pine species during the 2020 and 2021 breeding seasons at YWC and SCR. Gray band represents the 85% confidence interval around the prediction.

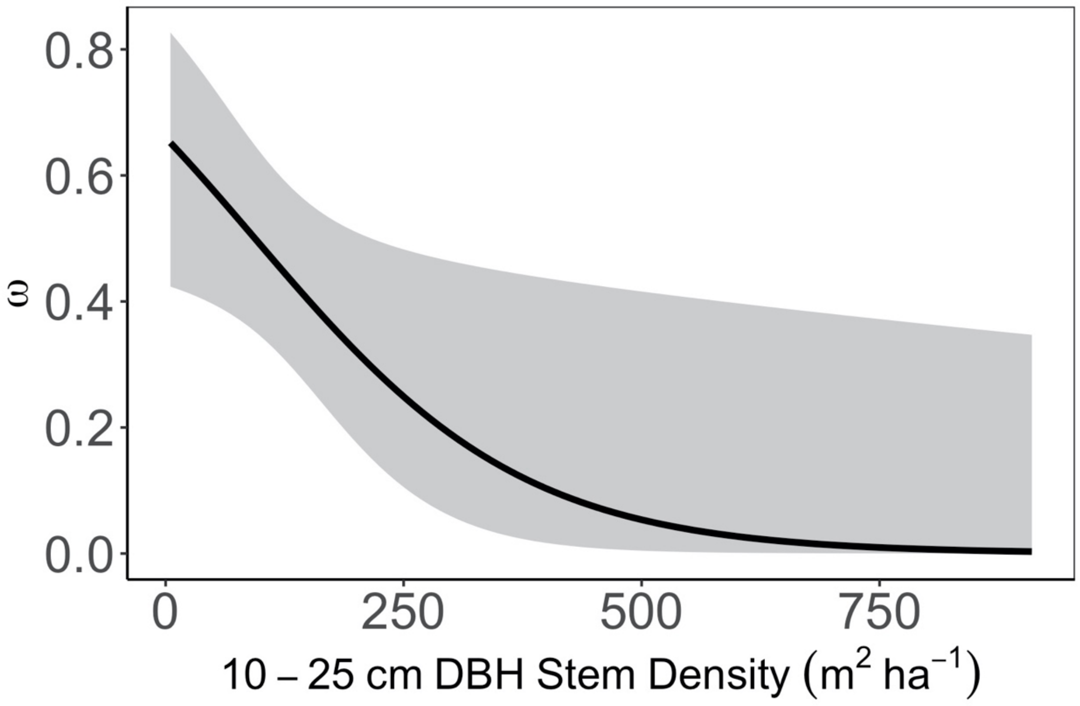

Figure 7. Predicted apparent survival probability (probability of survival or site-fidelity between primary periods, *ω*) of adult male Bachman's Sparrows at survey sites in response to small stem density (10-25 cm DBH stems per hectare) during the 2020 and 2021 breeding seasons at YWC and SCR. Gray band represents the 85% confidence interval around the prediction.

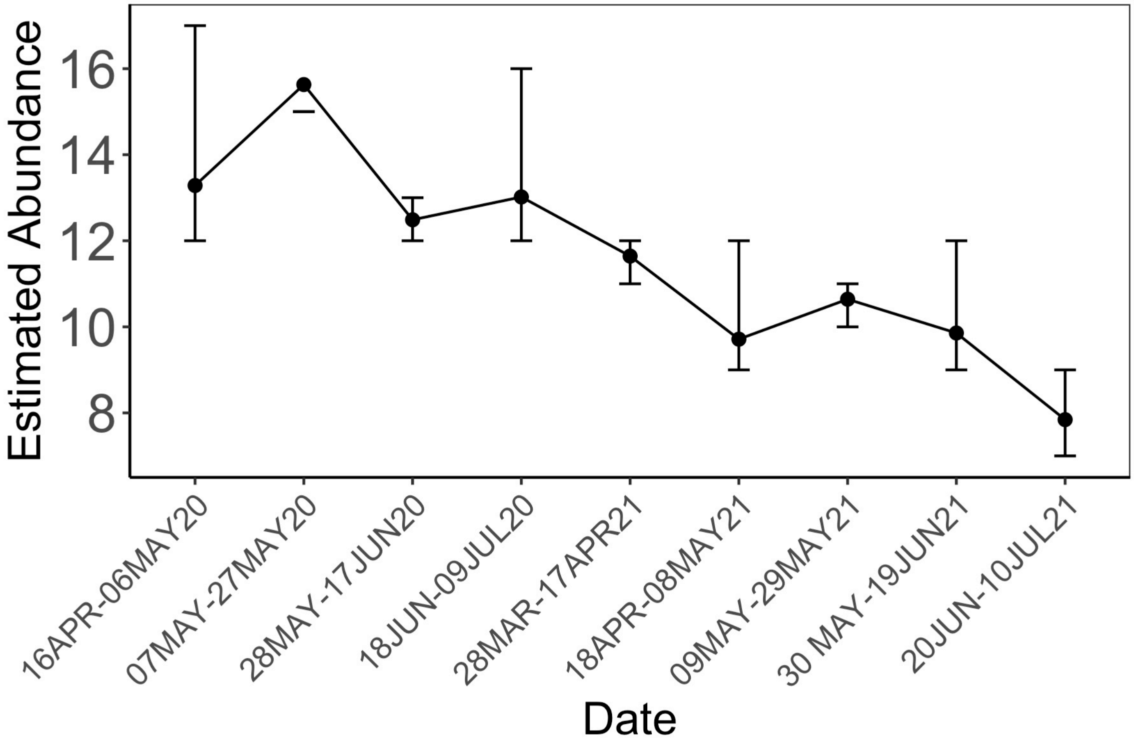

Figure 8. Bachman's Sparrow abundance at sites across the nine primary periods during the 2020 and 2021 breeding seasons at YWC and SCR. Error bars represent 85% confidence intervals around the predictions.

CHAPTER THREE

NEST-SITE SELECTION AND NEST SURVIVAL IN A WIREGRASS-FREE ECOSYSTEM

INTRODUCTION

Resource selection is a decision-making process in animals, driven by environmental perception, which results in disproportionate resource use (e.g. forest stands, denning sites, food items) in regards to resource availability (Johnson 1980, Manly et al. 2002). In theory, resource selection should be adaptive, as choices in resource use ultimately affect fitness (Hildén 1965, Rozenzweig 1981, Jaenike and Holt 1991, Martin 1998). If resource selection returns fitness benefits, natural selection should increase the frequency of that behavioral phenotype in the population. According to resource selection theory, birds should select nest-sites with characteristics that increase fitness, such as increased cover from predators or proximity to food sources. Nest success is a component of fitness; however, correlations between nest-site selection and nest success are not always observed (Chalfoun and Schmidt 2012; e.g. Filliater et al. 1994, Stillman et al. 2019). Maladaptive nest-site selection may be the result of ecological traps (i.e. when organisms prefer to use habitat or resources that are of low quality and decrease fitness; Dwernychuck and Boag 1972, Gates and Gysel 1978, Robertson and Hutto 2006), or perceptual traps, (i.e. when organisms underutilize habitats or resources that are of high quality and afford the most fitness benefits; Patten and Kelly 2010). Thus, linking habitat variables to use alone may fail to provide complete information for increasing population growth rates. Identifying potential ecological traps, or other sources on non-adaptive selection, is necessary for improving habitat management, particularly for declining species and species using atypical habitat.

When atypical habitat use does not lower fitness, it can reveal the adaptive capacity of a population (Sogge et al. 2006, Gailly et al. 2020). In cases of atypical habitat use, individuals may be making choices based on structural cues rather than vegetation associations (Kennedy et al. 2018). The relative importance of physiognomy versus floristics in influencing species habitat use has a long history of investigation and may vary among species and guilds (MacArthur and MacArthur 1961, Wiens and Rotenberry 1981, Rotenberry 1985, Fleishman et al. 2003, Hewson et al. 2011, Seavy and Alexander 2011). If vegetation structure influences selection more than vegetation composition, different plant communities that adequately replicate the structure of typically used species can provide the same benefits to wildlife, such as forage, shelter, and nesting substrate. Studies of atypical habitat use, such as use of non-native plant communities (Heckscher 2004, Jones and Bock 2005, Kennedy et al. 2009, Meyer et al. 2015) or human-modified areas (Davidson and Fitzpatrick 2010, Gailly et al. 2020), highlight the importance of vegetation structure above composition in selection processes and thus have implications for habitat management, conservation planning, and ecosystem restoration (Kennedy et al. 2009, 2018, Davidson and Fitzpatrick 2010).

Bachman’s Sparrow (*Peucaea aestivalis*) is a small, ground-nesting passerine endemic to frequently burned pine-grass woodlands, especially longleaf pine (*Pinus palustris*) forest, and other open habitat in the Southeastern United States. Habitat loss and degradation due to deforestation and fire suppression has driven population declines over the last half century (Sauer 2017). In response, states across its range have listed Bachman's Sparrow as a species of conservation concern, including South Carolina (SCDNR 2015). Across much of its range, Bachman's Sparrow uses the dense wiregrass (*Aristida spp.*) understory typical of longleaf pine forest. However, the central South Carolina "wiregrass gap" lies between the ranges of *Aristida stricta* and *A. beyrichiana*, where understories are instead dominated by bluestem species (*Schizachyrium spp*. and *Andropogon spp*.; Peet 1993, 2006) and generally have a higher shrub density. Nest-site selection and nest survival of Bachman's Sparrow in the unique wiregrass-free longleaf pine ecosystem of the South Carolina Coastal Plain has been little studied, and efforts to conserve the species require an understanding of regional habitat use.

Despite regional differences, Bachman's Sparrow nesting habitat shares some generalities. Bachman's Sparrows typically select nest-sites that have low grass ground cover or low to intermediate grass density and more woody vegetation than the surrounding nest area (Jones et al. 2013, Winiarski et al. 2017a). Bachman's Sparrows also select nest sites with patchy bare ground, especially by the nest entrance (Haggerty 1995, Jones et al. 2013). Bare ground and lower vegetation density at nesting sites of Bachman's Sparrow and other ground-nesting species are thought to increase accessibility to the nest for feeding, minimize moisture retention, provide escape routes, and increase fledgling mobility (Götmark et al. 1995, Brooks and Stouffer 2010, Jones et al. 2013, Taillie et al. 2015). However, regional differences in understory vegetation may lead to different patterns of selection and survival, raising the question of whether vegetation composition or structure drives nest-site selection and whether there are differences in reproductive success due to this selection.

Despite previous attempts to find correlates of Bachman’s Sparrow nest survival, preferred nest-site vegetation characteristics have not yet been linked to increased nest survival (Haggerty1995, Jones et al. 2013, Winiarski et al. 2017a). However, the vegetation community and structure within the wiregrass gap of the outer South Carolina Coastal Plain differs from those of past study areas. Thus, further research is warranted to determine if there is regional variation in selective pressures. In this study, I investigated whether Bachman’s Sparrow nest-site selection is adaptive within the unique wiregrass-free habitat of the outer South Carolina Coastal Plain. I also considered whether differences in vegetation composition in the region changes nest-site selection patterns, particularly whether Bachman’s Sparrows select nest-sites based on structure or vegetation class. To meet these objectives, I estimated the relative probability of selection and daily survival rates of nest-sites under varying vegetation characteristics. I then used these estimates to compare vegetation characteristics that Bachman’s Sparrows select for nest-sites to vegetation characteristics that increase nest survival. Given the results of previous studies and the dominance of shrubby species over grass in my study sites, I hypothesized that Bachman’s Sparrows would select nest-sites that allow escape but provide sufficient cover, and thus have higher groundcover density and patchy bare ground. Additionally, I hypothesized that nest-site selection in Bachman’s Sparrow is adaptive and thus nest-site selection and nest survival would increase under the same predictors, namely intermediate percent bare ground and groundcover density.

METHODS

Study Area

The study sites, Tom Yawkey Wildlife Center Heritage Preserve (YWC), Georgetown County, South Carolina and Santee Coastal Reserve Wildlife Management Area (SCR), Charleston County, South Carolina, are coastal properties managed by South Carolina Department of Natural Resources (SCDNR). YWC and SCR are both approximately 97 km^2 and contain diverse habitat including upland pine, maritime forest, marsh, and freshwater wetlands. Study areas are dominated by longleaf and loblolly (*Pinus taeda*) pine as well as mixed pine and hardwood forest. The understory vegetation composition of YWC and SCR is unique because the sites fall between the *Aristida stricta* and *Aristida beyrichiana* ranges and thus are free of wiregrass. Instead, understories are composed of predominantly bluestem grasses, bracken fern (*Pteridium aquilinum*), and short-statured shrubs (e.g. *Ilex glabra*, *Gaylussacia dumosa*, *Gaylussacia frondosa*, *Vaccinium spp*., *Lyonia lucida*). Switchcane (*Arundinaria tecta*) was common in areas, particularly those bordering hardwood slough. Longleaf, mixed pine, and mixed pine and hardwood stands at both sites are managed through dormant season prescribed burning, primarily in January through early April. Stands at YWC and SCR are typically burned every one to five years (YWC: mean = 1.33, SD = 2.67; SCR: mean = 2.11, SD = 1.38).

Nest Searching and Nest Monitoring

I searched for Bachman's Sparrow nests between 10 April and 31 July during the 2020 and 2021 breeding seasons. During point count surveys being conducted for another research objective, I noted locations of individuals demonstrating potential breeding activity (i.e. nest building, food carry, mate guarding, territoriality). I returned to the locations of potential breeders to search for nests using behavioral observation. I revisited each active nest every two to four days (mean = 2.82, SD = 0.82) to monitor nest survival following Martin and Geupel (1993). At each visit, I recorded the nesting stage, i.e. building, incubating, nestling, fledgling, or failed (abandoned, depredated, hatch failure, or unknown). If there were nest contents, I recorded the number of eggs and/or the number and age of young. I calculated nest ages based on the first day of incubation (penultimate egg laying) being Age 0. If lay date was unknown due to locating the nest after laying, I calculated approximate ages based on hatch dates. Bachman's Sparrows typically hatch 12-14 days after incubation begins (Haggerty 1994). Nests that hatched but had an unknown incubation period length were assigned an age of 13 days at hatching. For nests with ambiguous nest initiation dates, such as those that were found during incubation and were depredated before hatching, I estimated the incubation date by subtracting half of the maximum remaining incubation days from the location date. Nestlings on average fledge after nine days (Haggerty 1994), so survival rates for the whole nesting period were calculated based on a 22 day nesting period. Observations after 22 days were not included in analyses.

Vegetation Surveys

I measured nest-site vegetation characteristics between 06 May and 17 August 2020 and 15 May and 11 August 2021. I measured nest-site characteristics 30±3 days after nest initiation (from first day of incubation) and compared these measurements to available nest-site characteristics. Measuring nests after the nesting attempt is complete decreases the likelihood of nest abandonment or predation due to human presence (Götmark 1992, Martin and Geupel 1993). Measuring vegetation characteristics at a consistent time in the nesting period rather than at the inconsistent times of nest detection, failure, or fledging reduces bias in estimated effects of vegetation characteristics on nest-site selection and nest survival due to vegetation growth (McConnell et al. 2017).

To quantify habitat characteristics of available nesting locations within Bachman's Sparrow home ranges, I randomly selected a paired available nest-site for vegetation surveys from within the assumed home range of the individual. I considered each home range to be a circle, centered on the nest, with a radius of 160 m. This delineation is based on 95% fixed kernel home range estimates of Bachman's Sparrow from past studies (Brown 2012, Winiarski et al. 2017b) that produced estimates using radio telemetry. Following Taillie et al. (2015) and Winiarski et al. (2017a), I measured vegetation characteristics along two 10 m perpendicular transects centered at the nest site or available nest site. I measured vegetation characteristics along each transect at 1 m increments away from the nest, totaling 20 vegetation survey points plus the central nest location. The vegetation measurements taken at the 21 points were averaged for analysis (Table 1). I measured vegetation density using methods established by Wiens and Rotenberry (1981). I measured vertical density by quantifying the number of "hits" of each vegetation class along 0.1 m increments of a pole 1.5 m long and 6 mm in diameter. I quantified groundcover density as the number of "hits" of each vegetation class along the first 0.1 m of the pole. Using a 0.5 m x 0.5 m quadrat, I visually determined percent bare ground and percent composition of five vegetation classes (grass, switch cane, forb/fern, shrub, and dead) making up > 5% of the ground cover, excluding litter, within the quadrat. I measured the maximum height of each vegetation class using a measuring tape. I counted the number of perches at each survey point, defined as the number of alive or dead woody plants > 1 m that can support the weight of a sparrow. I measured canopy closure using a spherical densiometer and pine basal area at the nest-site using a 10-factor prism.

Weather

I used daily summary weather data from station WBAN:03728, McClellanville 7 NE, SC (33.1532°, -79.3637°, NOAA 2021) to determine maximum temperature and total precipitation over nesting intervals. This weather station was selected because it was the closest station (distance = 2.42 – 15.42 km) to YWC and SCR nests that had the most complete records.

Statistical Analyses

Nest-site Selection

To assess potential drivers of nest-site selection, I considered vegetation structure and composition covariates that, based on existing literature and preliminary field observations, might have impacted nest-site selection. I formulated 20 *a priori* models based on hypothesized effects of vegetation composition and structure on Bachman's Sparrow nest-site selection using conditional logistic regression models (Hosmer and Lemeshow 1989, Compton et al. 2002, Duchesne et al. 2010; Table 2). Nest ID was included as a stratum in each model in order to compare each used nest-sites to its paired available nest-sites. Models were restricted to one or two covariates because of small sample size. A null model was not included in this candidate set because conditional logistic regression does not support intercept estimation. I incorporated pine basal area at the nest, canopy closure, number of perches, groundcover density, vertical density, maximum vegetation height, percent bare ground, and percent cover of five vegetation types (grass, switch cane, forb/fern, shrub, and dead) as covariates in the nest-site selection models. Following the results of Winiarski et al. (2017a), I considered quadratic effects of percent grass, percent bare ground, and vegetation density measurements because high-density vegetation can inhibit the ground movement of Bachman's Sparrows, including foraging and escape (Götmark et al. 1995, Brooks and Stouffer 2010, Jones et al. 2013, Taillie et al. 2015). I also considered quadratic effects of canopy closure and pine basal area because past studies have demonstrated that Bachman's Sparrows use habitat with intermediate canopy cover (Hannah et al. 2017). Some nests were likely attempted by the same individuals; however, because the identity of all nesting pairs could not be confirmed, I assumed that all nesting attempts were independent. I screened for collinearity between covariates in the same models by calculating Pearson's correlation coefficients for covariate pairs. When $|r| > 0.6$, I removed the variable with less hypothesized ecological significance. Candidate models were fitted in the survival package (Therneau 2020) in R 4.0.3 (R Core Team 2020). I used the package AICcmodavg (Mazerolle 2020) to calculate AICc and rank candidate models. I retained a confidence set of models that held 95% of the Akaike weight on which to make inference (Burnham and Anderson 2002). I considered variables important if 85% confidence intervals around the beta coefficients did not overlap zero (Arnold 2010). I exponentiated the top fitted model to formulate a Resource Selection Function (RSF) that estimates relative probability of nest-site selection under the modeled habitat covariates (Manly et al. 2002).

Nest Survival

I used the logistic exposure method (Shaffer 2004) to model the daily survival rate (DSR) of Bachman's Sparrow nests across nest-site vegetation characteristics. The logistic exposure method uses logistic regression with a modified logit link which accounts for exposure days to fit logistic regression models with or without random effects to formulate estimates of daily nest survival rates when nest exposure time varies. Nests survived (1) the interval between each nest check if at least one viable egg or one live nestling remained in the nest, or if at least one nestlings was confirmed fledged. If no viable eggs or live nestlings or fledglings remained, the nest failed (0) during that interval. Nests were considered successful if at least one nestling fledged.

I formulated 28 *a priori* models based on hypothesized effects of vegetation composition and structure, weather, and nest timing on Bachman's Sparrow nest survival (Table 3). Twenty of these models share the same covariates as the nest-site selection model set in order to determine if the same characteristics that Bachman's Sparrow select at nest-sites increase survival, supporting adaptive nest-site selection. In addition, I included linear and quadratic models for the effect of years since burn on daily survival rate. Because weather can impact nest survival (Skagen and Yakel Adams 2012, Sherry et al. 2015), I included three models with temperature and precipitation covariates. The last three models explore the effect of nest age and ordinal day on daily survival rate. I included nest ID as a random effect. Site and year random effects were not included to simplify models and aid in convergence. I screened for collinearity between covariates in the same models by calculating Pearson's correlation coefficients for covariate pairs. When $|r| > 0.6$, I removed the variable with less hypothesized ecological significance. Candidate models were initially fitted in lme4 (Bates et al. 2015) in R 4.0.3 (R Core Team 2020); however, many models did not converge. Convergence issues were remedied by fitting models using package blme (Chung et al. 2013) and using theta values from corresponding models fitted in lme4 when it aided in convergence. I used the package AICcmodavg (Mazerolle 2020) to calculate AICc and rank candidate models. I retained a confidence set of models that held 95% of the Akaike weight on which to make inference (Burnham and Anderson 2002). I considered variables important if 85% confidence intervals around the beta coefficients did not overlap zero (Arnold 2010). I used the modified logit link on the fitted models to estimate daily survival rates under the modeled covariates. I calculated bootstrapped 85% confidence intervals (n sims = 10000) around predicted daily survival rates using the function bootMer in lme4. I exponentiated the estimated daily survival rate to the 22 day nesting period to estimate the nest survival rate over the whole nesting period, or the probability of fledging at least one young. 85% confidence intervals for estimates of nest and stage survival were calculated using the delta method (Powell 2007).

RESULTS

Nest-site Selection

I found 47 active Bachman's Sparrow nests in 2020 and 2021 (Figures 1-2). Nests were strongly associated with bluestem grasses, with 34 nests (72.3%) placed in predominantly bluestem sp. clumps. Ten nests (21.3%) were placed at the base of short statured shrubs including *Gaylussacia frondosa, Gaylussacia dumosa, Ilex glabra, Quercus sp.*, and *Morella cerifera,* two nests (4.3%) were placed in unknown grass species, and one nest (2.1%) was placed in primarily *Tephrosia virginiana*. Live and dead bracken fern (*Pteridium aquilinum*) was often incorporated as nesting substrate (n = 20), especially for cover.

The top conditional logistic regression model included the quadratic form for groundcover density (Table 4). This model carried 63% of the Akaike weight and was 5.7 times more likely to be the best predicting model than the second-best model which included the quadratic form for percent bare ground (Table 4). The relative probability of nest-site selection was highest at intermediate groundcover densities (Table 5). The quadratic form for percent bare ground was included in the second through fourth ranked models and was also an important predictor of nest-site selection (second ranked model: $\beta_{\text{BARE}}= 0.708$, 85% CI = 0.080 – 1.336; $\beta_{\text{BARE}^2}= -0.739$, 85% CI = -1.119 – -0.358).

Nest Survival

I monitored 47 nests of which 29 fledged and 18 failed. Groundcover density best predicted daily nest survival rates (Table 6). The quadratic groundcover density model was the top model in the candidate set but it only carried 25% of the Akaike weight

(Table 6). The quadratic groundcover density model and the nesting stage model were the only two models to rank higher than the null model (Table 6). The quadratic groundcover density model was 2.1 times more likely to be the best predicting model than the second-best model which only included nest stage (incubating or nestling) as a predictor and was 3.6 times more likely to be the best predicting model than the null model. Daily survival rates of nests were lowest at intermediate groundcover densities (Table 7, Figure 3). Nesting stage was an important predictor of nest survival, with a lower DSR observed in the nestling stage than the incubation stage ($\beta_{STAGE:N}$ = -1.332, 85% CI = -2.342 – -0.322). However, nesting stage was not included in models with vegetation covariates because of issues with model convergence due to small sample size.

Across the range of groundcover densities observed, the top-ranked model indicated that daily survival rates ranged from 0.947 (85% CI: 0.919 – 0.980) to 1.000 (85% CI: 0.998 – 1.000; Figure 3) and survival across the 22-day nesting period ranged from 0.301 (85% CI: 0.112 – 0.491) to 0.999 (85% CI: 0.995 – 1.000). Nest survival was lowest when nest sites had an average groundcover density of 0.262 vegetation hits in the first 10 cm. Using the second-ranked model which included a covariate for nesting stage, daily survival rates were estimated to be 0.990 (85% CI: 0.982 – 1.000) for the incubation stage and 0.962 (85% CI: 0.942– 0.999) for the nestling stage. Survival rate across the 13-day incubation period was estimated to be 0.875 (85% CI: 0.749 – 1.000), survival rate across the nine-day nestling period was estimated to be 0.709 (85% CI: 0.568 – 0.849), and survival rate across the whole 22-day nesting period was estimated to be 0.621 (85% CI: 0.441 – 0.800).

DISCUSSION

I found no evidence for adaptive nest-site selection in Bachman's Sparrow at the study sites. Given the opposite trends in selection and survival, selection may actually be maladaptive. However, daily nest survival rates at groundcover densities with the greatest probability of selection were fairly high when compared to nest survival estimates from other regions and likely do not suggest that low nest survival alone would be a source of population declines in Bachman's Sparrow at the study sites. I therefore suspect that within the studied Bachman's Sparrow population, fitness benefits may be gained at a life history stage that we did not observe.

Nest-site Selection

I hypothesized that Bachman's Sparrows would select nest-sites that had high groundcover density and patchy (intermediate percent cover) bare ground compared to available nest-sites within their assumed home ranges. My results demonstrated that Bachman's Sparrows selected nest-sites with intermediate groundcover density. Additionally, vegetation structure and density played a stronger role in selection at my study sites than understory composition. Likely, as proposed by Winiarski et al. (2017a), site selection is driven by both perceived predation risk and likelihood of female survival, as intermediate groundcover density provides sufficient nest cover while allowing escape paths from the nest. Contrary to previous studies of Bachman's Sparrow nest-site selection which emphasize the importance of grass in Bachman's Sparrow nesting habitat (Jones et al. 2013, Winiarski et al. 2017a), I found that the amount of grass within the nest-site was not as important for selection. Winiarski et al. (2017a) observed that

Bachman's Sparrow nest-sites in the North Carolina Sandhills ecoregion had intermediate vertical grass densities while in the Coastal Plain ecoregion, nest sites had lower grass vertical density compared to available nest-sites. The differing relationships between grass density and nest-site selection across the North Carolina Coastal Plain and Sandhills as well as the lack of relationship between grass cover and nest-site selection in the wiregrass gap of South Carolina affirms the importance of identifying regional differences in habitat selection in order to make targeted management plans.

Bachman's Sparrows may have selected sites based on total vegetation density (i.e. structure) instead of the amount of grass cover (i.e. composition) at my study sites because availability differs between the wiregrass gap populations and other regional populations. Longleaf pine habitat in the Coastal Plain wiregrass gap typically has lower grass density and higher shrub density than habitat with wiregrass dominated understories (Peet 2006, Fill et al. 2017). Additionally, although wiregrass and bluestem are both bunchgrasses, they have different growth habits. Wiregrass is cespitose while bluestems are more columnar. Bluestem understories likely do not provide the same structure as wiregrass, but additional shrub density may offset lower grass density. Although Bachman's Sparrows strongly associated with understory grasses (bluestem spp., primarily) as a nesting substrate, populations in the wiregrass gap may have adapted to a wider range of nest-site characteristics due to reduced availability of grassy sites. Availability drives resource use (Johnson 1980); however, low availability of a preferred resource (e.g. grass) can lead to alternative selection strategies, or a functional response in habitat selection (Mysterud and Ims 1998, Bremset et al. 2009, Monroe et al. 2019).

For example, Bachman’s Sparrows may select nest sites based on understory density of all vegetation types because areas with preferred grass densities are scarce. Selection of scarce resources may lower fitness if the cost of selection (time spent searching for optimal nesting location) outweighs the benefits (increased probability of nest success). As Bachman’s Sparrow nest success has not been linked to any habitat covariates (Haggerty 1995, Jones et al. 2013, Winiarski et al. 2017a), there may be little cost for selecting a resource that is not preferred but more abundant. Thus, Bachman’s Sparrows may be cueing into total understory structure as it may sufficiently mimic the structure of the preferred resource (i.e. grass density).

By recognizing that some species can adapt to the loss or decline of associated flora through flexible resource selection, a greater emphasis can be put on simulating the structure of optimal habitat through management actions rather than replicating the historic species composition. This emphasis may increase restoration success when goals are to increase wildlife use of degraded ecosystems. Both within and outside of the wiregrass range, land managers are working to restore longleaf pine forest (USDA 2020). However, restoring the understory plant community – especially wiregrass – is challenging. Unsuccessful or slow wiregrass regeneration can be caused by the dependency on growing season burns for flowering and seed production and sensitivity to soil disturbances (Clewell 1989, Platt et al. 1991, Cox et al. 2004). Although wiregrass is a critical component of the longleaf pine ecosystem, forests in the process of restoration can still support wildlife, including at-risk species. By identifying the structural and floristic components of naturally wiregrass-free ecosystems that longleaf pine forest specialists select, such as intermediate groundcover densities, we can improve wildlife management in forests where understory restoration is in process or has proved problematic.

Nest Survival and Adaptive Selection

I hypothesized that Bachman's Sparrow nest-sites that had high groundcover density and patchy bare ground would have the highest daily survival rates, as I predicted that these vegetation characteristics would have a higher probability of selection. I found that nest survival was lower at intermediate groundcover densities and that nest-site selection and nest survival showed opposite trends. This observed relationship could suggest an ecological trap; however, it is also possible that fitness benefits of selection are accrued at a different temporal or spatial scale. Daily nest survival rates were also lower in the nestling stage than in the incubation stage. Nests of altricial species may be more likely to be predated in the nestling stage because the female spends less time brooding and guarding the nest, the male and female make more frequent trips to and from the nest to feed the young, and nestlings draw attention to the nest by moving and vocalizing (Skutch 1949, Haskell 1994, Martin et al. 2000, Haff and Magrath 2011, Cox et al. 2012).

Data limitations require that inference from these results are made with caution. First, the sample size of nests was small. Although small sample size is unlikely to bias nest survival estimates, estimate variance is high (Weiser 2021). Second, nests at intermediate groundcover densities were sampled at higher intensities than nests with low or high groundcover densities because they had a higher probability of selection. Thus, with the smaller sample of low and high groundcover density nests, the likelihood that failed nests at low and high groundcover densities were simply not sampled (i.e., not detected by observers) is higher. Third, nests with high groundcover density may have been undersampled because they may have been more covered and thus less likely to be detected by observers.. Although I support further research to clarify this relationship, groundcover density is likely affecting survival in the YWC and SCR study populations given I did find significant relationships with groundcover density and nest survival.

Predation by snakes, mesomammals, and small mammals is the primary cause of nest failure in Bachman's Sparrow (Malone et al. 2019, Malone et al. 2021). Given that predation occurred more often at nests with intermediate groundcover densities, it is likely that predators also use understory with intermediate groundcover densities with greater frequency. This could be because both Bachman's Sparrows and predators are trying to maximize concealment from predators with movement and escape efficiency. Information about fine-scale habitat use and movement (third order selection, Johnson 1980) of common Bachman's Sparrow nest predators such as black racers (*Coluber constrictor*) and corn snakes (*Pantherophis guttata*) in longleaf pine habitats is limited, however. Black racers do associate with areas with less canopy cover, less midstory, and more ground-level vegetation in pine woodlands and burned oak-savanna (Perry et al. 2009, Fleet et al. 2009, Howey et al. 2016), which are similar to habitat characteristics that Bachman's Sparrows select on the home-range scale (Dunning and Watts 1990, Haggerty 2000, Brooks and Stouffer 2010, Jones et al. 2013, Taillie et al. 2015, Winiarski et al. 2017b). It is also possible that nest predator populations at YWC and SCR have changed over time and Bachman's Sparrows have not yet adapted to increased predation pressure through changes in nest-site selection behavior, creating an ecological trap. Cues and habitat characteristics that once presented fitness benefits may no longer signal optimal habitat due to ecosystem changes over time, such as increased predator density (Misenhelter and Rotenberry 2000) or shifts in vegetation composition (Fierro-Calderón and Martin 2020). Longleaf pine forest in particular has experienced both varied land-use and heavy management historically, which in turn alters understory species richness and composition (Brudvig and Damschen 2011).

Nests with intermediate groundcover densities had a higher probability of selection but reduced survival rates, indicating maladaptive selection. This could be due to a functional response in selection (Mysterud and Ims 1998) within the wiregrass gap, as there may be a tradeoff between locating rare nest-sites with ideal grass density and more common nest sites with adequate total groundcover density. If there is a functional response in selection in the wiregrass gap, total groundcover density may be a poor substitute for grass density. However, daily survival rates at nest-sites with the highest probability of selection still had relatively high daily survival rates (0.96). At this daily survival rate, approximately 41% of nests would fledge at least one young. This estimate is equal to or higher than other estimates of daily nest survival rates from other parts of the Bachman's Sparrow range (min DSR: 0.88-0.94, Red Hills, GA, FL [Malone et al. 2021]; max DSR: 0.96, Red Hills, GA, [Jones et al. 2013]; see also Haggerty 1988 [AR], Perkins et al. 2003 [FL], Tucker et al. 2006 [AL], Stober and Krementz 2000 [SC], Winiarski et al. 2017a [NC], Fish et al. 2019 [NC]). Although nest survival was not maximized at groundcover densities with the highest probability of selection, it is unlikely that this nonadaptive nest-site selection in regards to nest success would cause declines in the study population long-term if daily survival rates remained high. Research into other vital rates, such as female and fledgling survival (Fish et al. 2020, Choi et al. 2021), and dispersal behavior may reveal more about sources of population declines.

Bachman's Sparrow nest survival has yet to be linked to any measured habitat characteristic during previous studies (Haggerty 1995, Jones et al. 2013, Winiarski et al. 2017a) despite resource selection theory stating that selection should be adaptive (Hildén 1965, Rozenzweig 1981). The broad time scale over which natural selection occurs may be obscuring evidence for adaptive habitat selection. The stochasticity of predation and other sources of nest failure during the short duration of most habitat selection studies may prevent the correlation between nest-site selection and long-term fitness trends from being detected (Clark and Shutler 1999). Long-term studies on nest survival may depict the fitness benefit of selection more accurately. For ground-nesting grassland birds such as the Bachman's Sparrow which experience high levels of predation compared to other guilds (Ricklefs 1969, Martin 1993), nest-sites may be selected to ensure female survival over survival of the nest contents. In a short study, there may be no correlates of survival based on nest-site characteristics. However, long-term survival of the female may increase her genetic output more than if she were to be predated earlier but had slightly higher nest survival rate during her shorter life. The estimated survival rate of females during the breeding season, 0.94 (Choi et al. 2021), is similar to estimates of male survival over the same period and thus provides support for this hypothesis.

Alternatively, the results of an experiment conducted by Latif et al. (2012) support an "adaptive peak" hypothesis in which nest-site choice in some species has received so much selective pressure over time that only a small range of nest-choice phenotypes are present within a highly adapted population. A difference in survival between nests with highly selected characteristics and all used characteristics cannot be detected because the variance among used characteristics is too small. If this hypothesis were true, survival rates would be dictated by stochastic events.

Nest survival may not be linked to nest-site selection because nest survival is only one component of fitness and is not a complete measure of lifetime fitness. Rather, fitness benefits may be accrued at a different life history stage. For example, individuals may gain more fitness benefits from increasing fledgling survival rather than nest survival (Chalfoun and Martin 2007, Streby et al. 2014). Despite nest predation rates being higher at intermediate groundcover densities at the nest-site scale, fledglings may be more likely to survive because parents can provision them easily and they can move easily on the ground before they begin flying. Instead of solely cueing into characteristics of the exact nest location, breeding pairs may also select nesting locations based on cues within the proximity of the nest or even the home range. Fledglings select habitat with greater shrub, forb, and grass cover and less bare ground (Fish et al. 2020), and thus adults may nest in areas close to more cover but not within a 5 m radius of the nest. A tradeoff in selection between nest and fledgling survival may ultimately maximize fitness. Lastly, nest success is not a complete measure of fitness, as it does not provide information about how many offspring are produced. For example, nests with intermediate groundcover densities may fail at higher rates; however, if nests with intermediate groundcover densities can support higher clutch sizes or more fledglings, higher offspring output may compensate for lower nest survival rates. Because I did not observe fledging events and could not relocate fledglings, I could not accurately use fledgling success as another measure of fitness. Similarly, I could not relate clutch size to habitat variables because nests were located during varying times in the nesting period and may have experiences clutch or brood reductions. Additional research on fledgling success and survival in response to varying habitat would provide insights into these potential tradeoffs in nest-site selection.

In this study, I provide preliminary evidence for non-adaptive, and potentially maladaptive, nest-site selection in Bachman's Sparrow. Bachman's Sparrow is a declining species (Sauer 2017) and thus it is important to verify whether these results accurately demonstrate maladaptive selection or whether survival estimates were biased due to small sample size and stochastic events. Further study of other measures of fitness of Bachman's Sparrow such as fledgling survival and reproductive success over the lifetime of a female, can improve understanding of the breeding ecology and population dynamics of Bachman's Sparrows in this region. Lastly, if further investigation reveals that nest-site selection is non-adaptive, traditional avian management strategies based in augmenting habitat for selected characteristics may need to be reconsidered.

Management Implications

In this study, I found that the relative probability of nest-site selection in Bachman's Sparrow was highest at intermediate groundcover densities; however, because nest survival decreased at intermediate groundcover densities, I suggest that further research into other components of fitness in relation to groundcover density is completed to determine if this selection is adaptive or evidence of an ecological trap. If other components of fitness, such as fledgling success or adult survival, are found to compensate for reduced nest survival at intermediate groundcover densities, increasing the availability of areas with intermediate groundcover densities may support population growth in wiregrass-free ecosystems. Additionally, managers may choose to replicate selected groundcover densities at longleaf pine restoration sites where wiregrass understories could not be successfully restored to increase use by Bachman’s Sparrow. However, if nest-site selection based on groundcover density truly is maladaptive, managers may prioritize reducing the abundance of common Bachman’s Sparrow predators to increase nest survival rates.

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TABLES AND FIGURES

Table 1. Summary statistics (mean ± SD) for Bachman's Sparrow nest-site vegetation composition and structure variables at both YWC and SCR, South Carolina, 2020-2021.

		Nest Vegetation Plot	
Code	**Variable**	**Used**	**Available**
CLOS	Canopy Closure (%)	47.63±7.85	45.80±10.19
NBAP	Basal Area: Pine (m^2/ha)	22.76±6.77	19.54±6.73
YSB*	Years Since Last Burn	1.32±0.73	NA
TALL	# Shrub (Live or Dead) > 1 m	1.77±3.13	2.62±4.93
BARE	% Bare	46.09±10.22	44.88±16.29
GRAS	% Grass	7.55±5.02	7.46±7.50
SWIT	% Switch Cane	0.36±0.94	0.74±1.73
FOFE	% Forb/Fern	16.79±8.07	18.17±10.45
WOOD	% Shrub	25.87±8.87	25.35±11.13
DEAD	% Dead	3.34±3.31	3.40±3.72
MAXH	Max. Height: All Veg. Types	46.18±8.25	49.09±14.07
VDEN	Vertical Density: Total (hits 0 – 1.5 m)	0.77±0.25	0.79±0.41
GDEN	Groundcover Density: Total (hits < 0.1 m)	0.22±0.09	0.18±0.14

* Nest Survival Analysis Only

Table 2. Candidate set of 20 conditional logistic regression nest-site selection models based on the hypothesized effects of vegetation composition and structure on nest-site selection. Models are conditional on nest ID.

HYPOTHESIS	**COVARIATES**	**MODEL STRUCTURE**
BACS select nest sites based on nest-site structure.	Maximum Veg. Height	β_1 (MAXH)
BACS select nest sites based on nest-site structure.	Groundcover Density	β_1 (GDEN)
BACS select nest sites based on nest-site structure.	Groundcover Density^2	β_1 (GDEN) + β_2 (GDEN^2)
BACS select nest sites based on nest-site structure.	Vertical Density	β_1 (VDEN)
BACS select nest sites based on nest-site structure.	Vertical Density^2	β_1 (VDEN) + β_2 (VDEN^2)
BACS select nest sites based on availability of perches.	Number of Perches	β_1 (TALL)
BACS select nest sites based on nest-site floristics.	% Grass	β_1 (GRAS)
BACS select nest sites based on nest-site floristics.	% Grass^2	β_1 (GRAS) + β_2 (GRAS^2)
BACS select nest sites based on nest-site floristics.	% Switch Cane	β_1 (SWIT)
BACS select nest sites based on nest-site floristics.	% Woody	β_1 (WOOD)
BACS select nest sites based on nest-site floristics.	% Forb/Fern	β_1 (FOFE)
BACS select nest sites based on nest-site floristics.	% Dead	β_1 (DEAD)
Predator avoidance/foraging efficiency strategies impact nest-site selection.	% Bare Ground	β_1 (BARE)
Predator avoidance/foraging efficiency strategies impact nest-site selection.	% Bare Ground^2	β_1 (BARE) + β_2 (BARE^2)
Predator avoidance/foraging efficiency strategies impact nest-site selection	% Bare Ground^2 Groundcover Density	β_1 (BARE) + β_2 (BARE^2) + β_3 (GDEN)
Predator avoidance/foraging efficiency strategies impact nest-site selection	% Bare Ground^2 Tall	β_1 (BARE) + β_2 (BARE^2) + β_3 (TALL)
Stand thinning impacts nest-site selection.	Canopy Closure	β_1 (CLOS)
Stand thinning impacts nest-site selection.	Canopy Closure^2	β_1 (CLOS) + β_2 (CLOS^2)
Stand thinning impacts nest-site selection.	Pine Basal Area	β_1 (NBAP)
Stand thinning impacts nest-site selection.	Pine Basal Area^2	β_1 (NBAP) + β_2 (NBAP^2)

Table 3. Candidate set of 28 logistic exposure nest survival models based on the hypothesized effects of vegetation composition and structure, timing, and weather. Nest ID is included as a random effect in all models.

HYPOTHESIS	**COVARIATES**	**MODEL STRUCTURE**
VEGETATION MODELS		
No covariates impact daily survival rate (DSR).	Intercept Only	β_0
Nest-site structure impacts DSR.	Maximum Veg. Height	$\beta_0 + \beta_1$ (MAXH)
Nest-site structure impacts DSR.	Groundcover Density	$\beta_0 + \beta_1$ (GDEN)
Nest-site structure impacts DSR.	Groundcover Density^2	$\beta_0 + \beta_1$ (GDEN) + β_2 (GDEN^2)
Nest-site structure impacts DSR.	Vertical Density	$\beta_0 + \beta_1$ (VDEN)
Nest-site structure impacts DSR.	Vertical Density^2	$\beta_0 + \beta_1$ (VDEN) + β_2 (VDEN^2)
Number of perches impacts DSR.	Number of Perches	$\beta_0 + \beta_1$ (TALL)
Nest-site floristics impact DSR.	% Grass	$\beta_0 + \beta_1$ (GRAS)
Nest-site floristics impact DSR.	% Grass^2	$\beta_0 + \beta_1$ (GRAS) + β_2 (GRAS^2)
Nest-site floristics impact DSR.	% Switch Cane	$\beta_0 + \beta_1$ (SWIT)
Nest-site floristics impact DSR.	% Woody	$\beta_0 + \beta_1$ (WOOD)
Nest-site floristics impact DSR.	% Forb/Fern	$\beta_0 + \beta_1$ (FOFE)
Nest-site floristics impact DSR.	% Dead	$\beta_0 + \beta_1$ (DEAD)
Predator avoidance/foraging efficiency strategies impact DSR.	% Bare Ground	$\beta_0 + \beta_1$ (BARE)
Predator avoidance/foraging efficiency strategies impact DSR.	% Bare Ground^2	$\beta_0 + \beta_1$ (BARE) + β_2 (BARE^2)
Predator avoidance/foraging efficiency strategies impact DSR.	% Bare Ground^2 Groundcover Density	$\beta_0 + \beta_1$ (BARE) + β_2 (BARE^2) + β_3 (GDEN)
Predator avoidance/foraging efficiency strategies impact DSR.	% Bare Ground^2 Tall	$\beta_0 + \beta_1$ (BARE) + β_2 (BARE^2) + β_3 (TALL)
Stand thinning increases DSR.	Canopy Closure	$\beta_0 + \beta_1$ (CLOS)
Stand thinning increases DSR.	Canopy Closure^2	$\beta_0 + \beta_1$ (CLOS) + β_2 (CLOS^2)
Stand thinning increases DSR.	Pine Basal Area	$\beta_0 + \beta_1$ (NBAP)
Stand thinning increases DSR.	Pine Basal Area^2	$\beta_0 + \beta_1$ (NBAP) + β_2 (NBAP^2)
Prescribed burning increases DSR.	Years Since Burn	$\beta_0 + \beta_1$ (YSB)
Prescribed burning increases DSR.	Years Since Burn^2	$\beta_0 + \beta_1$ (YSB) + β_2 (YSB^2)
AGE/TIMING MODELS		
DSR changes with nest stage.	Stage	$\beta_0 + \beta_1$ (NEST)
DSR changes with time of year.	Julian Day	$\beta_0 + \beta_1$ (DAYS)
WEATHER MODELS		
DSR changes with temperature.	Maximum Temperature	$\beta_0 + \beta_1$ (MAXT)
DSR changes with precipitation.	Total Precipitation	$\beta_0 + \beta_1$ (PREC)
DSR changes weather.	Maximum Temperature Total Precipitation	$\beta_0 + \beta_1$ (MAXT) + β_2 (PREC)

Table 4. 95% confidence set of nest-site selection models for 47 nest-site and available nest-site pairs at YWC and SCR, South Carolina, 2020-2021. All models are stratified by nest ID. *K* = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, ΔAIC_c = the difference between the model AIC_c value and the top model AIC_c value, and w_i = Akaike weight.

MODEL	***K***	**Log-likelihood**	**AIC_c**	**ΔAIC_c**	**w_i**	***Cum.* w_i**
GDEN + $GDEN^2$	2	-24.10	52.33	0	0.63	0.63
BARE + $BARE^2$	2	-25.86	55.86	3.53	0.11	0.74
BARE + $BARE^2$ + GDEN	3	-24.80	55.87	3.54	0.11	0.85
BARE + $BARE^2$ + TALL	3	-25.64	57.54	5.21	0.05	0.89
VDEN + $VDEN^2$	2	-27.05	58.23	5.90	0.03	0.93
GRAS + $GRAS^2$	2	-27.33	58.80	6.47	0.02	0.95

Table 5. Parameter estimates of the scaled predictors for the top nest-site selection model with 85% confidence intervals. GDEN = groundcover density.

Predictor	**β**	**7.5%**	**92.5%**
GDEN	1.440	0.710	2.170
$GDEN^2$	-0.709	-1.073	-0.346

Table 6. 95% confidence set of nest survival models for 47 nests and 207 interval observations at YWC and SCR, South Carolina, 2020-2021. All models include nest ID as a random effect. *K* = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, ΔAIC_c = the difference between the model AIC_c value and the top model AIC_c value, and w_i = Akaike weight.

MODEL	***K***	**Log-likelihood**	**AIC_c**	**ΔAIC_c**	**w_i**	**Cum. w_i**
GDEN + $GDEN^2$	4	-57.73	123.67	0.00	0.25	0.25
STAGE	3	-59.52	125.17	1.50	0.12	0.37
NULL	2	-61.12	126.30	2.63	0.07	0.43
PREC	3	-60.54	127.21	3.54	0.04	0.47
MAXT	3	-60.80	127.72	4.06	0.03	0.51
WOOD	3	-60.81	127.75	4.08	0.03	0.54
GDEN	3	-60.85	127.81	4.14	0.03	0.57
SWIT	3	-60.89	127.90	4.24	0.03	0.60
YSB	3	-60.89	127.91	4.24	0.03	0.63
GRAS	3	-60.90	127.91	4.24	0.03	0.66
VDEN	3	-60.90	127.92	4.25	0.03	0.69
GRAS + $GRAS^2$	4	-59.89	127.98	4.31	0.03	0.72
TALL	3	-60.93	127.99	4.32	0.03	0.75
DEAD	3	-61.00	128.13	4.46	0.03	0.77
NBAP	3	-61.02	128.16	4.49	0.03	0.80
DAYS	3	-61.06	128.23	4.56	0.03	0.82
CLOS	3	-61.07	128.25	4.58	0.03	0.85
BARE	3	-61.11	128.34	4.68	0.02	0.87
FOFE	3	-61.12	128.36	4.69	0.02	0.90
MAXH	3	-61.12	128.36	4.69	0.02	0.92
MAXT + PREC	4	-60.31	128.81	5.15	0.02	0.94
VDEN + $VDEN^2$	4	-60.71	129.62	5.96	0.01	0.95

Table 7. Parameter estimate of the scaled predictor for the top nest survival model with 85% confidence interval. GDEN = groundcover density.

Predictor	**β**	**7.5%**	**92.5%**
Intercept	3.131	2.625	3.636
GDEN	-0.883	-1.591	-0.175
GDEN^2	0.785	0.172	1.397

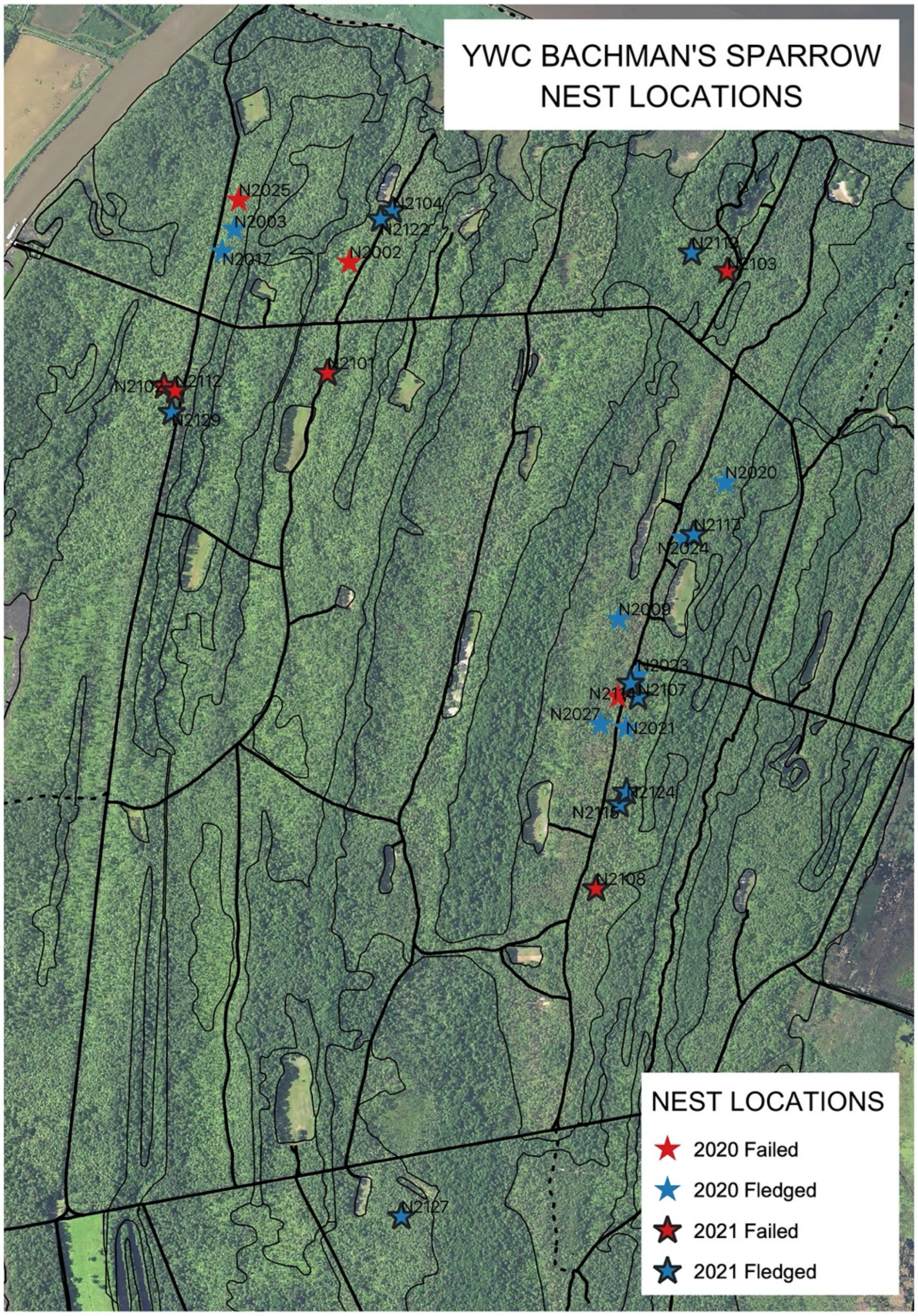

Figure 1. 2020 and 2021 nest locations and fates at Yawkey Wildlife Center.

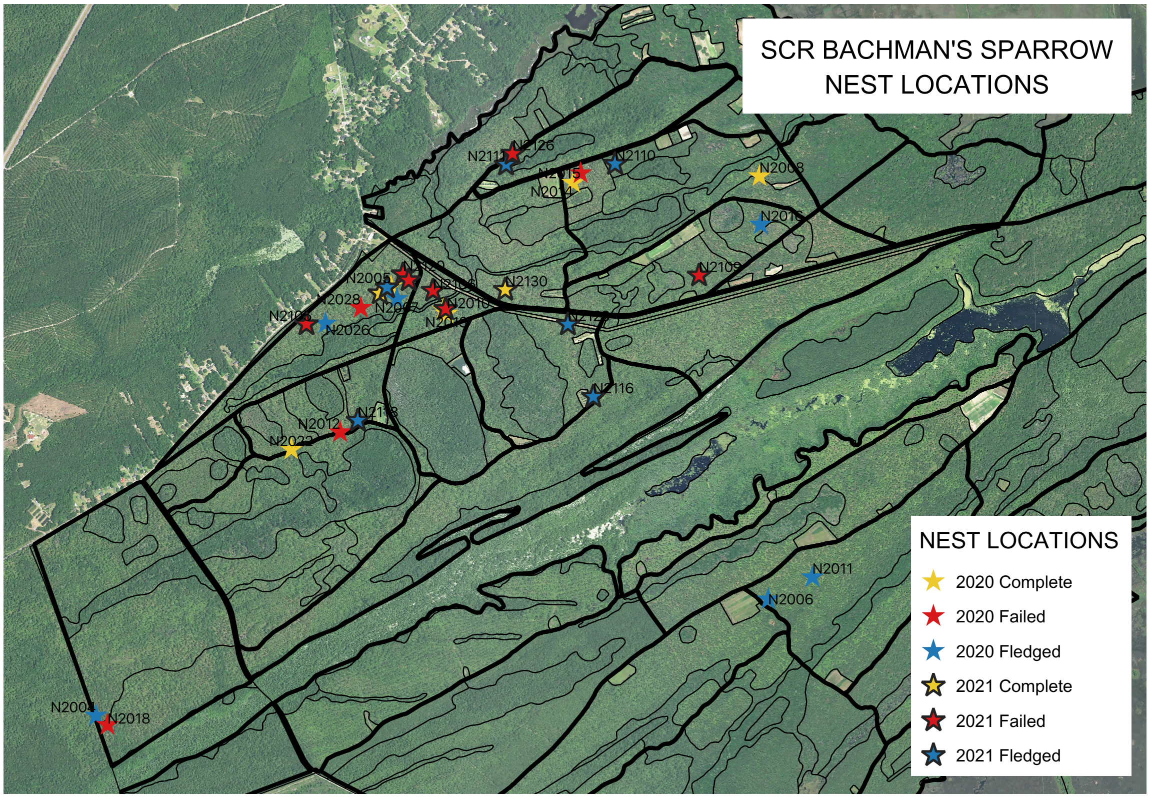

Figure 2. 2020 and 2021 nest locations and fates at Santee Coastal Reserve. Complete nests are nests that were found after fledging or failure and were not included in analyses.

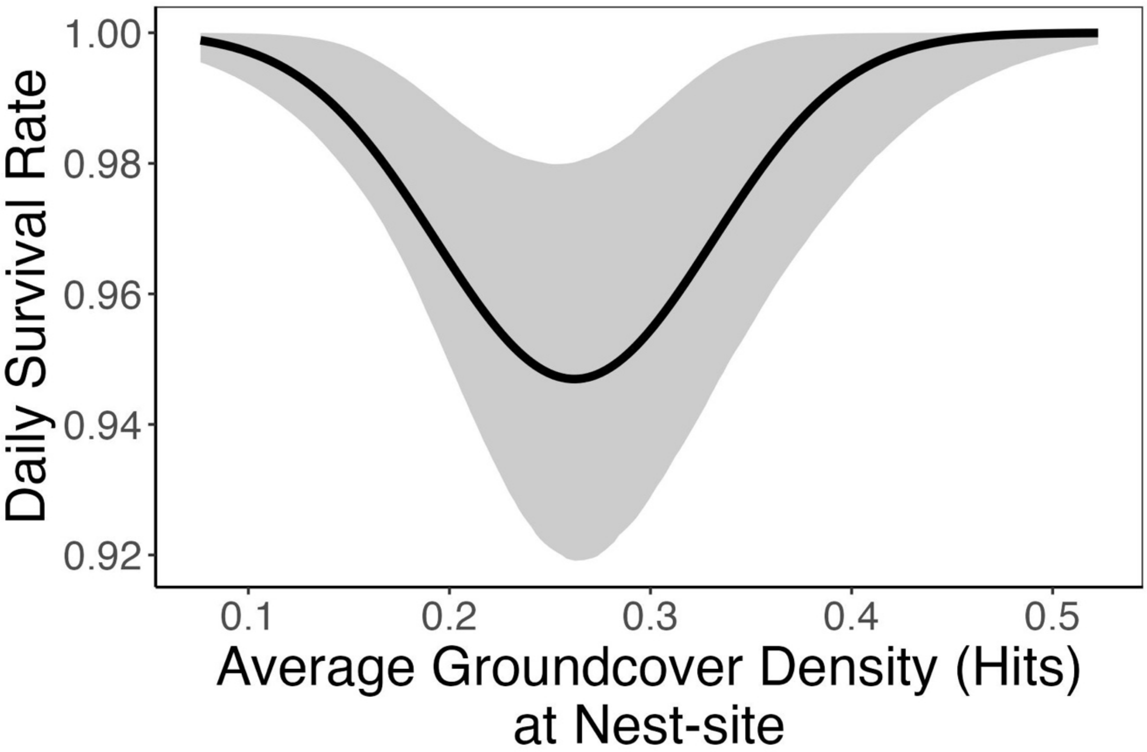

Figure 3. The predicted daily nest survival rate as is relates to groundcover density within the nest-site at YWC and SCR, South Carolina, 2020-2021. Gray band represents the bootstrapped 85% confidence interval around the prediction.

APPENDIX

PRELIMINARY FINDINGS ON APPARENT SURVIVAL AND MOVEMENT OF BACHMAN'S SPARROW

INTRODUCTION

Movement and survival of Bachman's Sparrow (*Peucaea aestivalis*) is not well understood. Current knowledge is a synthesis of short-term and small-scale studies from various parts of the species' range (but see Cox and Jones 2010 for long-term research). As populations have declined since the 1960's (Sauer 2017), estimates of nest, fledgling, and adult survival as well as estimates of emigration are needed to understand the population dynamics of Bachman's Sparrow across its range. Regional data and small-scale studies can contribute to knowledge of the species' demographic parameters as a whole and increase the accuracy of range-wide population models (Pulliam et al. 1992).

A base understanding of regional Bachman's Sparrow population dynamics is needed to identify populations at greatest risk of steep declines. Additionally, monitoring vital rates can inform actions taken to increase populations, as it can target management strategies (e.g. improving nesting habitat to improve birth rates, increasing foraging habitat to improve adult survival, increasing habitat connectivity to promote immigration and gene flow). When combined with estimates of reproductive success, estimates of dispersal distances in juvenile Bachman's Sparrows will reveal whether local habitat quality is influencing recruitment (Pulliam 1988). To achieve species conservation goals, land managers and policy makers must understand whether habitat improvements to increase nest success on their property are influencing population growth locally or whether birds are dispersing off-site. If birds typically disperse off-site in their first year and new recruits immigrate from neighboring properties, a concerted effort will be needed to ensure population stability.

Movement in Bachman’s Sparrow is poorly understood and may vary by region and habitat type. Additionally, little is known about natal dispersal in Bachman’s Sparrow. A genetic analysis of Bachman’s Sparrows across their range and across significant natural barriers showed high levels of genetic diversity and low levels of genetic population structure, both representative of a panmictic population (Cerame et al. 2014). This connectivity suggests that despite habitat fragmentation, Bachman’s Sparrows are able to successfully disperse across large distances (Cerame et al. 2014). This may be an adaptation to locate suitable habitat immediately after fire or once understories have become overgrown (Travis and Dytham 1999, Cerame et al. 2014). Evidence for long dispersal capacity also include the existence of migratory populations at the northern edge of their range and a rapid range expansion in the early 1900s (Eifrig 1915, Brooks 1938). However, recent land-use change may limit dispersal success despite adaptation to patchy or ephemeral habitat (Fahrig 2007). Although Bachman’s Sparrow has adapted to fire-prone landscapes through dispersal mechanisms, landscape changes, including increased fragmentation, may reduce survival probability when navigating a complex habitat matrix (Dunning et al. 1995, Fahrig 2007, Taillie et al. 2015) as unsuitable patches may act as boundaries (Jones et al. 2017).

Movement and survival rates of a study species must inform study design and modeling decisions. For example, occupancy and abundance estimates can be biased if counted individuals immigrate into or emigrate from the study area (Rota et al. 2009). Thus, traditional occupancy models and *N*-mixture models assume population closure within the season being sampled (MacKenzie et al. 2002, Royle 2004). To guarantee population closure over a sampling period, one must consider the length of each sampling period and ensure that within this time, (1) no individuals are moving in or out of the site and (2) there are no births or deaths. In order to account for movement and avoid biased estimates when the closure assumption cannot be met, analyses that incorporate estimates of dynamic parameters (e.g. colonization, extinction, recruitment rate, apparent survival) should be used (MacKenzie et al. 2003, Dail and Madsen 2011).

In order to collect preliminary data on Bachman's Sparrow movement (i.e. dispersal distances within sites), site fidelity, and apparent survival rates within the wiregrass gap, I opportunistically banded and resighted Bachman's Sparrows at Yawkey Wildlife Center (YWC) and Santee Coastal Reserve (SCR). I originally intended to look at effects of habitat characteristics and age class on dispersal distances. I was unable to run formal analyses on collected data because of my limited sample size and opportunistic resighting procedures. However, I present my observations to report the preliminary trends I detected, contribute to the understanding of Bachman's Sparrow survival and dispersal, and defend my decision to use open *N*-mixture models (Dail and Madsen 2011, Chapter 2) due to violation of the population closure assumption. These data only provide a snapshot of the demographic parameters and extended mark-resight efforts, and other population modeling will be needed to fully understand the population dynamics of Bachman’s Sparrow.

METHODS

I opportunistically captured and banded adult Bachman’s Sparrows following Jones and Cox (2007). I only attempted to capture males when I could confirm that there was no active nest on the territory or that the male was not provisioning young fledglings so that I would not influence reproductive success. I confirmed the sex of captured individuals through behavior (i.e. singing, aggressive response to playback) and presence of an enlarged cloacal protuberance as well as the age through plumage characteristics. Although I targeted males for capture, I unintentionally captured one adult female and four juveniles which I opportunistically banded. Each individual was fitted with one USGS aluminum leg band as well as a unique combination of three colored leg bands. I similarly banded nestlings at nests located for another study objective (Chapter 3). Nestlings were banded when they were aged to be approximately five days old. Jongsomjit et al. (2007) suggest nestlings should be banded when alar feather sheaths have erupted. By day 5, alar feather sheaths should be ruptured but by day 6, nestlings are more active and may be prone to premature fledging (Haggerty 1994).

In 2021, I resighted individuals opportunistically and following all detections on point count surveys (Chapter 2). Band combinations were recorded along with the approximate location of the resighted individual. I determined the minimum and maximum distances moved between 2020 and 2021 for each banded demographic. I also calculated distances moved by banded males between 28 March and 10 July 2021 to determine if within breeding season dispersal occurred.

RESULTS

In 2020, I banded 16 adult males, one adult female, four juveniles, and 20 nestlings. In 2021, I banded an additional 17 males and 39 nestlings. I resighted 10 of 16 males, two of four juveniles, and four of 20 nestlings banded in 2020 (Table 1). Naïve apparent survival rates based on this raw resighting data were 62.5%, 50%, and 20%, for males, juveniles, and nestlings, respectively. Seven of the 16 males banded as adults and resighted in 2021 survived overwinter and remained in their 2020 territory. The maximum distance moved by a resighted banded male was approximately 2000 m (Table 1). The two resighted males banded as juveniles moved about 600 m from their initial capture location (Table 1). Resighted male nestlings moved between 1700 and 2700 m away from the natal site and the one resighted female nestling moved 700 m away from the natal site (Table 1). During the 2021 breeding season, eight of 27 males that were resighted at least twice moved a distance of over 400 m (Table 2).

DISCUSSION

In examining the raw banding and resighting data, I made four conclusions. (1) The apparent survival rate of males from one breeding season to the next appeared to be on par with other studies, (2) the apparent survival rate of hatch year birds from fledging to the next breeding season was similar to estimates of other grassland birds, (3) males displayed moderate levels of site fidelity, and (4) some males did move during the breeding season.

The naïve apparent survival rate of the 16 males I banded in 2020 was 62.5%. This is likely a lower estimate than true survival rate, as I may have failed to detect males onsite or males may have survived and dispersed off of the study sites. Despite only having one year of data and a small sample of individuals, my results suggest that yearly survival rate was similar to previous annual survival estimates for Bachman's Sparrow. On the Wade Tract in southwestern Georgia, annual survival rate for adult male Bachman's Sparrows was estimated to be ≥ 0.68, accounting for an estimated emigration rate of ≤ 0.14 and a detection probability of ≥ 0.86, using mark-resight data of 132 individuals on and off of the study area (Cox and Jones 2010). Additional estimates of annual survival were 0.58 (Cox and Jones 2007) and 0.41 (Malone et al. 2021), however emigration was not considered. Addition survival estimates were 0.94 over one month during the breeding season (Krementz and Christie 1999) and 0.89 over three months during the breeding season (Stober and Krementz 2000). Assuming constant survival probability across the year, annual survival estimates were 0.48 and 0.63, respectively.

There are currently no estimates of Bachman's Sparrow survival over the full first year of life in the literature to my knowledge. In one study in Arkansas, 60 banded nestlings were confirmed to have fledged, yet no individuals marked as nestlings were resighted during subsequent breeding seasons (Haggerty 1988). Fish et al. (2020) estimated fledgling survival rate to be 0.31 and reported that majority of mortality occurred within the first four days of leaving the nest. Across species, post-fledging survival is lowest in the first three weeks after leaving the nest (Cox et al. 2014). Estimates of grassland bird survival in the first year are limited, especially for annual residents; however, first year survival rate of migratory Savannah Sparrow and Bobolink is estimated to be 0.412 (range = 0.322 – 0.577, Perlut and Strong 2016). Of the 20 nestlings I banded in 2020, all were expected to have fledged and four were resighted. Thus, the naïve apparent survival rate in the first year was 20%. Again, this is likely a lower estimate than true survival rate. In similar species, behavioral differences in second-year (SY) birds may limit resighting. For example, SY birds may be less likely to successfully establish a territory and breed in the first year and may exist as "floaters" (Smith 1978, Arcese 1987). In their first year, Bachman's Sparrows may also be dispersing off the property. The individuals I resighted that were banded as nestlings dispersed 700 – 2700 m from the natal site. Of the five male SY birds resighted in 2021, three successfully nested, one held a consistent territory but breeding was never confirmed, and one was resighted only once.

Seven of 10 males banded in 2020 and resighted in 2021 showed fidelity to their 2020 territory. Males that did not disperse were in territories that were not burned or only partially burned before the breeding season. Of the males that dispersed and were resighted, two were in territories that completely burned and one was in a territory that did not burn. In Arkansas, 22% of males returned to a territory occupied in a previous year (Haggerty 1988). However, Cox and Jones (2007, 2010), report that Bachman's Sparrows show high site fidelity because they observed territory overlap over several years of their study. Although dispersal is common in species that inhabit ephemeral habitat (Travis and Dytham 1999, Cerame et al. 2014), resident species frequently demonstrate high site fidelity (Paradis 1998).

I observed a small number of male Bachman's Sparrows depart from their defended territories during the 2021 breeding season. Some individuals moved early in the breeding season and likely had not yet established a territory or were responding to prescribed burns in late March and early April that overlapped with the beginning of the breeding season (Seaman and Krementz 2000, Cox and Jones 2007, Jones et al. 2014). For species that occupy frequently disturbed and ephemeral habitat, breeding season dispersal is likely an adaptation to find suitable habitat after summer wildfires or, if vegetation becomes overgrown after initial site selection, to find recently burned areas to repopulate (Cox and Jones 2007, Jones et al. 2014, Cerame et al. 2014). Breeding season dispersal in Bachman's Sparrow was observed to be low in areas (clearcuts) without summer burns (Krementz and Christie 1999); however, breeding season dispersal has been documented in other grassland bird species outside of the context of breeding season burns (Williams and Boyle 2018, 2019). Although drivers of dispersal vary across species, breeding season dispersal is likely triggered by changes in resource availability, nesting failure, or perceived predation risk (Greenwood and Harvey 1982, Jackson et al. 1989, Williams and Boyle 2018, 2019). In some circumstances, breeding season dispersal may be a response to pairing failure or mate loss (Forero et al. 1999, Catlin et al. 2005, Fuirst et al. 2021). Although anecdotal, movement at YWC and SCR seemed to be linked to pairing failure, as male behavior (i.e. frequent singing, broadcasting higher in trees, longer flights) seemed to correlate with site abandonment. Additionally, Cox and Jones

(2007) report that males may move over 500 m from the breeding territory while tending fledglings.

Although the inference that can be made from this initial band-resighting effort is limited due to small sample size and only one year of resighting data, I can report that adult male survival from 2020-2021 was comparable or higher than estimates from other regions, some males showed site-fidelity, fledglings and juveniles from the previous year survived, dispersed, and bred on-site, and males moved during the breeding season. This is the first description of survival and movement within the South Carolina wiregrass gap to my knowledge. Additional information on Bachman's Sparrow survival and dispersal in the wiregrass gap would aid in the understanding of local population dynamics.

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TABLES

Table 1. Banding and resighting data with approximate distances moved for Bachman's Sparrows banded in 2020 at YWC and SCR. Individuals that moved < 160 m remained in their territory. AHY = After Hatch Year, J = Juvenile, L = Local (Nestling), M = Male, F = Female, U = Unknown

AGE	**SEX**	**NUMBER BANDED (2020)**	**NUMBER RESIGHTED (2021)**	**DISTANCE MOVED (MIN)**	**DISTANCE MOVED (MAX)**
AHY	M	16	10	< 160 m	2000 m
	F	1	0	NA	NA
J	M	2	2	600 m	600 m
	F	0	0	NA	NA
	U	2	0	NA	NA
L	M	3	3	1700	2700 m
	F	1	1	700 m	700 m
	U	16	0	NA	NA

Table 2. Movement of banded males within the 2021 breeding season point count surveys period (28 Mar – 10 Jul 2021) at YWC and SCR. Approximate distance moved is only reported if > 400 m (diameter of point count survey area) away from initial resighting or 2021 banding location. AHY = After Hatch Year, J = Juvenile, L = Local (Nestling).

BAND NUM.	COLOR COMBO	DATE BANDED	AGE BANDED	SITE	DISTANCE MOVED (m)
2811-82502	WB-GS	5/31/20	AHY	YWC	< 400
2811-82507	OY-BS	6/11/20	L	YWC	< 400
2811-82513	RW-GS	6/25/20	AHY	SCR	< 400
2811-82517	OS-YB	7/14/20	L	YWC	2540
2811-82520	WW-WS	7/16/20	AHY	YWC	440
2811-82522	KG-RS	7/17/20	J	SCR	< 400
2811-82523	RR-BS	7/19/20	AHY	YWC	840
2811-82524	OK-WS	7/20/20	AHY	SCR	< 400
2811-82525	YG-WS	7/20/20	AHY	SCR	< 400
2811-82526	WR-OS	7/20/20	AHY	SCR	< 400
2811-82527	OK-YS	7/22/20	L	SCR	UNK
2811-82531	BW-BS	7/24/20	AHY	SCR	< 400
2811-82532	OW-GS	7/27/20	J	SCR	< 400
2811-82533	RW-KS	7/29/20	AHY	YWC	450
2811-82535	WW-OS	7/30/20	AHY	SCR	< 400
2811-82542	YO-WS	3/12/21	AHY	SCR	< 400
2811-82543	BR-OS	3/12/21	AHY	SCR	610
2811-82545	KW-WS	3/17/21	AHY	SCR	< 400
2811-82546	WR-BS	3/19/21	AHY	SCR	2160
2811-82547	OG-KS	3/22/21	AHY	YWC	< 400
2811-82548	BY-WS	3/25/21	AHY	SCR	< 400
2811-82549	BB-OS	3/25/21	AHY	SCR	< 400
2811-82551	GK-GS	3/28/21	AHY	YWC	460
2811-82552	YW-YS	3/30/21	AHY	SCR	UNK
2811-82553	RO-KS	3/31/21	AHY	YWC	800
2811-82554	YO-OS	4/2/21	AHY	SCR	< 400
2811-82555	RG-WS	4/9/21	AHY	WR	< 400
2811-82556	BK-YS	4/13/21	AHY	WR	< 400
2811-82557	RY-GS	4/15/21	AHY	WR	UNK
2811-82558	WO-RS	4/26/21	AHY	SCR	< 400