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Spatiotemporal Factors Affecting the Occupancy and Phenology of a Declining Songbird (Bachman's Sparrow - Peucaea aestivalis) at the Western Extent of its Range

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SPATIOTEMPORAL FACTORS AFFECTING THE OCCUPANCY AND PHENOLOGY OF A DECLINING SONGBIRD (BACHMAN'S SPARROW – *PEUCAEA AESTIVALIS*) AT THE WESTERN EXTENT OF ITS RANGE

By

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ABSTRACT

The Bachman’s Sparrow (*Peucaea aestivalis*) is a declining songbird that occurs throughout the southeastern United States. Bachman’s Sparrow is a Species of Greatest Conservation Need in Texas, but information crucial to management efforts, such as factors affecting their detectability and occupancy, is lacking. I investigated the predictors of Bachman’s Sparrow occupancy and phenology in Texas using detections from autonomous recording units coupled with site characteristics and weather data. My results indicate that Bachman’s Sparrow occupancy is associated with increasing herbaceous ground cover and decreasing basal area, distance to the nearest source population, and basal area when canopy height is high. Singing phenology is affected by photoperiod and precipitation, with singing occurring between January and October. These results highlight the optimal spatial and temporal conditions for this species to guide future management and monitoring efforts.

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INTRODUCTION

Habitat is among the most crucial requirements for the success of a species in its environment as it provides the resources needed for survival and reproduction (Odum 1971, Jourdan et al. 2021). Each species is adapted uniquely to the biotic and abiotic components of its habitat and this uniqueness improves fitness (MacArthur 1958, Block and Brennan 1993, Matich et al. 2017, Wei et al. 2021). While some species are habitat generalists and can tolerate a wide range of habitat conditions, other species are habitat specialists and are highly reliant on certain characteristics of their habitat for survival (Pandit et al. 2009). Habitat generalists can persist following habitat alteration (e.g., those associated with land use change) due to their wide niche breadth enabling them to adapt to new conditions or move to different habitats (Feinsinger et al. 1981). Habitat specialists, however, are more sensitive to deviation from optimal conditions as specialization limits their ability to move into other habitat types (Hansson 1991, Beger 2021). Because they are adapted to a narrow range of conditions, specialist species in suboptimal habitat experience lower fitness, resulting in decreased population sizes and in some cases, extirpation (McKinney 1997, Beger 2021). Consequently, habitat fragmentation, degradation, or loss has a severe negative impact on populations of specialist species (Winiarski et al. 2017, Betts et al. 2021). A species' tolerance to diverse environmental conditions may limit its distribution (Sexton et al. 2009). Distributions are often defined by a gradient of environmental conditions (biotic and abiotic) that a species can tolerate, with the least tolerable conditions at range edges (Sexton et al. 2009). Populations at range edges are therefore subject to less optimal conditions than interior populations and are further faced with increased variability in gene flow and abundance (and consequently fitness) due to fewer and less varied source populations (Sexton et al. 2009). Because of this, local extinctions are more likely at range edges than in interior populations (Doherty et al. 2003). Specialist species are particularly vulnerable at the fringe of their distribution as their narrow niche breadth exacerbates the effects of occupying regions with suboptimal habitat (Doherty et al. 2003, Swihart et al. 2006).

Habitat fragmentation and isolation of populations further exacerbate these issues by inhibiting movement among populations (Devictor et al. 2008). Where range boundaries exist in severely fragmented regions, the risk for extirpation and range reduction is enhanced (Hornseth et al. 2014). It is crucial to understand the factors that influence site occupancy on range edges to mitigate population losses through habitat management. This is especially critical for species of concern that are already experiencing population declines due to habitat fragmentation and loss, including some species of birds in the southeastern USA, such as Red-cockaded Woodpecker (*Dryobates borealis*) and Bachman's Sparrow (*Peucaea aestivalis*).

Bachman's Sparrow is a declining specialist in woodland savannas and early successional fields with sufficient grass cover in the southeastern United States (Dunning and Watts 1990, Allen and Burt 2014). Sites supporting Bachman's Sparrow have been described as park-like, with reduced density of overstory trees and a minimal or absent woody midstory component (Plentovich et al. 1998, Brooks and Stouffer 2010, Allen and Burt 2014, Hannon et al. 2021). Most importantly, a copious amount of bunchgrass present in the understory is necessary for the persistence of this species, as it uses grass for foraging, cover, and nesting (Jones et al. 2014, Taillie et al. 2015, Fish et al. 2018). These habitat characteristics are maintained by fire, as it mitigates woody overgrowth in the understory, promoting the success of fire-adapted grasses and forbs (Tucker et al. 2004, Conner et al. 2005, Fish et al. 2018, Hannon et al. 2021). Individuals are known to abandon sites burned less frequently than 3 years and a burning regime of 2-3 years is necessary for continued occupancy by the species (Tucker et al. 2004).

Pine and oak savanna are the primary habitat types associated with Bachman's Sparrow due to low tree density and frequent fires allowing for an increased amount of grass (Dunning and Watts 1990, Farley et al. 2008). These habitat types reach their western edge in the West Gulf Coastal Plain ecoregion along with their associated species, including Bachman's Sparrow. Although pine savanna (primarily longleaf pine [*Pinus palustris*] savanna) once dominated upland landscapes across the southeast, it persists in a severely fragmented 3% coverage across its original range (Van Lear et al. 2005). Similarly, post oak (*Quercus stellata*) savanna experienced a 99% decrease since

European colonization (Nuzzo 1986). With these losses in suitable habitat, Bachman's Sparrow populations have plummeted by 76% in the last century (Rosenberg et al. 2016). As pine and oak savannas have been severely fragmented, populations of Bachman's Sparrow are now isolated, exacerbating their population declines (Winiarski et al. 2017).

The majority of information on Bachman's Sparrow comes from populations on the eastern portion of their range (i.e., east of the Mississippi River) (Dunning and Watts 1990, Brooks and Stouffer 2010, Taillie et al. 2015, Fish et al. 2018, Fish et al. 2020) and information on habitat preferences on the western range edge (Texas, Oklahoma, and Arkansas) come from small-scale surveys (Conner et al. 2002, Conner et al. 2005, Farley 2008, Allen and Burt 2014). Given the decline of the species across its range and the increased vulnerability of specialists on the periphery of their distribution, it is crucial to understand the habitat requirements of Bachman's Sparrow across the entirety of the Gulf Coastal Plain. To determine the habitat covariates associated with Bachman's Sparrow occupancy on its western range edge in Texas, I used an occupancy modeling approach with ecologically relevant observation-level and site-level covariates that not only elucidated local-scale predictors of detection and occupancy, but also investigated the importance of habitat connectivity using a regional-scale covariate. I hypothesized that occupancy would be associated with sites with an open understory (i.e., reduced basal area and shrub foliage density and little to no midstory) and abundant grass and forb ground cover. I also hypothesized that because of habitat fragmentation, isolation of populations would result in a decrease in occupancy probability at sites far from established populations (Dunning et al. 1995). This study builds on the current knowledge of Bachman's Sparrow ecology by offering results of site occupancy on the western fringe of its range. These results may better inform management efforts for Bachman's Sparrow in the West Gulf Coastal Plain. Furthermore, because Bachman's Sparrow is regarded as an indicator for pine savanna quality (Hannah et al. 2017, McIntyre et al. 2019), these results could have a broader application as a metric for habitat quality in this region or across the range of Bachman's Sparrow.

METHODS

Study Area

In the West Gulf Coastal Plain, Bachman’s Sparrow is restricted to the Pineywoods and Post Oak Savanna ecoregions (Griffith et al. 2007), limiting the range of Bachman’s Sparrow to east of the Brazos River (Lockwood and Freeman 2004). The geography in this region is characterized by xeric, sandy uplands historically dominated by longleaf pine, shortleaf pine (*P. echinata*), and post oak (*Quercus stellata*) and bottomlands dominated by an oak-gum-cypress cover type (Griffith et al. 2007). Replacement of longleaf and shortleaf pine by short-rotation plantations of the more commercially viable loblolly pine (*P. taeda*) has severely fragmented the pine savanna ecosystems in this region and across its range (Van Lear et al. 2005). These savanna ecosystems are fire-maintained and fire regimes less frequent than 3 years can cause the understory of dense herbaceous ground cover to become shaded beneath less fire-resistant successional species, such as American sweetgum (*Liquidambar styraciflua*) and yaupon holly (*Ilex vomitoria*) (Tucker et al. 2004). The sites I surveyed contained areas of pine and hardwood habitats at varying levels of succession. Habitat types included upland pine and post oak savanna, upland loblolly-shortleaf pine stands, upland oak-hickory forests, restored prairie with Osage-orange (*Maclura pomifera*) and eastern red cedar (*Juniperus virginiana*) mottes, and oak-gum-cypress bottomlands.

Survey Sites

I surveyed 10 study sites (accessible properties containing multiple survey locations) within the Pineywoods and Post Oak Savanna ecoregions of Texas representing a variety of wooded habitats with varying ground cover types. I placed plots (specific survey locations within study sites) in areas of low, medium, and high likelihood of Bachman's Sparrow occurrence based on a species distribution model (SDM) developed by Andersen and Beauvais (2013). This SDM used training data (confirmed records of Bachman's Sparrow) paired with data on climate, topography, land use/landcover, soils and substrate, and surface water to develop a spatial model that predicts the distribution of Bachman's Sparrow in Texas by low, medium, and high relative likelihood of occurrence (Andersen and Beauvais 2013). In 2020 and 2021 between April and August, I surveyed 40 plots in each habitat quality category (low, medium, and high) per year for a total of 120 plots per survey season (n = 240 plots total).

I selected study sites in 3 United States Forest Service National Forests (NFs) and 1 National Grassland (NG), 2 Texas Parks and Wildlife Department Wildlife Management Areas (WMAs), and 2 privately-owned properties (see Appendix 1). I sampled a total of 12 counties across eastern Texas: Anderson, Angelina, Fannin, Freestone, Houston, Jasper, Nacogdoches, Newton, Sabine, San Augustine, Shelby, and Trinity. The northmost and southmost latitude I surveyed were 33.44° N and 31.02° N, respectively, while the westmost and eastmost longitudes I surveyed were 96.04° W and 93.70° W, respectively (Figure 1.1).

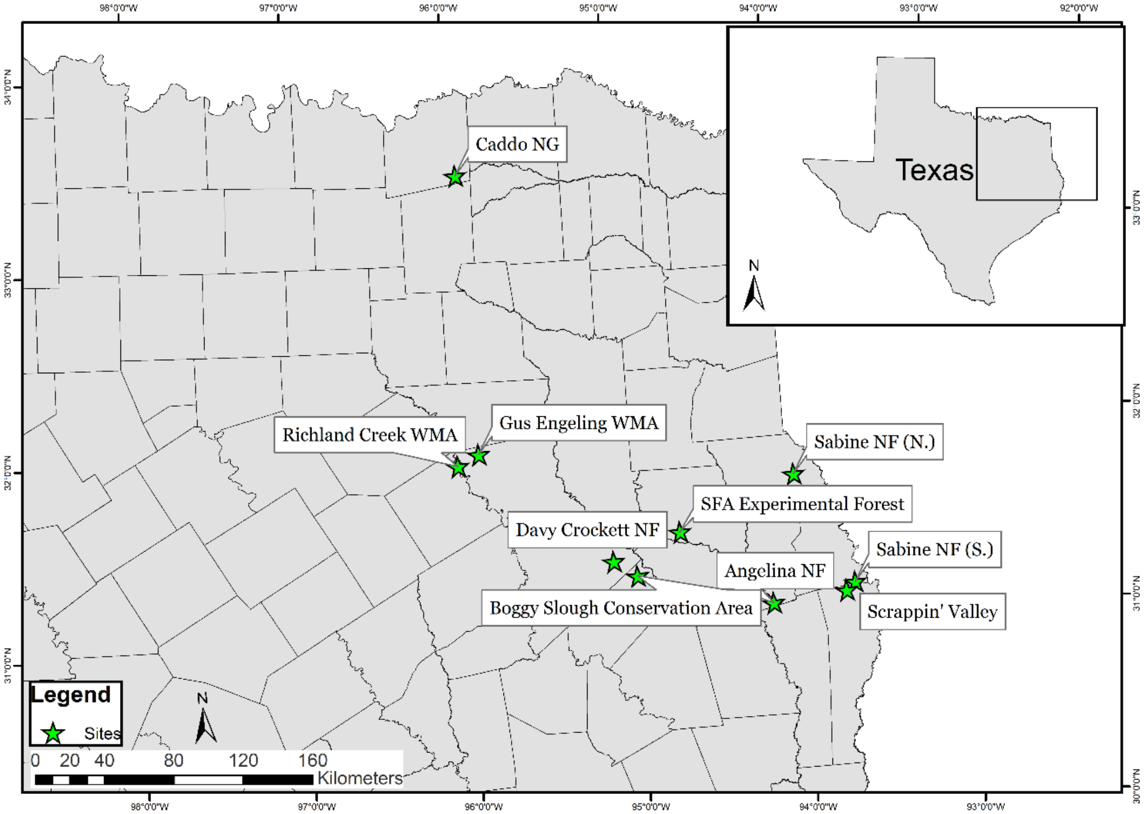

Figure 1.1. Sites selected for occupancy surveys of Bachman's Sparrow in eastern Texas in 2020 and 2021. Sites were selected based on their occurrence in low, medium, and high relative likelihood of Bachman's Sparrow occurrence based on Andersen and Beauvais' (2013) species distribution model. Abbreviations are NF and NG for National Forest and National Grassland, respectively, and WMA for Wildlife Management Area.

I selected study sites in ArcMap (Version 10.6.1, Environmental Systems Research Institute, Redlands, CA) by overlaying the Andersen and Beauvais (2013) model raster over accessible properties to determine which possible study sites fell within each category of Bachman's Sparrow occurrence. To ensure plots were selected in homogeneous landscapes, I filtered the model raster to minimize patchiness of each category. I overlaid a 400 m by 400 m grid of points (i.e., plots) over each study site using the Create Fishnet tool and manually removed inaccessible points (in bodies of water, on roads, beyond impassable creeks or rivers). I included a buffer zone of 200 m for each plot to ensure independence of plots. At most study sites, I randomly selected plots using a command in the ArcPy tool that removed a random set of points. At study sites with a limited amount of space to fit plots (Caddo NG, Gus Engeling WMA, and both north and south Sabine NF sites), I selected all possible plots instead of randomly removing plots. If space allowed, I randomly selected a maximum of ten plots per site as back-up plots in case the originally selected plots were inaccessible in the field. At Sabine NF (S.), I determined 3 plots to be inaccessible in the field due to steep ravines, so I subsequently randomly selected 3 plots from another study site, Angelina NF, to replace them.

Data Collection

I used autonomous recording units (ARU; Wildlife Acoustics SM4s and SM Minis) to gather Bachman's Sparrow detection data. I deployed up to 30 ARUs at their respective plots simultaneously, programming a schedule to record daily for 5 consecutive days, recording 5 minutes every half-hour from sunrise until 3 hours after sunrise. This time window is the period of the day that songbirds are most likely to exhibit singing behavior and therefore most likely to be detected (Leopold and Eynon 1961). I deployed ARUs (*n* = 120) between May 18 and July 12 in 2020, and April 17 and June 16 in 2021, during the peak season for Bachman's Sparrow singing phenology (see Chapter 2). I attached ARUs at the base of a tree or at breast height, depending on susceptibility of the plot to fire or flooding. To account for any changes in detection within a season, plots were resampled with ARUs between July 19 and August 17 in 2020, and June 22 and July 22 in 2021. Some ARUs (*n* = 3) failed to record due to memory card errors during the resampling period of 2021.

Following retrieval of ARUs, I downloaded recorders and scanned recordings using Wildlife Acoustics Kaleidoscope software. Although Wildlife Acoustics offers a version of Kaleidoscope with cluster analysis that can be used to isolate bird song by type, I opted to scan all recordings by visual scanning of the spectrogram paired with listening. Bachman's Sparrow has a diverse repertoire with at least 6 different song types with multiple sub-types (Borror 1971, Wolff, unpublished data), making cluster analysis a potentially time-consuming process. Additionally, I opted to scan recordings to reduce the chances of false negative detections from the automated cluster analysis.

At each plot, I measured ecologically relevant habitat covariates to be used as predictors of occupancy based on results from prior studies (Table 1.1) (Brooks and Stouffer 2010, Allen and Burt 2014, Taillie et al. 2015, Fish et al. 2018). I centered plots at the ARU attachment tree and measured subplots at 25 m and 50 m in each cardinal direction away from the tree (Table 1.1). Basal area was measured with a 10-factor wedge prism at plot center and at 50 m subplots, canopy cover was measured with a spherical densiometer at 25 m and 50 m subplots, midstory density was categorized from 1-5 sensu Conner et al. (1999) from plot center, percent ground cover of grass, forbs, leaf litter, and bare ground were estimated using Daubenmire classes in a 1 m^2 quadrat (Daubenmire 1968) at 25 m and 50 m subplots, and foliage density was measured with a density board at plot center and 50 m subplots. I also collected observation-level data to use as predictors of detection based on previous studies (Taillie et al. 2015, Fish et al. 2018). I recorded hourly weather data (rain, wind, and temperature) from the nearest United States Forest Service Remote Automated Weather Station and averaged values from the 3-hour recording window of the ARU for each survey date. The average distance to a weather station was 23 km (range 1.9 km–43 km). I also recorded Julian date for each date the ARUs surveyed.

Table 1.1. Habitat covariates measured at each plot as potential predictors of Bachman's Sparrow detection and occupancy. Observation-based covariates were measured to be included in detection models while state-based covariates were measured to be included in both detection and occupancy models.

Covariate	Description	Subplot Measured
Observation-based		
Julian Date	Number of days since the beginning of the Julian Year	-
Temperature (°C)	Temperature values averaged across the 3-hr recording period	-
Wind (m/s)	Wind values averaged across the 3-hr recording period	-
Precipitation (mm)	Rain values averaged across the 3-hr recording period	-
State-based		
Local Scale		
Basal Area (m^2/ha)	Square meters per hectare occupied by tree stems	Plot center
Canopy Cover (%)	Percentage of canopy foliage covering the plot	Plot center
Midstory Density (1-5)	Density of sub-canopy trees over 3 m tall at plot	Plot center
Grass Ground Cover (%)	Percentage of ground covered by grass in a 1 m^2 quadrat	25m, 50m
Herbaceous Ground Cover (%)	Percentage of ground covered by herbaceous plants in a 1 m^2 quadrat	25m, 50m
Leaf Litter Ground Cover (%)	Percentage of ground covered by leaf litter in a 1 m^2 quadrat	25m, 50m
Bare Ground Cover (%)	Percentage of bare ground in a 1 m^2 quadrat	25m, 50m
Foliage Density (m^2/m^3)	Area of density board covered by shrub foliage	Plot center, 50m
Regional Scale		
Distance to Nearest Source Population (km)	Distance of the plot to the nearest known population location	-

Data Cleaning

Prior to analysis, I averaged habitat measurements from plot center, 25 m, and 50 m subplots after proofing all data from each site. I converted ground cover percentage classes from ordinal data to continuous by replacing categories with their median percentage value and averaging across subplots. I converted foliage density measurements from raw values (distance in meters from observer to density board) to m^2/m^3 of foliage density using the formula derived from MacArthur and MacArthur (1961) and adjusted by Conner and O'Halloran (1986). I used variance inflation factor (VIF) to evaluate collinearity among all variables in global model and found that only ground cover covariates were collinear (VIF >5). Because grass and forb ground cover have been previously implicated as important predictors of Bachman's Sparrow occupancy, I combined the two covariates into one covariate, herbaceous ground cover, by summing their values prior to averaging. By only including one ground cover covariate or the combined herbaceous cover covariate in any one model, I was able to investigate whether these covariates affected occupancy without violating the assumption of the independence of independent variables. I used a Mann-Whitney U test to determine if sites with Bachman's Sparrow detections and sites without detections were significantly different in their habitat characteristics.

Occupancy Modeling

I used an occupancy modeling approach to determine which habitat covariates were the most important predictors of Bachman's Sparrow site occupancy. To meet the assumptions of single-season occupancy modeling (MacKenzie 2006), I repeated surveys by recording 5 consecutive days to keep my detection data within a closed season (i.e., there were no colonization or extinction events), which ensures that probability of occupancy (ψ) does not change between surveys and that the probability of detection (p) and ψ remain equal across all plots. The plot selection process established plot independence, reducing the chance an individual is detected at more than one site.

Although I sampled plots during two 5-day sampling events in the same season, sufficient time had passed between the two sampling events that they could not be treated as a closed season (MacKenzie 2006). Because colonization and extinction dynamics modeled in multi-season occupancy modeling were not within the scope of this study, I utilized a single-season occupancy modeling approach and treated the second survey dataset as unique plots sharing habitat data with the first survey data, but with unique detection histories, resulting in 477 total unique plots.

I developed single-species, single-season hierarchical occupancy models using the *unmarked* package of R 4.0.3 (Fiske and Chandler 2011, R Core Team 2019). I assessed model fit of the saturated model using the MacKenzie and Bailey Goodness-of-fit Test for single-season occupancy models (MacKenzie and Bailey 2004). Using the saturated model for goodness-of-fit provides a baseline to assess the fit of less complex *a priori* models (Cooch and White 2002). Because the $\hat{c}$ statistic indicated slight overdispersion ($\hat{c}$ = 2.17), I ranked models using Quasi-Akaike Information Criterion (QAIC) and inflated nominal variance by multiplying the estimated standard error of each parameter by the square-root of $\hat{c}$. This method accounts for overdispersion by penalizing more complex models during model ranking and by correcting any bias in the standard error from possible collinearity of covariates (Cooch and White 2002). If any of the models were competitive with the top model (ΔQAIC less than 2 units from the top model), I selected the most parsimonious of the competitive models (Burnham and Anderson 2002).

I fit 9 detection-based *a priori* detection models with different combinations of Julian date and weather data. I included a variation of Julian date with a quadratic effect as well as an interaction term of Julian date with temperature. Occupancy modeling can incorporate state-based covariates as predictors of detection as well, so I included combinations of ecologically relevant habitat covariates in some detection models.

Using the parameters from the top-ranked detection model, I then fit 20 *a priori* state-based occupancy models with ecologically relevant habitat covariates. Previous studies on Bachman's Sparrow habitat preferences have implicated basal area, canopy height, foliage density, herbaceous ground cover, and woody midstory components as predictors of Bachman's Sparrow occupancy (Plentovich et al. 1998, Conner et al. 2005, Brooks and Stouffer 2010, Allen and Burt 2014, Taillie et al. 2015, Fish et al. 2018, Fish et al. 2020, Hannon et al. 2021), so *a priori* models had varying combinations of these covariates. I expected herbaceous ground cover and basal area to have a quadratic relationship with site occupancy (Taillie et al. 2015) or to only be a strong predictor of Bachman's Sparrow occupancy when canopy height was high, suggestive of savanna-type habitats over prairie-type habitats. Because of this, I included variants of herbaceous ground cover and basal area with a quadratic effect and with interactions with canopy height. I also included a regional-scale covariate, distance of each plot to the nearest source population, in case dispersal barriers limit individuals from occupying suitable habitat far from source populations. Using the training points from the Andersen and Beauvais (2013) model as source populations, I calculated the distance in kilometers from each plot to the closest model training point in ArcMap. Some sites, such as Davy Crockett NF, have areas with dense herbaceous cover and moderately low basal area, but are far enough from source populations that dispersing Bachman's Sparrow have a decreased chance of discovering them, or have not had sufficient time since the site was restored to do so. Furthermore, some individuals may occupy habitat that is suboptimal but close to conspecifics within their source population. A distance to source population covariate may therefore explain variance in the data caused by either occupancy of poor habitat near source populations or lack of occupancy in adequate habitat far from source populations.

Model inference was performed using the *linearComb* function of the *unmarked* package of R, setting all coefficients at their mean (Fiske and Chandler 2011). Because of the wide range of values for the distance to source population covariate, the median was used for model inference instead of the mean. I used the R package *ggplot2* to construct plots of the marginal effect of each covariate to visualize relationships between the covariate and ψ.

In addition to performing this modeling procedure with all plots, I also repeated it with only the plots located within the high likelihood of Bachman's Sparrow occurrence as suggested by the Andersen and Beauvais (2013) model. Because of the localness of most of the habitat covariates measured, I proposed that they may be stronger predictors of Bachman's Sparrow occupancy at a more local scale. All plots with Bachman's Sparrow detections were within the high likelihood category of the Andersen and Beauvais (2013) model and all plots in this category were relatively close together (<60 km), limiting variation in the data caused by distance and multiple disparate habitat types. Because I developed the 20 *a priori* occupancy models before analyses, I used the same set of candidate models in both modeling efforts.

RESULTS

Bachman’s Sparrow Surveys

During 2020 and 2021, I detected Bachman’s Sparrow at a total of 40 unique plots (Figure 1.2). Across both 2020 surveys, I detected Bachman’s Sparrow at 12 unique plots. During the first 2020 survey, Bachman’s Sparrow was detected at all 12 plots, but only 8 of those plots retained Bachman’s Sparrow detections during the second 2020 survey. Across both 2021 surveys, I detected Bachman’s Sparrow at 28 unique plots. During the first survey, I detected Bachman’s Sparrow at 23 plots, 22 of which retained detections in the second 2021 survey. However, Bachman’s Sparrow was detected at 5 additional plots in the second 2021 survey for a total of 27 plots with Bachman’s Sparrow.

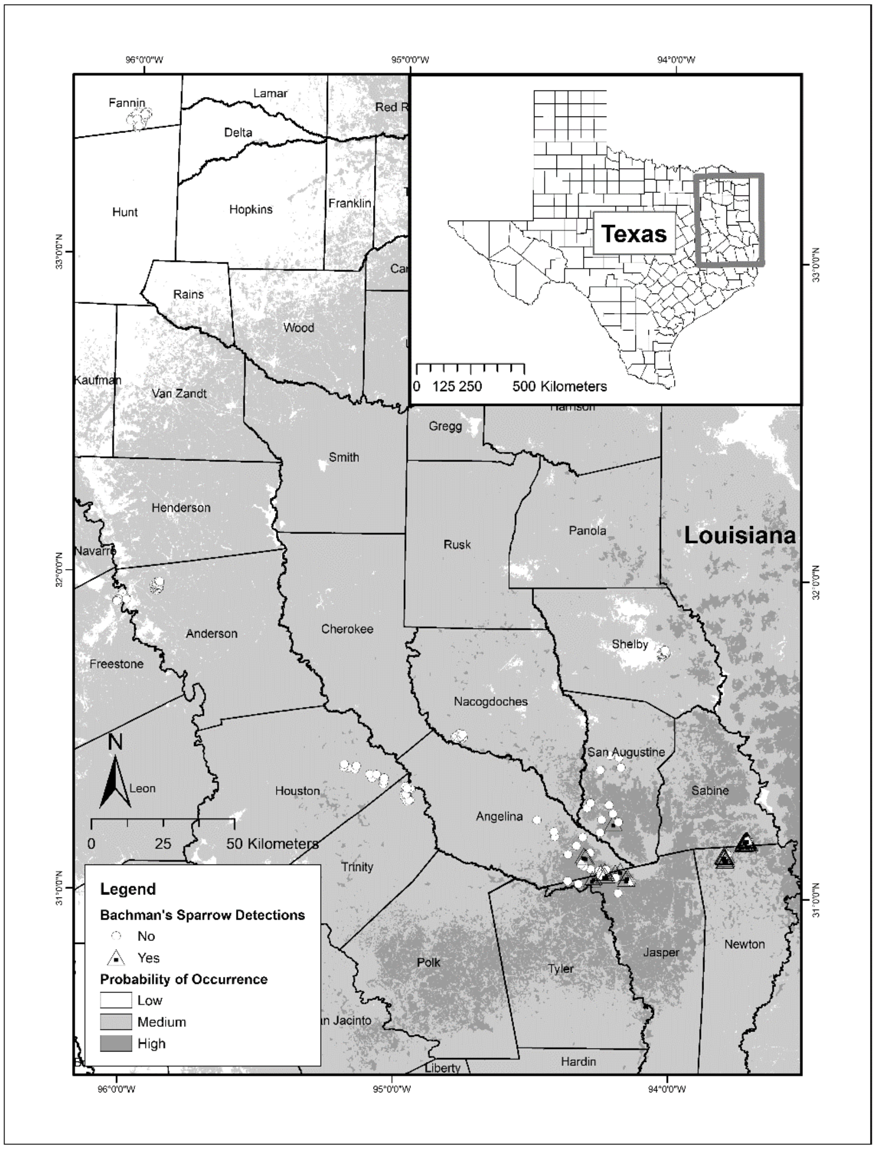

Figure 1.2. Plots surveyed in 2020 and 2021. Sites with Bachman's Sparrow detections are represented by triangles while sites without detections are represented by white circles. Areas of low, medium, and high probability of Bachman's Sparrow occurrence from the Andersen and Beauvais (2013) species distribution model are represented by white, light gray, and dark gray, respectively.

Plots with Bachman’s Sparrow detections were located in Angelina, Jasper, Newton, Sabine, and San Augustine counties (Appendix 1). All plots with detections from both years were located in the high likelihood of Bachman’s Sparrow occurrence category of the Andersen and Beauvais (2013) species distribution model (Appendix 1). Furthermore, all these plots except one were located within the 93,000 ha Longleaf Ridge Conservation Area (LRCA), which has been identified by the United States Forest Service as an area of “excellent habitat” for Bachman’s Sparrow (United States Forest Service 2011). The single plot outside of this area was located nearby in San Augustine County <10 km from LRCA (Appendix 1). Bachman’s Sparrow was detected at plots with lower median values of midstory density ($U = 5870$, $p < 0.01$) and distance to source population ($U = 6783$, $p = <0.01$) and higher median values of canopy height ($U = 3038$, $p = 0.02$), herbaceous ground cover ($U = 2637$, $p < 0.01$), and foliage density ($U = 2931$, $p < 0.01$) (Table 1.2).

Table 1.2. The median (min – max) values of habitat variables measured at unoccupied and occupied plots in 2020 and 2021. Plots were considered occupied if they had at least one Bachman’s Sparrow detection. All occupied plots were within a region of high likelihood of Bachman’s Sparrow occurrence as defined by a species distribution model by Andersen and Beauvais (2013). Asterisks indicate a statistically significant difference between the median values for that covariate at $p <0.05$ (*) and $p < 0.01$ (**) as determined by a Mann-Whitney U test.

Habitat Variable	Unoccupied Plots Median (min – max)	Occupied Plots Median (min – max)
All Plots	**(*n* = 200)**	**(*n* = 40)**
Basal Area (m^2/ha)	63.27 (1.51 – 165.70)	67.79 (24.10 – 158.17)
Canopy Height (m) *	24.40 (2.74 – 42.98)	27.58 (11.89 – 34.44)
Midstory Density Category **	3.00 (1.00 – 5.00)	2.00 (1.00 – 4.00)
Canopy Cover (%)	27.03 (0.00 – 94.40)	23.35 (13.31 – 88.15)
Ground Cover – Grass (%)	22.06 (3.00 – 90.00)	29.50 (3.00 – 75.31)
Ground Cover – Forbs (%) **	19.75 (3.00 – 69.00)	32.34 (10.31 – 64.68)
Ground Cover – Herbaceous (%) **	54.00 (7.50 – 100.18)	66.93 (28.19 – 100.06)
Ground Cover – Bare Ground (%) **	8.81 (3.00 – 79.37)	3.00 (3.00 – 32.18)
Ground Cover – Leaf Litter (%)	33.52 (3.00 – 95.50)	31.50 (6.00 – 72.00)
Foliage Density (m^2/m^3) **	0.01 (0.00 – 0.08)	0.02 (0.00 – 0.06)
Distance to Nearest Source Population (km) **	56.83 (0.03 – 164.40)	0.86 (0.03 – 19.33)
High Likelihood of Occurrence Plots	**(*n* = 40)**	**(*n* = 40)**
Basal Area (m^2/ha) **	90.38 (22.60 – 165.70)	67.79 (24.10 – 158.17)
Canopy Height (m)	28.96 (11.89 – 36.88)	27.58 (11.89 – 34.44)
Midstory Density Category **	3 (1.00 – 5.00)	2.00 (1.00 – 4.00)
Canopy Cover (%) **	32.70 (8.98 – 92.28)	23.35 (13.31 – 88.15)
Ground Cover – Grass (%) **	16.43 (3.00 – 60.25)	29.50 (3.00 – 75.31)
Ground Cover – Forbs (%) **	23.56 (3.00 – 69.00)	32.34 (10.31 – 64.68)
Ground Cover – Herbaceous (%) **	44.25 (7.5 – 81.00)	66.93 (28.19 – 100.06)
Ground Cover – Bare Ground (%) **	4.5 (3.00 – 57.25)	3.00 (3.00 – 32.18)
Ground Cover – Leaf Litter (%) **	51.19 (14.94 – 95.50)	31.50 (6.00 – 72.00)
Foliage Density (m^2/m^3)	0.01 (0.00 – 0.08)	0.02 (0.00 – 0.06)
Distance to Nearest Source Population (km) **	4.23 (0.21 – 37.80)	0.86 (0.03 – 19.33)

Detection Modeling

State-based covariates were stronger predictors of Bachman's Sparrow detection than observation covariates alone. The top-ranked detection model (QAIC = 351.16; p = 0.962) included 2 state-based covariates, midstory density and herbaceous ground cover (Table 1.3). Probability of detection (p) increased with increasing herbaceous ground cover and decreased with increasing midstory density. The second-ranked model (QAIC = 353.72; p = 0.989) included midstory density and an interaction term of Julian date and temperature but was not considered competitive with the top model (ΔQAIC >2; Table 1.3). Additional detection models had a ΔQAIC >10 from the top-ranked model (Table 1.3).

Occupancy Modeling

From the dataset containing all categories of occurrence likelihood, 3 models were competitive and included various combinations of herbaceous ground cover, midstory density, foliage density, distance to nearest source population, and an interaction term of basal area with canopy height (Table 1.3). The most parsimonious model from this dataset, which was also the top-ranked model (QAIC = 263.04, ψ = 0.39), contained herbaceous ground cover, midstory density, distance to nearest source population, and an interaction of basal area and canopy height. For this dataset, values of ψ increased with increasing herbaceous ground cover and decreased with increasing midstory density and distance to source population as inferred from marginal effect of the covariate plots produced from the selected model (Appendix 2). The values of ψ were highest when basal area was low and canopy height was relatively high (Appendix 2).

Table 1.3. Top-ranked detection and occupancy models sorted by Quasi-Akaike's Information Criterion (QAIC). *K* represents number of parameters, ΔQAIC is change in QAIC value from the top model, ω is model weight, and –QLogLike represents –Quasi-log likelihood. Plots within the high likelihood of Bachman's Sparrow occurrence were based on the results from Andersen and Beauvais (2013).

Model	*K*	QAIC	ΔQAIC	ω	–QLogLike
Detection (*p*)					
MD[a] + Herb[b]	5	351.16	0.00	0.67	170.58
MD + JD*Temp[c]	7	353.72	2.55	0.19	169.86
Occupancy (ψ)					
All plots					
Herb + MD + DNSP[d] + BA*CH[e]	11	263.04	0.00	0.36	120.52
Herb + MD + DNSP + FD[f] + BA*CH	12	264.10	1.06	0.21	120.05
Herb^2 + MD + DNSP + FD + BA*CH	12	265.03	1.99	0.13	120.52
Herb + MD + DNSP^2 + BA*CH	12	265.17	2.13	0.12	120.58
Herb*CH + MD + DNSP + FD + BA*CH	13	265.80	2.76	0.09	119.90
Plots in high likelihood of Bachman's Sparrow occurrence					
Herb + MD + DNSP + BA*CH	11	254.05	0.00	0.35	116.02
Herb + MD + DNSP + FD + BA*CH	12	255.87	1.82	0.14	115.93
Herb^2 + MD + DNSP + BA*CH	12	256.02	1.97	0.13	116.01
Herb + MD + DNSP + BA*CH^2	13	256.95	2.90	0.08	115.48
Herb^2 + MD + DNSP + FD + BA*CH	13	257.85	3.80	0.05	115.92

[a] Midstory Density
[b] Herbaceous Ground Cover
[c] Julian Date × Temperature
[d] Distance to the Nearest Source Population
[e] Basal Area × Canopy Height
[f] Foliage Density

Results for the analysis containing the high likelihood of Bachman's Sparrow occurrence were similar to those with all plots surveyed, with the top 2 competitive models remaining the same (Table 1.3). The most parsimonious model (QAIC = 254.05) was selected for inference and had a ψ estimate of 0.90. Occupancy probability increased with increasing herbaceous ground cover and decreased with increasing midstory density and increasing distance to nearest source population based on marginal effect of the covariate plots (Figure 1.3) produced from the selected model. The values of ψ were highest when basal area was low and canopy height was moderately high (Figure1.3).

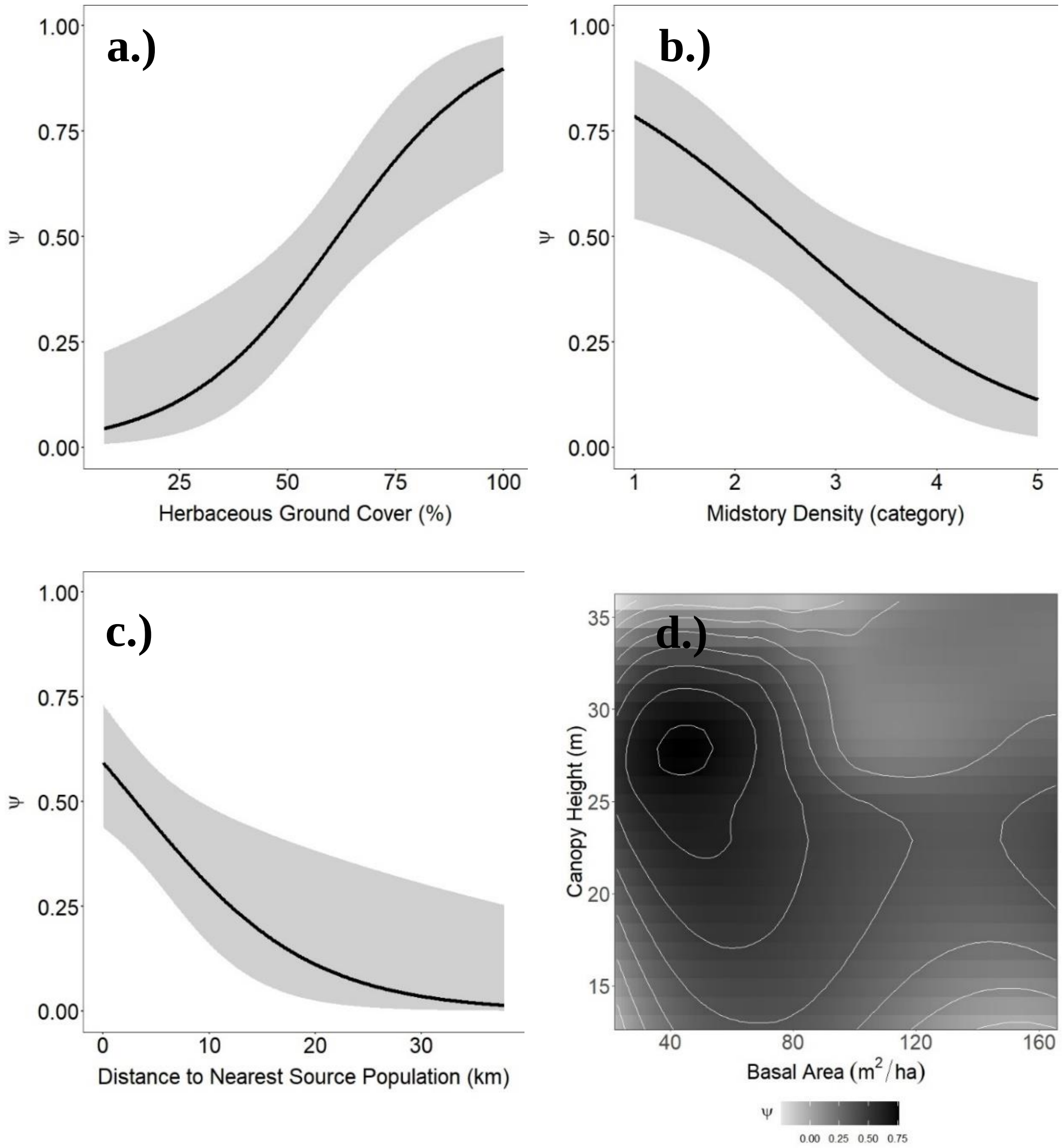

Figure 1.3. Occupancy probability (*Ψ*) and 95% confidence intervals (gray ribbon) for **a**. herbaceous ground cover, **b.** midstory density, and **c.** distance to the nearest source population from the top occupancy model for plots located within areas of high likelihood of Bachman's Sparrow occurrence. The interaction of basal area and canopy height is represented by a contour plot (**d.**) with the darker areas having increased probability of occupancy.

DISCUSSION

At the western fringe of its distribution, Bachman's Sparrow was found to occur in forested habitat types that have an open understory with dense grass and forb cover, characteristics restricted to pine savanna and post oak savanna habitat in this region (Griffith et al. 2007). These results support my hypothesis that Bachman's Sparrow occupancy would best be predicted by covariates associated with woodland savannas. The relationship of occupancy probability with herbaceous ground cover, midstory density, basal area, and canopy height is consistent with occupancy studies on eastern populations (Taillie et al. 2015, Fish et al. 2018, Hannon et al. 2021), suggesting that local-scale habitat requirements remain consistent across the range of Bachman's Sparrow. Furthermore, the relationship of occupancy with plot distance to nearest source population corroborate prior studies (Taillie et al. 2015, Winiarski et al. 2017) that large-scale factors such as habitat contiguity are important predictors of Bachman's Sparrow site occupancy on the fringe of their range.

Detection of Bachman's Sparrow may be enhanced by surveying with ARUs in place of point-counts and by surveying in optimal habitat. Prior studies suggest that use of ARUs increases the chance of detecting highly vocal species, as ARUs can survey a wider time window and more sites using significantly less effort (Zwart et al. 2014, Furnas and Callas 2015, Bobay et al. 2018). My use of ARUs likely enhanced my detection results since I was able to survey many plots simultaneously across the duration of peak singing hours. In my study, detection was better predicted by the presence of high-quality habitat than by weather and Julian date during the breeding season. At plots in poor quality habitat, individuals may have been detected singing from nearby, higher-quality habitat or may have been singing from the periphery of their territory and spent more time elsewhere in their territory out of range of detection, reducing their probability of being detected from repeated surveys. Although date appears frequently as an important predictor of Bachman's Sparrow detection in prior occupancy studies (Taillie et al. 2015, Fish et al. 2018), site-based covariates (basal area and shrub density) have also appeared in top prediction models (Taillie et al. 2015), corroborating my results. Furthermore, I surveyed almost entirely during the peak singing season for Bachman's Sparrow, May to August (Wolff, unpub. data), so singing detections may have been more consistent over time than in prior studies that surveyed earlier in the year (Taillie et al. 2015, Fish et al. 2018, Hannon et al. 2021).

Fragmentation may inhibit colonization or recolonization of Bachman's Sparrows at suitable but isolated sites. Occupancy probability decreased with increasing distance from a source population, suggesting that although suitable habitat may exist in a region, it may be difficult for Bachman's Sparrow to discover if it is isolated from established populations. Previous studies (Sexton et al. 2009) have highlighted that this lack of occupancy at suitable yet unoccupied sites is generally attributed to factors that limit its movement, such as a lack of habitat connectivity on the landscape. Although Bachman's Sparrow has previously been known to be an accomplished disperser, as demonstrated by its northward expansion in the early 1900s (Brooks 1938), the extent of this ability on the current landscape is unknown. Furthermore, the northward expansion of Bachman's Sparrow in the early 1900s was the result of conversion of optimal pine savanna habitat (that supported high population densities) to vast swaths of suboptimal early successional habitat (that supported low population densities) that spread from Texas to Illinois and Pennsylvania (Brooks 1938, Dunning and Watts 1991, Lee 1999).

Although some of the longleaf pine savanna habitat in the southeast has been restored, optimal habitat in the West Gulf Coastal Plain remains severely fragmented by not only the conversion of historic pine savanna to timber stands that prioritize product yield, but also by an increase of fire exclusion efforts that enables the persistence of woody plants in the understory (Brockway et al. 2005). This region is now dominated by private land that typically contains heavily grazed pasture or short-rotation timber plantations, neither of which support Bachman's Sparrow (Conner and Rudolph 1994). Short-rotation timber stands have been noted to have a negative association with Bachman's Sparrow, as they may not allow sufficient growth of bunchgrasses (Messick et al. 2021). The result is a patchy landscape that limits suitable habitat to isolated "islands" of pine savanna habitat among pine plantations or post oak savanna among pastures. Dunning et al. (1995) determined that this type of habitat fragmentation inhibits colonization of Bachman's Sparrow at sites with suitable habitat that are far from established populations. They further found that habitat corridors increase the ability of Bachman's Sparrow to find and colonize restored sites. Conner and Rudolph (1994) demonstrated that fragmentation in the West Gulf Coastal Plain negatively impacts clusters of Red-cockaded Woodpecker, a species that is commonly managed alongside Bachman’s Sparrow (Plentovich et al. 1998), so it is likely that Bachman’s Sparrow populations are similarly affected in this region. Fragmentation is known to heavily impact site occupancy of Bachman’s Sparrow at the northeast fringe of its range (Taillie et al. 2015, Winiarski et al. 2017) and the species likely suffers the same effects on the western fringe of its range as well.

Conversely, I did not detect Bachman’s Sparrow in the Post Oak Savanna ecoregion at locations that source populations had previously occupied in low abundances as recently as 2017 (McInnerney et al. 2021). Bachman’s Sparrow in post oak savanna habitat utilize similar habitat characteristics as in pine savanna (Farley et al. 2008). Despite my lack of detections, my top model likely predicts Bachman’s Sparrow occupancy probability with similar accuracy as in pine savanna because these habitat types are very similar in their structure (i.e., open understory with herbaceous ground cover) (Griffith et al. 2007). The lack of Bachman’s Sparrow detections in this region may be an example of a local extirpation resulting from habitat fragmentation and isolation of populations on the westernmost edge of their range. Farley et al. (2008) noted that populations in this ecoregion have extremely low abundances and known source populations are 80-160 km away, reducing the likelihood of immigration and recolonization (Andersen and Beauvais 2013, Pardieck et al. 2020). If this population has been extirpated from the central Post Oak Savanna ecoregion, it could indicate a range reduction of ~160 km from its western periphery south of the Ozark Plateau.

Previous studies have highlighted bimodality in Bachman's Sparrow habitat use, occupying mature woodland savanna habitat as well as early successional fields (Wan Ramle 1987, Dunning and Watts 1990, Brooks and Stouffer 2010, Allen and Burt 2014, Fish et al. 2018). This species is known to prefer mature forest over early successional fields and areas with reduced basal area and high canopy height are more likely to host Bachman's Sparrow (Dunning and Watts 1990, Allen and Burt 2014). It is also known to frequently occupy territories that include both enclosed woodland as well as forest edge or canopy gaps (Fish et al. 2018). Although I did not survey enough plots in early successional habitat, Allen and Burt (2014) provided a thorough examination of differences in Bachman's Sparrow habitat selection in these two habitats in Texas. Their findings in forested habitat types reflected the results of my study, but in early successional habitats, Bachman's Sparrow was associated with areas of increased grass cover and reduced bare ground. This emphasizes the importance of grass ground cover for the species, suggesting that Bachman's Sparrow will not occupy earliest successional habitat where dense grass is replaced by increased bare ground.

Frequent burning of sites is crucial for continued occupancy by Bachman's Sparrow (Tucker et al. 2004). Previous studies (Tucker et al. 2004, Conner et al. 2005, Hannon et al. 2021) have stressed the importance of fire for promoting the appropriate habitat characteristics for Bachman's Sparrow, emphasizing its role in eliminating woody growth in the understory, permitting the success of the fire-adapted grass that Bachman's Sparrow requires. Although I did not assess the effects of fire directly due to the challenge of acquiring time-since-fire data, the effects of fire disturbance can be inferred by the conditions of the habitat covariates associated with Bachman's Sparrow occupancy (Taillie et al. 2015).

In addition to fire, forest maturity may be beneficial for Bachman's Sparrow occupancy. In recent decades, management for old-growth conditions (i.e., forests with trees in the later stages of development and with the related site conditions such as tree size, coarse woody debris, and species composition) has gained traction (Glen et al. 1997). Old-growth conditions in pine savanna ecosystems favor Bachman's Sparrow, as they are fire-climax communities that have reduced tree density and increased grass cover compared to short-rotation plantations (Noel et al. 1998, Cox and Jones 2007). These old-growth pine savannas in the southeast host the federally endangered Red-cockaded Woodpecker, which requires living, mature trees for cavity excavation (Plentovich et al. 1998, Gault et al. 2004). Red-cockaded Woodpecker management has been shown to enhance habitat for Bachman's Sparrow and the two species can be managed for concurrently (Plentovich et al. 1998). Both species respond positively to fire and the usage of fire in maintaining habitat for both species is consistent across their ranges. However, differences in soil and vegetation across their ranges result in varying outcomes of burning. Martin et al. (2021) recommend that regional management practices based on local environmental conditions should be implemented to enhance habitat in that region.

My findings corroborate those of studies in the east on important predictors of Bachman’s Sparrow occupancy and build on the current knowledge of the species by offering results from the western fringe of its range. In Texas, Bachman’s Sparrow occupancy is predicted by similar covariates as populations in the east, indicating that populations may respond to management similarly across its entire distribution. However, at the western fringe of the range, habitat connectivity is crucial as increasing distance from source populations greatly reduces the probability of Bachman’s Sparrow site occupancy. On the western fringe of Bachman’s Sparrow’s distribution, management should not only focus on reducing basal area and midstory density to promote the growth of herbaceous ground cover but should also aim to increase habitat connectivity to reduce isolation of populations.

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CHAPTER II: THE SINGING PHENOLOGY OF BACHMAN'S SPARROW (*PEUCAEA AESTIVALIS*): IMPLICATIONS FOR MONITORING PROGRAMS

INTRODUCTION

Temporal patterns of activity of a species are critical to understanding its life history as these patterns are a response to ecological constraints or resources (Körner and Basler 2010, Haest et al. 2019). An organism's phenology can be a result of the interplay between biotic factors (e.g., antagonistic interactions, food resources, and mate availability) and abiotic factors (e.g., temperature and rainfall) (Schalk and Saenz 2016, Lautenschleger et al. 2020). The timing of these phenological events can have cascading effects on the type and strength of interactions that an organism may experience in an ecological community (Körner and Basler 2010, Carter et al. 2018).

Seasonal differences in photoperiod lead to cyclic changes in temperature and precipitation and these factors often regulate the availability of resources (e.g., food, water, and nutrients) an organism needs to survive and reproduce (Varpe and Fiksen 2010, Ernakovich et al. 2014). On a shorter temporal scale, species may respond to fluctuations in environmental conditions (e.g., temperature or precipitation) that affect activity and behavior (Schalk and Saenz 2016, Kucera et al. 2020). The relative importance of these factors to an organism's phenology is also a result of their life history or reproductive strategies. For example, aquatic or semiaquatic organisms such as fish and anurans, rely heavily on precipitation events to create suitable habitat for breeding (Saenz et al. 2006, Varpe and Fiksen 2010, Schalk and Saenz 2016) while terrestrial and aerial organisms such as birds and bats depend more on increasing temperatures to sustain food sources such as insects (Jenni-Eiermann et al. 2008, Kravchenko et al. 2017).

An important factor underlying songbird phenology is change in ambient temperature that coincides with increasing or decreasing periods of daylight (Schaper et al. 2012). Breeding behavior in songbirds begins as a hormonal response to ambient warming in late winter and spring caused by lengthening photoperiods (Frankl-Vilches et al. 2015). The increase in food availability associated with these seasonal shifts provides resources to meet demands associated with reproduction (Jenni-Eirmann et al. 2008), while increased hours of daylight enable them to extend their foraging period (Mieke et al. 2012). Changes in weather patterns that affect food availability (e.g., drought) can shift the timing of phenological events such as breeding by limiting the number of successful broods (Ganier 1941, Brown and Brown 2014). This mismatch between the phenology of a species and environmental conditions can have detrimental effects on populations, a subject that has gained much credence in light of global climate change (Gordo and Hoi 2012, Schaper et al. 2012, Brown and Brown 2014). It is therefore crucial to understand the cyclical dynamics of species to design monitoring programs and conservation efforts.

Baseline knowledge on the variability underlying a species' phenology can increase the effectiveness of monitoring programs as it can elucidate the ideal temporal windows and environmental conditions for surveys (Furnas and McGrann 2018). Such information can be acquired through various survey methodologies (e.g., mist-netting, nest box surveys), but among the most time- and cost-effective methods for highly vocal species is detection of songs or calls (Strebel et al. 2014, Furnas and McGrann 2018). During the breeding season, songbirds defend their territory and advertise to mates by singing, not only increasing their probability of detections, but also enabling researchers to track important life history events (e.g., breeding) with these acoustic signals (Strebel et al. 2014, Wood et al. 2021). However, challenges arise from the variability of detection caused by factors that might affect singing behavior on a smaller temporal scale (e.g., daily wind speed, heavy rainfall, extreme temperatures). To maximize the efficacy of monitoring programs, efforts should consider the role that abiotic factors have on the singing behavior across broader (i.e., seasonal) and short-term (i.e., daily) temporal scales.

The Bachman's Sparrow is a species of conservation concern that inhabits the southeastern United States (Allen and Burt 2014, Taillie et al. 2015, Malone et al. 2021). Following habitat fragmentation and loss due to conversion of suitable pine savanna habitat to pasture, cropland, or short-rotation pine plantations, Bachman's Sparrow experienced, and continues to experience, severe population declines (Dunning and Watts 1990, Taillie et al. 2015, Winiarski et al. 2017), resulting in many U.S. states listing it as a threatened or endangered species (Dunning et al. 2020). Although Bachman's Sparrow is difficult to detect by visual observation, it is easily detected by its song (Meanley 1959). Despite this, little empirical information exists on its singing phenology across its range. Anecdotal accounts have indicated that it sings from late winter until early fall (Meanley 1990, Farley et al. 2008) and other shorter-term studies have investigated song rate within the breeding season (Allen 2004), but no empirical studies have investigated its singing phenology across the entire year nor the abiotic factors that predict its singing behavior.

For over 2 years, I surveyed for Bachman's Sparrow at sites of known occupancy to determine the abiotic factors that affect the singing phenology of the species. I hypothesized that singing phenology would be associated with an increase in temperature and daylength, as these conditions correspond to optimal breeding periods for the species, and that wind and precipitation would decrease the day-to-day chances of singing. The singing season should therefore extend from warm days in late winter until the end of the breeding season in early fall. These results of the optimal conditions and seasons to detect Bachman's Sparrow are important not only for conservation efforts for the species (i.e., monitoring and management), but also because Bachman's Sparrow detections can be used as a bioindicator of habitat quality in pine ecosystems (Hannah et al. 2017, McIntyre et al. 2019).

METHODS

Study Area and Survey Sites

This study was conducted in the West Gulf Coastal Plain of Texas, near the southwestern edge of Bachman's Sparrow's distribution in the Longleaf Ridge Conservation Area (United States Forest Service 2011). This region is characterized by hilly, xeric longleaf pine savanna habitat with an open understory containing dense bluestem (*Schizachyrium* spp.) and bracken fern (*Pteridium aquilinum*) and sparse bluejack oak (*Quercus incana*), sassafras (*Sassafras albidum*), and American beautyberry (*Callicarpa americana*) in restored areas (Griffith et al. 2007). Restoration efforts by the U.S. Forest Service (USFS) have created over 4,000 ha of longleaf savanna that are frequently managed with thinning operations and prescribed fire (United States Forest Service 2011). Much of this restored area contains optimal habitat for Bachman's Sparrow (United States Forest Service 2011, Allen and Burt 2014).

Survey sites ($n = 9$) for Bachman's Sparrows were located within the Angelina National Forest in Angelina and Jasper counties, Texas, at USFS point-count survey sites that had Bachman's Sparrow detections consistently in the 5 years prior to 2020 (USFS, unpublished data). These sites were regularly burned to maintain the appropriate pine savanna habitat of the region (Appendix 3), and more than half of the sites ($n = 5$) were associated with Red-cockaded Woodpecker clusters. All sites had an overstory characterized by mature longleaf pine, but vegetation in the midstory and understory varied with some sites having more woody shrubs in the understory and less grass cover and more bluejack oak and immature longleaf pine in the midstory.

Data Collection

I used Wildlife Acoustics SM4 and SM Mini autonomous recording units (ARUs) to detect singing behavior at each site. ARUs recorded daily from February 8, 2020 to March 3, 2022 on a schedule of 5 minutes every half-hour starting at sunrise and ending at 3 hours after sunrise for a total of 30 minutes of recording per day. Recordings were scanned for Bachman's Sparrow songs using Kaleidoscope (Version 5.3.0, Wildlife Acoustics, Inc. Maynard, MA). Some data loss occurred at various sites over the survey years due to equipment failure and damage from prescribed fires, but every date had data from at least one site for the entire study period. To assess the window during which Bachman's Sparrow sang, I plotted the presence of detections for each site against Julian date using the absolute presence of detections across all survey years (2020, 2021, and 2022).

I downloaded daily weather data (temperature, precipitation, and wind) from the nearest USFS Remote Automated Weather Station in Zavalla, Texas (range of distance to each site 13.85–20.63 km) and averaged hourly values from the 3-hour recording window for each day. Daily photoperiod values were calculated using the daylength formula derived by Kirk (1994) and Julian date was recorded for each date as well.

Statistical Analysis

I used multiple logistic regression to assess the effect of each independent variable on singing behavior ($\alpha = 0.05$). Variance inflation factor (VIF) was used to assess potential multicollinearity among independent variables in the global. Temperature, Julian date and photoperiod were moderately collinear (VIF between 1 and 5), so I only used one of these three parameters in any given model. I ranked models with varying combinations of the independent variables and interaction terms using Quasi-Information Criterion (QIC) and selected the highest-ranked, most parsimonious model. Because my data were repeated measurements, I fit generalized estimating equations (GEE) with a first-order autoregressive correlation structure using SAS (version 9.4, SAS Institute, Inc., Cary, USA). GEE models average population responses (Ballinger 2004) and therefore it was not necessary to consider variation caused by differences in site characteristics (Ballinger 2004). Since I surveyed the same sites across 3 years, I included year as an independent variable in each model to account for any yearly variation in singing. Two top-ranked models were competitive (QIC = 5740.17 and 5740.47) and differed only in the inclusion of wind as an independent variable, so I proceeded with the more parsimonious model for inference. I modeled the relationship between observed singing behavior (where 0 = no singing and 1 = singing) and year, photoperiod, and precipitation. This analysis was conducted only on data from months with Bachman’s Sparrow detections (January to October) to avoid nuance in the effects of parameters derived from modeling dates in the late fall and early winter when Bachman's Sparrow do not sing.

RESULTS

Bachman's Sparrow Surveys

The first and last dates Bachman's Sparrow was detected were February 8 and September 10, respectively, in 2020 and January 21 and October 6, respectively, in 2021. Singing in 2022 began on January 19, but recorders were pulled on March 3 so no inference on singing cessation dates could be made for that year. Most sites had consistent singing detections between late February and early August (Figure 2.1). The proportion of sites with singing detections slowly increased between late January and late February and steeply declined in late August (Figure 2.1). Bachman's Sparrow was detected most consistently across sites between March and July of each year (Figure 2.1). During January, September, and October, Bachman's Sparrows were noted to sing subsongs, which are low-amplitude and unstructured song types (Dabelsteen et al. 1998), in place of regular, higher amplitude songs.

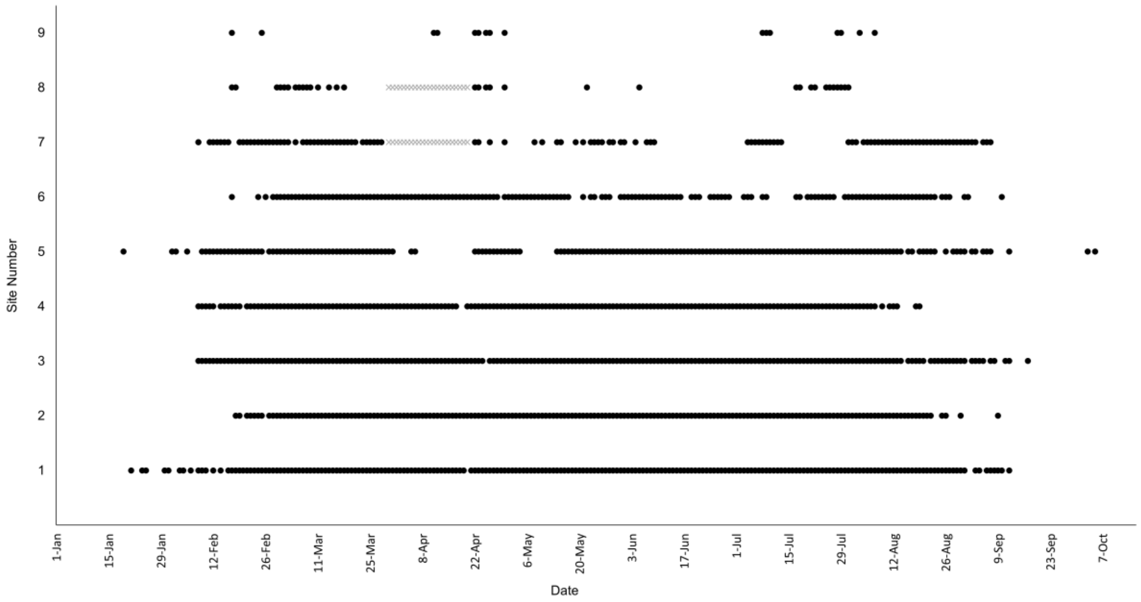

Figure 2.1. Bachman's Sparrow singing detections across the singing season (January 19 to October 6) at 9 sites in the Angelina National Forest, Texas, USA pooled from all survey years (2020-2022). Sites are arrayed along a gradient of decreasing detections. Singing detections for each date and site are represented by black dots while missing data are represented by gray x symbols. Sites 7 and 8 are missing data between March 28 and April 22 due to equipment malfunction in 2020 and fire damage in 2021. Bachman's Sparrow songs were not detected between October 6 and January 19 across all years, so dates from October 8 to December 31 are not displayed in this figure.

Abiotic Influences on Singing Behavior

Precipitation occurred on 68 days across the 3 singing seasons (January to October) and totaled 61.67 mm of precipitation (daily max = 14.61 mm) (Figure 2.2; Appendix 4). Wind speeds were relatively low (mean = 0.66 m/s), with a max of 6.30 m/s across the 3 singing seasons (Appendix 4). Temperature increased with photoperiod (mean = 18.95 °C, range = -10.58–28.88 °C) during the singing season (Appendix 4). Average temperature across all years exhibited high daily fluctuations in fall, winter, and spring, but were consistently high during the summer (Figure 2.2).

Bachman's Sparrow was more likely to sing as photoperiod increased ($P < 0.01$) (Table 2.1). Precipitation had a negative relationship with the probability of singing, though this effect was not statistically significant ($P = 0.06$) (Table 2.1). Wind and temperature did not occur in any of the top models and models including temperature had ΔQIC values of 418 or more, suggesting that they did not explain as much of the variation in the data as models with photoperiod.

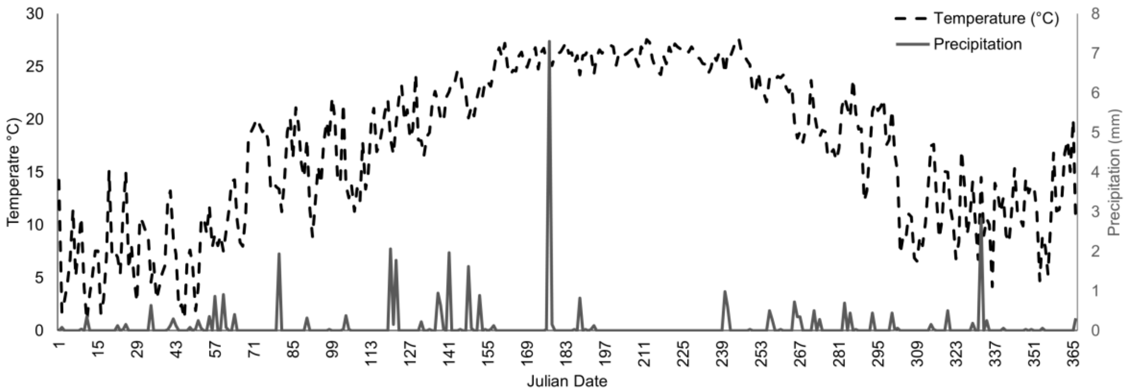

Figure 2.2. Average temperature (black dashed line) and precipitation (gray solid line) values for each Julian date surveyed in the Angelina National Forest, Texas, USA, averaged across all survey years (2020, 2021, and 2022).

Table 2.1. Logistic regression model based on a survey of 9 sites in the Angelina National Forest, Texas, USA between January and October 2020-2022, showing the relationship between Bachman's Sparrow singing and year, photoperiod, and precipitation.

Parameter	Estimate	SE	LCL95	UCL95	Z	*P*
Intercept	-9.45	1.16	-11.73	-7.17	-8.12	<0.01
Year-2020	-0.06	0.28	-0.61	0.50	-0.20	0.84
Year-2021	-0.23	0.28	-0.79	0.33	-0.81	0.42
Year-2022	0.00	0.00	0.00	0.00	–	–
Photoperiod	0.74	0.11	0.52	0.95	6.72	<0.01
Precipitation	-0.15	0.08	-0.31	0.01	-1.89	0.06

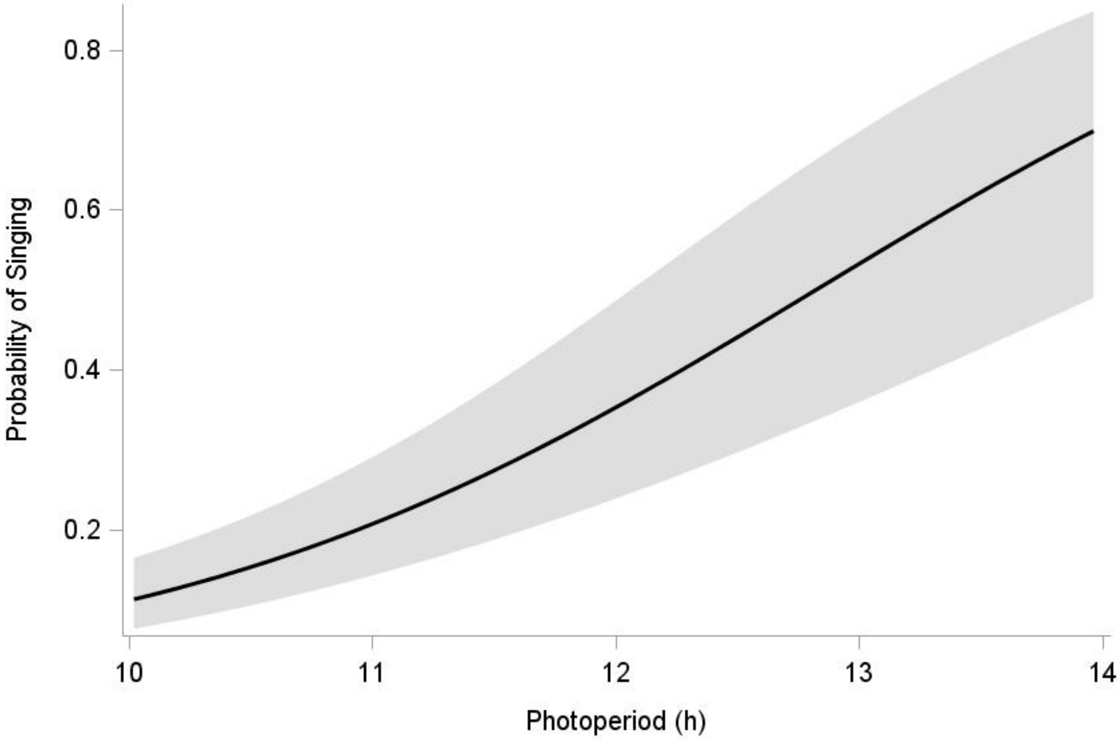

Figure 2.3. The relationship of photoperiod and the probability of Bachman's Sparrow singing. The bold line represents the marginal effect with 95% confidence intervals represented by the shaded blue region. These results were based on a survey of 9 sites in the Angelina National Forest, Texas, USA from 2020-2022.

DISCUSSION

My results indicate that Bachman’s Sparrow in Texas are most likely to sing from February to August, reflecting anecdotal observations that note singing in other populations starts in mid-February (Farley et al. 2008) and continues into August, with few birds continuing singing behavior into September (Brooks 1938, Meanley 1990). Singing detections of Bachman’s Sparrow are most frequent in March, consistent with the Allen (2004) study conducted in east Texas. My results also supported my hypothesis that Bachman’s Sparrow singing phenology is affected by photoperiod. Although I was not able to model temperature and photoperiod simultaneously, daily averages in temperature increased with daily increases in photoperiod, suggesting that it may still play a role in determining singing behavior. The relationship between precipitation and singing further agree with my hypothesis that precipitation influences daily variation in singing behavior, although this relationship was not significant in this study. Wind was not found to be a strong influence on Bachman’s Sparrow singing behavior, likely due to the consistency of low to absent wind speeds throughout the year at these sites.

Photoperiod is likely the primary driver of singing phenology of Bachman’s Sparrow, with the likelihood of singing increasing as daylength increases. This is consistent with the current knowledge of how photoperiod regulates hormonal activation of breeding behavior by increasing testosterone levels (Smith et al. 1997). This increase in testosterone triggers gonadal growth and promotes singing behavior (Gahr 2014). Bachman’s Sparrow is known to sing after dark on moonlit nights (Brooks 1938), a phenomenon observed in many songbirds that is likely a photosensitive response to an increase in ambient light (Bruni et al. 2014). Photoperiods in southern latitudes are less extreme than in northern latitudes, resulting in longer photoperiods at earlier dates. Bachman’s Sparrow may start singing in mid-winter (i.e., mid-January) in southeastern Texas as a result of increasing daylength at early dates. However, Bachman’s Sparrow ranges as far north as Kentucky (Hockman 2013) and singing phenology may differ at more northerly latitudes. Further studies are needed to assess latitudinal variation in singing phenology for this species.

Temperature changes, associated with changes in photoperiod, likely also affect the singing phenology of Bachman’s Sparrow. Temperature is known to affect singing behavior in other songbirds with individuals more likely to sing during warmer temperatures (Bruni et al. 2014, Kucera et al. 2020). Anecdotal accounts of Bachman’s Sparrow singing have noted similar patterns, especially early in the season (Meanley 1959), and cold spells in spring result in interruptions in seasonal singing behavior (Brooks 1938). Furthermore, prior studies on songbirds have indicated that increasing temperatures are stronger drivers of breeding behavior than mean temperatures at the beginning of the breeding season (Schaper et al. 2012). Highly variable temperature in late winter and early spring across the range of Bachman’s Sparrow likely underlies why its singing behavior has a strong association with high temperatures (Brooke 1938, Meanley 1959) and why March has the highest detection rate (Allen 2004).

Photoperiod may also drive singing cessation in Bachman’s Sparrow in late summer. As photoperiod decreases in September, birds become photorefractory from hormonal deactivation of photosensitivity, leading to reductions in gonad size and cessation of singing behavior (Nicholls et al. 1988, Wilson and Reinert 1993). I observed a decrease in the frequency of Bachman’s Sparrow singing detections in August and September as photoperiod, and to a lesser extent temperature, decreased over time. This period is also associated with fledgling care and the prebasic molt (Willoughby 1986, Haggerty 1988), so breeding males may expend less energy on territory defense during this time to accommodate parental responsibilities and molt.

Precipitation may influence daily variation in singing behavior in Bachman’s Sparrows. The pattern I found of decreasing singing detections as precipitation increased is supported by prior studies that have demonstrated negative associations of singing and precipitation (Catchpole and Slater 2008, Keast 1994, Hasan 2010, Bruni et al. 2014). Detection of singing birds during rain events is challenging due to rainfall filling acoustic space and masking other sounds (Smith et al. 2014). Birds singing during rain events may go undetected if their song is masked by the sound of rain (Bruni et al. 2014, Smith et al. 2014). However, this phenomenon may extend to a bird’s ability to detect conspecifics, and individuals might not expend energy advertising during rain events when vulnerability to predation and thermal stress increases (Keast 1994, Link et al. 2011).

Bachman’s Sparrow sings potentially non-territorial songs (subsongs) outside of the breeding season in late winter and fall. Singing behavior in songbirds can take the form of whisper songs (low amplitude variations of territorial song types) or subsongs (soft and unstructured non-territorial songs) during certain times of the year (Schafer 1916, Dabelsteen et al. 1998). Although whisper songs are known to be a form of aggressive signaling during the breeding season in Bachman's Sparrows and Song Sparrows (*Melospiza melodia*) (Searcy et al. 2014, Ali and Anderson 2018), the function of subsongs in songbirds during the non-breeding season is enigmatic and does not appear to occur in antagonistic contexts (Janes 2017). Unstructured subsongs are associated with song development in young male birds during the fall but are also exhibited by adults during the non-breeding season (Thorpe 1958, Dabelsteen et al. 1998). I noted Bachman's Sparrow singing unstructured subsongs in place of primary songs during the fall following the breeding season and in late winter preceding the breeding season. This could be non-territorial singing from young males developing their song repertoire or adults practicing singing and may not be reflective of breeding behavior in the species, per se.

Implications for Monitoring Programs

The reliability of monitoring programs is dependent on correct spatial and temporal coverage for a species and study designs should consider phenology in addition to spatial factors to accurately monitor species. Poorly designed monitoring programs can lead to false negative detections which can misconstrue occupancy and abundance estimates and result in misled policy decisions (Thompson 2002, Amundson et al. 2014, Kellner and Swihart 2014). This is especially significant for monitoring programs that focus on species of conservation concern, as results have inferences on the success or failure of management applications (Oppel et al. 2014).

Surveys should therefore be conducted when detections are most likely and using optimal survey methods to maximize detections. Surveys for songbirds (e.g., point-count surveys) emphasize the importance of focusing surveying efforts on when temperatures are moderately warm and wind and precipitation are minimal (Ellis and Taylor 2018, Holt and Butler 2019). My results corroborate this for Bachman’s Sparrow, suggesting that detection is most likely on days without precipitation and during warmer months during the year (March to early August). If surveys are conducted prior to March, temperature should be considered as an influence on the probability of detecting a Bachman’s Sparrow and efforts should be focused on warmer days. Bachman’s Sparrow is a highly vocal species during this period and the use of ARUs in this study demonstrates their efficacy for detecting Bachman’s Sparrow. This knowledge on the optimal survey conditions and methods for Bachman’s Sparrow should be used in concert with information on their ideal habitat characteristics (see Chapter 1) for accurate monitoring efforts.

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Appendix 1. Plots surveyed for Bachman's Sparrow between May and August 2020 and April and July 2021. Plots were placed in regions of low, medium, and high likelihood of Bachman's Sparrow occurrence (*n* = 40 plots per category per year) based on a species distribution model developed by Andersen and Beauvais (2013). Plots were placed randomly on accessible sites using an ArcMap random selection Python command. Wildlife Management Area is abbreviated to "WMA" in the site names and National Forest and National Grassland are abbreviated to "NF" and "NG," respectively. Latitude and longitude are in World Geodetic System (WGS84) decimal degrees. Bachman's Sparrow detections are designated by an X. The latitude and longitude of plots at Boggy Slough Conservation Area have been obscured per request of the landowner.

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2020	Low	Freestone	Richland Creek WMA	RC01	31.9104	-96.0454	
2020	Low	Freestone	Richland Creek WMA	RC02	31.9085	-96.0427	
2020	Low	Freestone	Richland Creek WMA	RC05	31.9118	-96.0433	
2020	Low	Freestone	Richland Creek WMA	RC07	31.9127	-96.0385	
2020	Low	Freestone	Richland Creek WMA	RC08	31.9138	-96.0103	
2020	Low	Freestone	Richland Creek WMA	RC10	31.9151	-96.0352	
2020	Low	Freestone	Richland Creek WMA	RC11	31.9174	-96.013	
2020	Low	Freestone	Richland Creek WMA	RC12	31.9161	-96.0109	
2020	Low	Freestone	Richland Creek WMA	RC14	31.9185	-96.0315	
2020	Low	Freestone	Richland Creek WMA	RC15	31.9174	-96.0275	
2020	Low	Freestone	Richland Creek WMA	RC16	31.9183	-96.0242	
2020	Low	Freestone	Richland Creek WMA	RC17	31.9201	-96.0129	
2020	Low	Freestone	Richland Creek WMA	RC19	31.9217	-96.0268	
2020	Low	Freestone	Richland Creek WMA	RC20	31.9215	-96.0245	
2020	Low	Freestone	Richland Creek WMA	RC21	31.9164	-96.031	
2020	Low	Freestone	Richland Creek WMA	RC22	31.9219	-96.0171	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2020	Low	Freestone	Richland Creek WMA	RC25	31.9243	-96.0239	
2020	Low	Freestone	Richland Creek WMA	RC31	31.9286	-96.0276	
2020	Low	Freestone	Richland Creek WMA	RC32	31.9287	-96.0245	
2020	Low	Freestone	Richland Creek WMA	RC37	31.9304	-96.0276	
2020	Low	Freestone	Richland Creek WMA	RC38	31.9315	-96.0246	
2020	Low	Freestone	Richland Creek WMA	RC69	31.9195	-96.0171	
2020	Low	Freestone	Richland Creek WMA	RC99	31.9069	-96.045	
2020	Low	Shelby	Sabine NF	SNF00	31.762	-94.0359	
2020	Low	Shelby	Sabine NF	SNF02	31.762	-94.0323	
2020	Low	Shelby	Sabine NF	SNF03	31.765	-94.0323	
2020	Low	Shelby	Sabine NF	SNF04	31.7685	-94.0355	
2020	Low	Shelby	Sabine NF	SNF05	31.7681	-94.0323	
2020	Low	Shelby	Sabine NF	SNF06	31.7681	-94.0251	
2020	Low	Shelby	Sabine NF	SNF07	31.7712	-94.0359	
2020	Low	Shelby	Sabine NF	SNF08	31.7712	-94.0323	
2020	Low	Shelby	Sabine NF	SNF09	31.7712	-94.0287	
2020	Low	Shelby	Sabine NF	SNF10	31.7713	-94.0205	
2020	Low	Shelby	Sabine NF	SNF11	31.7711	-94.0212	
2020	Low	Shelby	Sabine NF	SNF12	31.7712	-94.0179	
2020	Low	Shelby	Sabine NF	SNF13	31.7742	-94.0179	
2020	Low	Shelby	Sabine NF	SNF14	31.7773	-94.0179	
2020	Low	Shelby	Sabine NF	SNF15	31.7803	-94.0215	
2020	Low	Shelby	Sabine NF	SNF16	31.7833	-94.0253	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2020	Low	Shelby	Sabine NF	SNF17	31.7834	-94.0215	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS01	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS02	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS03	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS04	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS05	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS06	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS07	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS08	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS09	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS10	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS11	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS12	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS13	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS14	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS16	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS17	–	–	
2020	Medium	Trinity	Boggy Slough Conservation Area	SBS19	–	–	
2020	Medium	Houston	Davy Crockett NF	DCNF00	31.3992	-95.1814	
2020	Medium	Houston	Davy Crockett NF	DCNF02	31.3502	-95.0504	
2020	Medium	Houston	Davy Crockett NF	DCNF03	31.3588	-95.0485	
2020	Medium	Houston	Davy Crockett NF	DCNF05	31.3696	-95.0469	
2020	Medium	Houston	Davy Crockett NF	DCNF07	31.3686	-95.0918	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2020	Medium	Houston	Davy Crockett NF	DCNF08	31.3801	-95.1006	
2020	Medium	Houston	Davy Crockett NF	DCNF10	31.3799	-95.0758	
2020	Medium	Houston	Davy Crockett NF	DCNF11	31.3954	-95.1552	
2020	Medium	Houston	Davy Crockett NF	DCNF12	31.4013	-95.1957	
2020	Medium	Houston	Davy Crockett NF	DCNF14	31.4061	-95.1504	
2020	Medium	Houston	Davy Crockett NF	DCNF15	31.4102	-95.1946	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF01	31.5005	-94.7599	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF02	31.503	-94.7645	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF03	31.4978	-94.7648	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF04	31.4976	-94.7648	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF05	31.508	-94.7645	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF06	31.4973	-94.7857	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF07	31.5006	-94.7826	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF08	31.5004	-94.7713	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF09	31.5036	-94.7821	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF10	31.5035	-94.7713	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF20	31.4972	-94.7768	
2020	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF21	31.5064	-94.7733	
2020	High	Angelina	Angelina NF	H011	31.0915	-94.2858	
2020	High	Angelina	Angelina NF	H013	31.1008	-94.3109	
2020	High	Angelina	Angelina NF	H014	31.1069	-94.3217	
2020	High	Angelina	Angelina NF	H018	31.1438	-94.2894	
2020	High	Angelina	Angelina NF	H020	31.1654	-94.3397	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2020	High	Angelina	Angelina NF	H021	31.193	-94.4187	
2020	High	Angelina	Angelina NF	H023	31.2084	-94.4223	
2020	High	Angelina	Angelina NF	H103	31.0878	-94.2549	
2020	High	Angelina	Angelina NF	H104	31.0865	-94.2346	X
2020	High	Angelina	Angelina NF	H105	31.1371	-94.3699	
2020	High	Angelina	Angelina NF	H107	31.1921	-94.3163	
2020	High	Angelina	Angelina NF	H111	31.2446	-94.4849	
2020	High	Angelina	Angelina NF	H200	31.054	-94.3699	
2020	High	Angelina	Angelina NF	H204	31.0817	-94.2298	X
2020	High	Angelina	Angelina NF	H205	31.0909	-94.2298	
2020	High	Angelina	Angelina NF	H206	31.1309	-94.3052	X
2020	High	Angelina	Angelina NF	H207	31.1342	-94.3115	X
2020	High	Jasper	Angelina NF	H001	31.0177	-94.1852	
2020	High	Jasper	Angelina NF	H004	31.0546	-94.1385	
2020	High	Jasper	Angelina NF	H005	31.0669	-94.275	X
2020	High	Jasper	Angelina NF	H006	31.0731	-94.2283	X
2020	High	Jasper	Angelina NF	H008	31.0822	-94.1959	X
2020	High	Jasper	Angelina NF	H010	31.0885	-94.178	X
2020	High	Jasper	Angelina NF	H100	31.0447	-94.3304	
2020	High	Jasper	Angelina NF	H101	31.0662	-94.1938	
2020	High	Jasper	Angelina NF	H201	31.0601	-94.2801	X
2020	High	Jasper	Angelina NF	H203	31.0632	-94.1547	X
2020	High	Jasper	Angelina NF	H300	31.0701	-94.1524	X

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2020	High	San Augustine	Angelina NF	H022	31.207	-94.2525	
2020	High	San Augustine	Angelina NF	H027	31.2668	-94.2069	
2020	High	San Augustine	Angelina NF	H029	31.2944	-94.2212	
2020	High	San Augustine	Angelina NF	H030	31.3006	-94.2894	
2020	High	San Augustine	Angelina NF	H109	31.2385	-94.2046	X
2020	High	San Augustine	Angelina NF	H110	31.2416	-94.1866	
2020	High	San Augustine	Angelina NF	H112	31.2476	-94.2478	
2020	High	San Augustine	Angelina NF	H114	31.2846	-94.3016	
2020	High	San Augustine	Angelina NF	H116	31.4042	-94.2549	
2020	High	San Augustine	Angelina NF	H117	31.4134	-94.1795	
2020	High	San Augustine	Angelina NF	H118	31.4441	-94.1866	
2020	High	San Augustine	Angelina NF	H119	31.4502	-94.219	
2021	Low	Fannin	Caddo NG	CNG00	33.4055	-96.0083	
2021	Low	Fannin	Caddo NG	CNG01	33.4137	-96.0228	
2021	Low	Fannin	Caddo NG	CNG03	33.4191	-96.0412	
2021	Low	Fannin	Caddo NG	CNG04	33.4196	-96.0318	
2021	Low	Fannin	Caddo NG	CNG05	33.4221	-96.0434	
2021	Low	Fannin	Caddo NG	CNG06	33.4241	-95.9972	
2021	Low	Fannin	Caddo NG	CNG07	33.4255	-96.0415	
2021	Low	Fannin	Caddo NG	CNG08	33.4265	-96.0373	
2021	Low	Fannin	Caddo NG	CNG10	33.428	-96.0197	
2021	Low	Fannin	Caddo NG	CNG11	33.4267	-96.0157	
2021	Low	Fannin	Caddo NG	CNG12	33.4274	-95.9973	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2021	Low	Fannin	Caddo NG	CNG14	33.4297	-96.0374	
2021	Low	Fannin	Caddo NG	CNG17	33.4303	-96.0158	
2021	Low	Fannin	Caddo NG	CNG18	33.4309	-95.9971	
2021	Low	Fannin	Caddo NG	CNG21	33.4338	-96.016	
2021	Low	Fannin	Caddo NG	CNG24	33.4348	-95.9902	
2021	Low	Fannin	Caddo NG	CNG29	33.4453	-96.0178	
2021	Low	Fannin	Caddo NG	CNG32	33.4096	-96.0068	
2021	Low	Fannin	Caddo NG	CNG35	33.442	-95.9821	
2021	Low	Fannin	Caddo NG	CNG36	33.3954	-96.0191	
2021	Low	Fannin	Caddo NG	CNG37	33.3987	-96.0185	
2021	Low	Fannin	Caddo NG	CNG38	33.4022	-96.0177	
2021	Low	Fannin	Caddo NG	CNG39	33.4086	-96.0157	
2021	Low	Fannin	Caddo NG	CNG40	33.4087	-96.0113	
2021	Low	Fannin	Caddo NG	CNG41	33.4093	-96.0025	
2021	Low	Fannin	Caddo NG	CNG43	33.4062	-96.0043	
2021	Low	Fannin	Caddo NG	CNG46	33.4453	-95.9904	
2021	Low	Fannin	Caddo NG	CNG47	33.4465	-95.9818	
2021	Low	Fannin	Caddo NG	CNG48	33.4419	-95.9907	
2021	Low	Fannin	Caddo NG	CNG49	33.4164	-96.03	
2021	Low	Fannin	Caddo NG	CNG50	33.4167	-96.0349	
2021	Low	Fannin	Caddo NG	CNG51	33.438	-95.9826	
2021	Low	Fannin	Caddo NG	CNG52	33.4384	-95.9876	
2021	Low	Fannin	Caddo NG	CNG55	33.4192	-96.0453	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2021	Low	Fannin	Caddo NG	CNG56	33.4355	-96.0222	
2021	Low	Fannin	Caddo NG	CNG57	33.436	-96.0264	
2021	Low	Fannin	Caddo NG	CNG58	33.4392	-96.0241	
2021	Low	Fannin	Caddo NG	CNG60	33.4238	-96.0206	
2021	Low	Fannin	Caddo NG	CNG61	33.4026	-96.0132	
2021	Low	Fannin	Caddo NG	CNG63	33.4392	-95.9918	
2021	Medium	Anderson	Gus Engeling WMA	GE00	31.9461	-95.9073	
2021	Medium	Anderson	Gus Engeling WMA	GE01	31.945	-95.9034	
2021	Medium	Anderson	Gus Engeling WMA	GE02	31.9443	-95.8993	
2021	Medium	Anderson	Gus Engeling WMA	GE03	31.9489	-95.9066	
2021	Medium	Anderson	Gus Engeling WMA	GE04	31.9489	-95.9005	
2021	Medium	Anderson	Gus Engeling WMA	GE05	31.9489	-95.8962	
2021	Medium	Anderson	Gus Engeling WMA	GE06	31.9506	-95.8919	
2021	Medium	Anderson	Gus Engeling WMA	GE08	31.952	-95.9003	
2021	Medium	Anderson	Gus Engeling WMA	GE10	31.9506	-95.8918	
2021	Medium	Anderson	Gus Engeling WMA	GE12	31.9552	-95.9005	
2021	Medium	Anderson	Gus Engeling WMA	GE13	31.9538	-95.8963	
2021	Medium	Anderson	Gus Engeling WMA	GE14	31.9542	-95.8917	
2021	Medium	Anderson	Gus Engeling WMA	GE15	31.9575	-95.9044	
2021	Medium	Anderson	Gus Engeling WMA	GE16	31.9587	-95.9005	
2021	Medium	Anderson	Gus Engeling WMA	GE17	31.9581	-95.8962	
2021	Medium	Anderson	Gus Engeling WMA	GE18	31.9579	-95.8915	
2021	Medium	Anderson	Gus Engeling WMA	GE20	31.9613	-95.9087	

(continued)

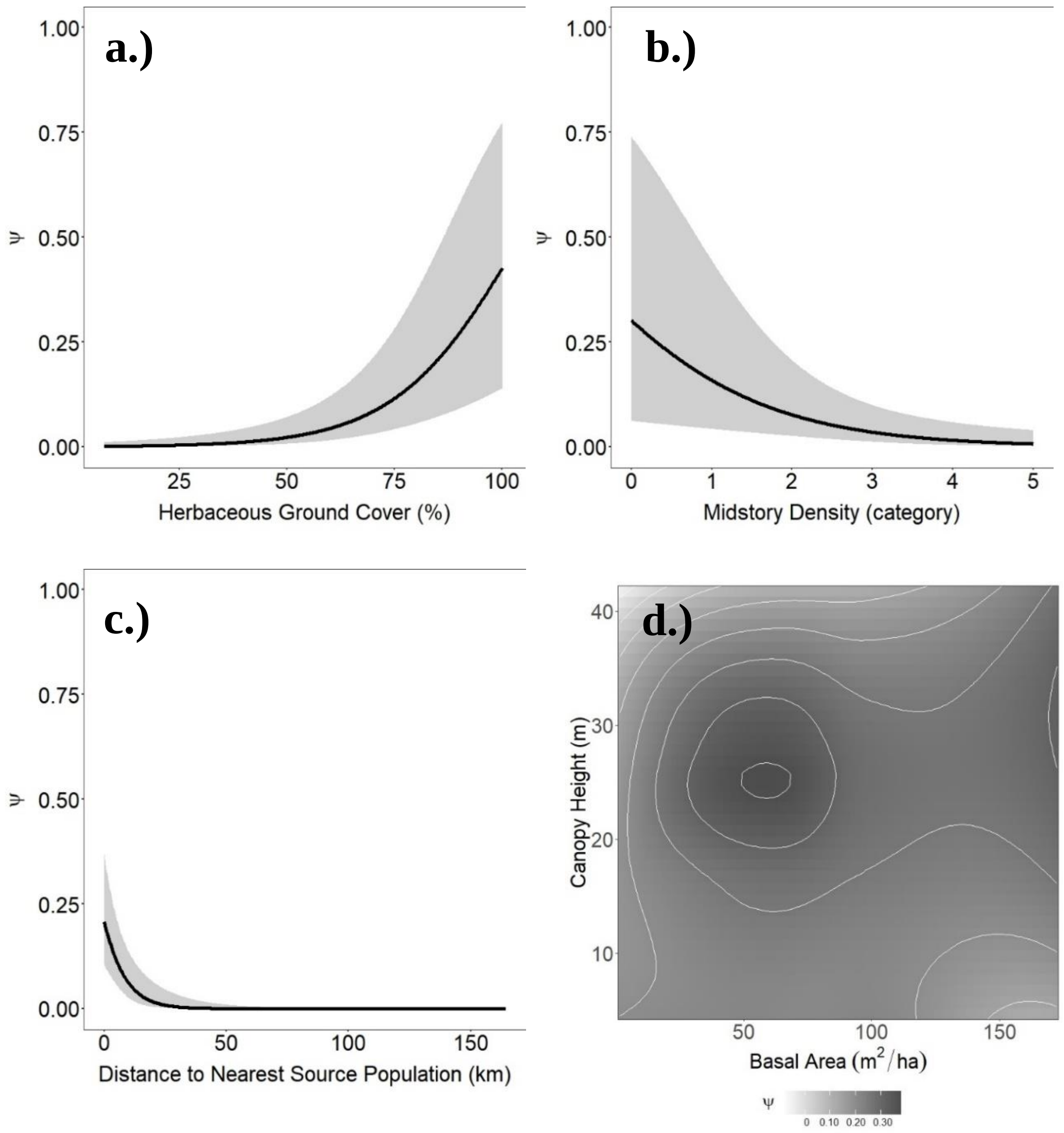
Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2021	Medium	Anderson	Gus Engeling WMA	GE21	31.961	-95.9045	
2021	Medium	Anderson	Gus Engeling WMA	GE22	31.9623	-95.9007	
2021	Medium	Anderson	Gus Engeling WMA	GE23	31.9614	-95.8961	
2021	Medium	Anderson	Gus Engeling WMA	GE24	31.9616	-95.8916	
2021	Medium	Anderson	Gus Engeling WMA	GE25	31.9645	-95.9041	
2021	Medium	Anderson	Gus Engeling WMA	GE26	31.9692	-95.8955	
2021	Medium	Anderson	Gus Engeling WMA	GE27	31.9648	-95.8956	
2021	Medium	Anderson	Gus Engeling WMA	GE28	31.9651	-95.8902	
2021	Medium	Anderson	Gus Engeling WMA	GE29	31.9682	-95.904	
2021	Medium	Anderson	Gus Engeling WMA	GE30	31.9684	-95.9	
2021	Medium	Anderson	Gus Engeling WMA	GE31	31.9725	-95.894	
2021	Medium	Anderson	Gus Engeling WMA	GE32	31.9689	-95.89	
2021	Medium	Anderson	Gus Engeling WMA	GE34	31.9721	-95.8892	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A01	31.496	-94.7817	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A03	31.5009	-94.7774	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A05	31.5033	-94.7893	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A06	31.5053	-94.7857	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A07	31.5043	-94.7756	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A08	31.5053	-94.7677	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A09	31.5106	-94.7622	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A11	31.51	-94.7749	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A12	31.5113	-94.769	
2021	Medium	Nacogdoches	Stephen F. Austin Experimental Forest	SFAEF-A13	31.5131	-94.7734	

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2021	High	Angelina	Angelina NF	ANF01	31.0818	-94.2486	X
2021	High	Jasper	Angelina NF	ANF02	31.0722	-94.2488	
2021	High	Jasper	Angelina NF	ANF03	31.0733	-94.2352	X
2021	High	Sabine	Sabine NF (S.)	FHH00	31.1713	-93.7315	X
2021	High	Sabine	Sabine NF (S.)	FHH01	31.1716	-93.7115	X
2021	High	Sabine	Sabine NF (S.)	FHH03	31.1749	-93.7266	X
2021	High	Sabine	Sabine NF (S.)	FHH04	31.1749	-93.7224	X
2021	High	Sabine	Sabine NF (S.)	FHH05	31.1749	-93.7182	
2021	High	Sabine	Sabine NF (S.)	FHH06	31.1757	-93.7139	
2021	High	Sabine	Sabine NF (S.)	FHH07	31.1749	-93.7098	
2021	High	Sabine	Sabine NF (S.)	FHH08	31.1749	-93.7055	
2021	High	Sabine	Sabine NF (S.)	FHH10	31.1785	-93.7309	
2021	High	Sabine	Sabine NF (S.)	FHH11	31.1785	-93.726	X
2021	High	Sabine	Sabine NF (S.)	FHH12	31.1785	-93.7224	
2021	High	Sabine	Sabine NF (S.)	FHH13	31.1781	-93.7179	X
2021	High	Sabine	Sabine NF (S.)	FHH14	31.1785	-93.714	X
2021	High	Sabine	Sabine NF (S.)	FHH15	31.1785	-93.7097	X
2021	High	Sabine	Sabine NF (S.)	FHH16	31.1785	-93.7055	X
2021	High	Sabine	Sabine NF (S.)	FHH17	31.1821	-93.7266	X
2021	High	Sabine	Sabine NF (S.)	FHH18	31.1821	-93.7224	
2021	High	Sabine	Sabine NF (S.)	FHH19	31.1821	-93.7182	X
2021	High	Sabine	Sabine NF (S.)	FHH20	31.1821	-93.714	X
2021	High	Sabine	Sabine NF (S.)	FHH21	31.1821	-93.7098	X

(continued)

Year Surveyed	Model Category	County	Site	Plot	Latitude	Longitude	Bachman's Sparrow detections
2021	High	Sabine	Sabine NF (S.)	FHH22	31.1842	-93.7064	
2021	High	Sabine	Sabine NF (S.)	FHH23	31.1858	-93.7224	X
2021	High	Sabine	Sabine NF (S.)	FHH24	31.1858	-93.7182	X
2021	High	Sabine	Sabine NF (S.)	FHH25	31.1858	-93.714	X
2021	High	Sabine	Sabine NF (S.)	FHH26	31.1855	-93.7098	
2021	High	Sabine	Sabine NF (S.)	FHH27	31.1894	-93.7182	X
2021	High	Sabine	Sabine NF (S.)	FHH28	31.1894	-93.714	X
2021	High	Newton	Scrappin Valley	SV00	31.1413	-93.7906	X
2021	High	Newton	Scrappin Valley	SV01	31.1411	-93.7868	
2021	High	Newton	Scrappin Valley	SV02	31.1366	-93.7946	X
2021	High	Newton	Scrappin Valley	SV03	31.1376	-93.7904	
2021	High	Newton	Scrappin Valley	SV04	31.1384	-93.7979	X
2021	High	Newton	Scrappin Valley	SV05	31.1364	-93.8014	X
2021	High	Newton	Scrappin Valley	SV06	31.1232	-93.7966	X
2021	High	Newton	Scrappin Valley	SV07	31.1293	-93.7917	X
2021	High	Newton	Scrappin Valley	SV08	31.1342	-93.7976	X
2021	High	Newton	Scrappin Valley	SV09	31.1232	-93.7924	X



Appendix 2. Occupancy probability (*Ψ*) and 95% confidence intervals (gray ribbon) for **a**. herbaceous ground cover, **b.** midstory density, and **c.** distance to the nearest source population from the top occupancy model for all plots surveyed. The interaction of basal area and canopy height is represented by a contour plot (**d.**) with the darker areas having increased probability of occupancy.

Appendix 3. Local-scale habitat characteristics measured at each survey site in the Angelina National Forest in March 2021. Sites are ordered according to their total number of days with Bachman's Sparrow detections (range 16 – 361 days). Basal area, foliage density, canopy cover, and ground cover values are the mean values averaged across all subplots. See Chapter 1 for methods on how habitat variables were measured.

Site	**Total Detections**	**Basal Area (m^2/ha)**	**Canopy Height (m)**	**Midstory Density (category)**	**Foliage Density (m^2/m^3)**	**Canopy Cover (%)**	**Grass Ground Cover (%)**	**Forb Ground Cover (%)**	**Herbaceous Ground Cover (%)**	**Bare Ground (%)**	**Leaf Litter (%)**
1	361	21.36	28.65	1	43.72	89.72	35.00	7.19	42.19	2.50	47.19
2	333	44.43	27.43	2	32.64	92.50	7.19	7.19	14.38	2.50	76.56
3	312	34.18	26.82	2	35.12	89.00	30.94	11.56	42.5	4.06	55.94
4	254	41.87	25.00	2	42.51	91.22	31.88	4.06	35.94	2.50	65.31
5	250	41.87	19.20	2	49.84	89.09	20.63	6.88	27.50	2.50	73.75
6	190	42.72	27.13	1	43.79	89.17	10.00	20.63	30.63	4.06	64.69
7	117	59.81	12.20	3	14.12	90.06	30.63	10.00	40.63	4.06	57.81
8	36	34.18	25.30	2	18.25	90.63	2.50	16.25	18.75	4.06	80.94
9	16	32.47	29.87	2	32.16	89.91	20.63	2.50	23.13	2.50	73.75

Appendix 4. Values of precipitation, temperature, and wind from all seasons and only the singing season (defined as the first and last dates Bachman's Sparrow was detected singing). Singing behavior extended from February 8 to September 10 in 2020 (recorders were set February 8), January 21 to October 6 in 2021, and January 19 to March 3 in 2022 (recorders were retrieved on March 3).

	Precipitation (mm)			**Temperature (°C)**			**Wind (m/s)**	
All Seasons	**Total**	**Max Daily**	**Average Daily**	**Min Daily**	**Max Daily**	**Average Daily**	**Max Daily**	**Average Daily**
2020[1]	45.25	14.61	0.14	-3.05	28.88	18.58	3.90	0.61
2021	31.98	4.07	0.09	-10.58	28.18	17.50	6.30	0.59
2022[2]	2.22	1.27	0.04	-2.53	23.47	6.30	2.45	0.70
All Years	110.61	14.61	0.07	-10.58	28.88	17.06	6.30	0.62
Singing Season								
2020[1]	31.16	14.61	0.14	-0.125	28.88	20.96	3.90	0.71
2021	28.55	4.07	0.11	-10.58	28.18	19.38	6.30	0.58
2022[2]	1.96	0.11	0.04	-2.53	21.95	6.12	2.45	0.69
All Years	61.67	14.61	0.10	-10.58	28.88	18.95	3.90	0.66

[1] Data from 2020 starts at February 8, when recorders were first placed (326 survey days).

[2] Data from 2022 ends at March 3, when recorders were retrieved (62 survey days).

VITA

Liam Wolff grew up outside of Augusta, Georgia where he attended Augusta University from 2014 until receiving his Bachelor of Science in Ecology in 2018. During this time, he worked as an intern at the Phinizy Center for Water Sciences in addition to as a teaching assistant at his university. Following graduation, he took a gap year from school, monitoring the endangered Golden-cheeked Warbler in Texas at Fort Hood for the University of Illinois Urbana-Champaign from February to June, 2019, and surveying and banding migratory songbirds in Alabama at Splinter Hill Bog for the University of Southern Mississippi from August to November, 2019. He accepted the position of Graduate Research Assistant at Stephen F. Austin State University in the Arthur Temple College of Forestry and Agriculture in January 2020. Liam received the degree of Master of Science in Forestry in May of 2022.

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Written in the style of the American Ornithological Society Journals

This thesis was typed by Liam G. Wolff.