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Reproductive consequences of habitat fragmentation for a declining resident bird of the longleaf pine ecosystem

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Citation: Winiarski, J. M., C. E. Moorman, J. P. Carpenter, and G. R. Hess. 2017. Reproductive consequences of habitat fragmentation for a declining resident bird of the longleaf pine ecosystem. Ecosphere 8(7):e01898. 10.1002/ecs2.1898

Abstract. Habitat loss and fragmentation are major threats to bird population persistence. Yet, our understanding of the demographic factors behind the adverse effects of fragmentation remains limited for many species. We studied the breeding demographics of the Bachman's Sparrow (*Peucaea aestivalis*), a species of conservation concern that is associated with highly imperiled longleaf pine ecosystems in the southeastern United States. We quantified the effects of local- and landscape-scale factors on different components of reproductive success (i.e., pairing success and probability of fledging offspring) for 96 male sparrows at eight sites in southeastern North Carolina. Pairing success of monitored sparrows was 69%, and 77% of paired males fledged ≥1 offspring. Habitat amount in the surrounding landscape, rather than local habitat quality, was the most influential predictor of pairing success for male Bachman's Sparrows. In contrast, we documented no predictors of successfully fledging offspring for paired males. We infer that reduced pairing success is limiting reproduction in isolated landscapes and may be a contributing factor for the low occupancy and declines of Bachman's Sparrow in our study region. Overall, our results suggest that managers can promote breeding opportunities for Bachman's Sparrows by prioritizing resources to patches near large, preexisting longleaf pine forest to ensure ≥20% habitat within the surrounding landscape.

Key words: Bachman's Sparrow; dispersal; fire; fragmentation; habitat amount; landscape; longleaf pine; North Carolina; pairing success; reproductive success.

Received 10 April 2017; revised 13 June 2017; accepted 15 June 2017. Corresponding Editor: Christopher Lepczyk.

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INTRODUCTION

Anthropogenic change in the amount and configuration of habitat is considered to be a major driver of bird population declines across landscapes (Herkert 1994, Robinson et al. 1995, Donovan and Flather 2002). Habitat destruction and fragmentation transform landscapes by reducing habitat area, increasing distance and isolation among remaining fragments, and increasing the amount of edge (Haddad et al. 2015). Consequently, these processes can adversely affect a suite of demographic rates that drive bird density, distribution, and species richness (McGarigal and McComb 1995, Villard et al. 1999, Donovan and Flather 2002, Lampila et al. 2005). While extensive research has shown that landscape changes can have widespread detrimental consequences for bird distribution and abundance, the specific demographic components involved in population declines often remain unknown for many species of conservation concern (Lampila et al. 2005).

Habitat loss and fragmentation can negatively influence bird demography and lead to reduced fitness in several ways. First, loss of habitat connectivity can impede mobility, potentially resulting in higher mortality for dispersing individuals and lower pairing success for males residing in isolated fragments (Dale 2001, Cooper and Walters 2002, Lampila et al. 2005, Robles et al. 2008). Second, increased isolation can lead to a reduction in the abundance of individuals in remaining habitat patches (Dale 2001). Because females may use conspecific density as a habitat selection cue, this change may further limit breeding opportunities for males (Villard et al. 1993, Ward and Schlossberg 2004). Third, alterations in landscape composition (e.g., patch size reduction and greater exposure to edges; Fahrig 2003) can initiate changes in predator and brood parasite abundance, leading to higher rates of nest predation and brood parasitism that negatively affect reproductive success (Robinson et al. 1995, Chalfoun et al. 2002). Finally, decreasing prey availability associated with declining fragment size can limit nest success, clutch size, and fledgling condition (Burke and Nol 1998, Zanette et al. 2000, Lampila et al. 2005). Given the myriad impacts of landscape change on breeding bird populations, a better understanding of the specific demographic mechanisms responsible for declines is crucial to address the adverse effects of habitat fragmentation and inform effective management strategies (Lampila et al. 2005).

We investigated the breeding response of the Bachman's Sparrow (*Peucaea aestivalis*) to habitat loss and fragmentation as a possible explanation for population declines. Bachman's Sparrow is a ground-nesting bird endemic to the southeastern United States and typically inhabits open pine woodlands maintained with frequent fire (Dunning 2006). Although it can occupy other habitat types created through disturbance (e.g., clearcuts, utility right-of-ways, and abandoned fields), the species is primarily associated with longleaf pine (*Pinus palustris*) ecosystems (Dunning and Watts 1990). Moreover, Bachman's Sparrow is considered to be an effective indicator species for healthy longleaf pine ecosystems because of its reliance on frequent fire (typically ≤3-yr return interval; Tucker et al. 2004, 2006), open canopy, and diverse groundcover characterizing these forests (Hannah et al. 2017). Due to extensive habitat loss and fire suppression, this ecosystem has been reduced to 3–5% of its historic range (Frost 2006), and much of the remaining habitat exists as scattered and degraded remnant patches (Van Lear et al. 2005). Consequently, Bachman's Sparrow is listed as a species of conservation concern across its range, and habitat loss and fragmentation have been implicated as serious threats to its population persistence (Dunning and Watts 1990) and other longleaf pine biota (Van Lear et al. 2005).

Throughout the species' range, suitable patches of longleaf pine forest often are unoccupied (Dunning and Watts 1990), and dispersal limitation and landscape structure appear to play an important role in shaping the spatial distribution of Bachman's Sparrow populations. Adult Bachman's Sparrows exhibit strong site fidelity (Cox and Jones 2007, 2010), and may innately lack the ability to make long-distance movements between habitat patches (Jones et al. 2017). Connected habitat patches, particularly those that are ≤2 km from source populations, appear more likely to be colonized by Bachman's Sparrows than isolated patches (Dunning et al. 1995). Taillie et al. (2015) showed that landscape-scale habitat amount within 3 km was the most influential predictor of Bachman's Sparrow occupancy. Most recently, translocation experiments demonstrated that fragmentation of pine savanna influenced the movement behavior of Bachman's Sparrows, and individuals avoided traversing long distances (>500 m) across large agricultural fields as they returned to capture locations (Jones et al. 2017). Despite the emergent characteristics of Bachman's Sparrow movement and occupancy that have been demonstrated by these studies, the potential demographic mechanisms underlying abundance and occurrence patterns have not yet been addressed.

In this study, we assessed breeding demographic variables for Bachman's Sparrows that are likely to be associated with fragmentation and relatively easy to measure: (1) pairing success, which may be indicative of disrupted landscape connectivity or lower habitat quality, and (2) fledging success, which may suggest increased nest predation, parasitism, or food shortages (Lampila et al. 2005). We examined these key components of reproductive success by comparing Bachman's Sparrows residing in highly fragmented and relatively continuous longleaf pine landscapes in southeastern North Carolina, USA.

METHODS

Study area

We studied Bachman's Sparrows at eight sites within the Middle Atlantic Coastal Plain physiographic region (hereafter, Coastal Plain) of southeastern North Carolina (Fig. 1). This region is part of the North American Coastal Plain, which recently has been recognized as a global biodiversity hot spot because of considerable plant endemism and >70% habitat loss (Noss et al. 2015). Longleaf pine ecosystems cover <20% of the study area, whereas urban development, agricultural lands, and loblolly pine (*Pinus taeda*) plantations are the most abundant land cover types (Southeast GAP Analysis Project 2008). The

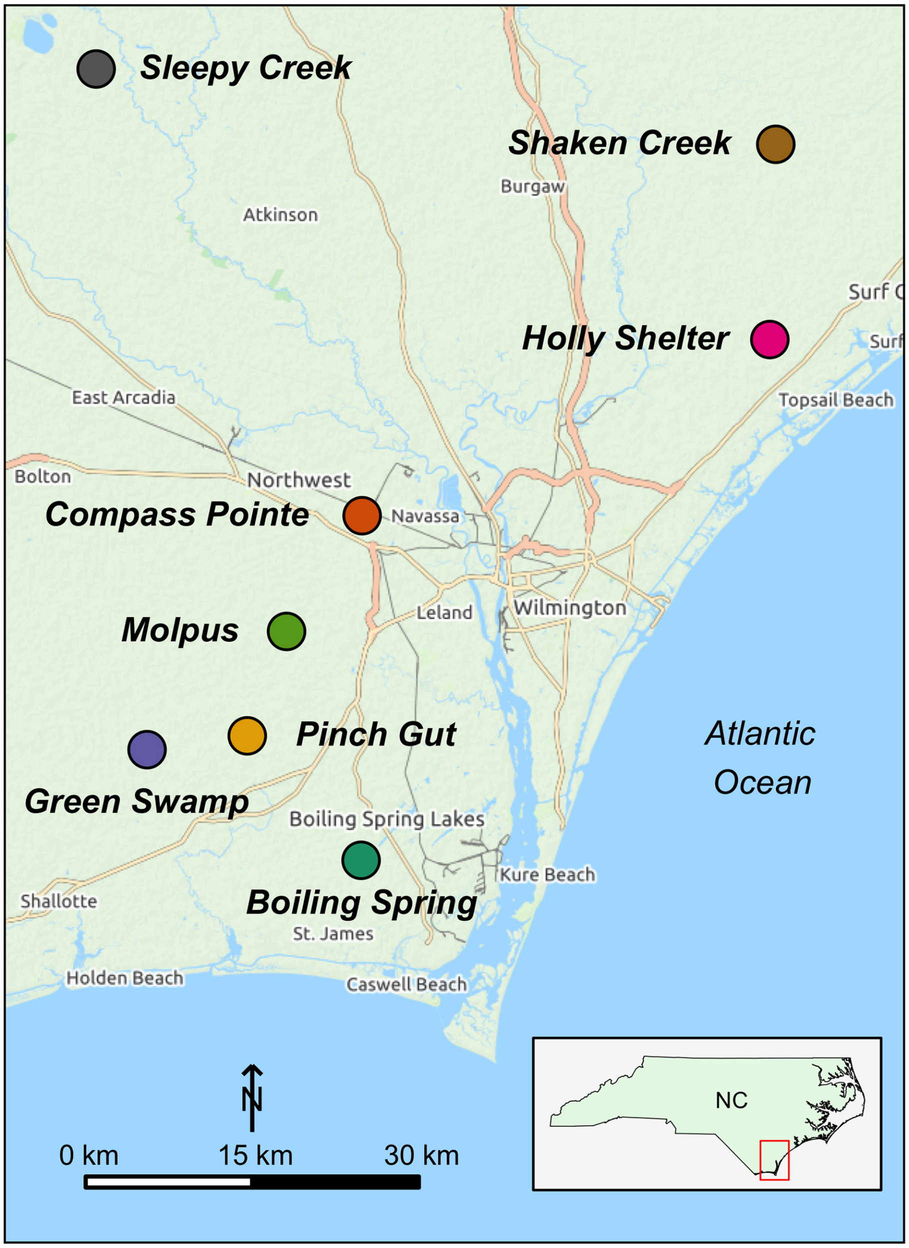

Fig. 1. Study sites (n = 8; colored points and bold labels) in southeastern North Carolina where reproductive data were collected for 96 Bachman's Sparrow territories, 2014–2015.

majority of longleaf pine woodlands occur on public landholdings, which comprise approximately 17% of the study area and are managed by the U.S. Department of Defense, North Carolina Forest Service, North Carolina Wildlife Resources Commission (NCWRC), and the North Carolina Plant Conservation Program (NCPCP). The Nature Conservancy (TNC) also manages several properties that comprise ~2% of land in the study area. Because of the species' rarity in the region, we relied on previously gathered information on Bachman's Sparrow distribution in North Carolina (Taillie et al. 2016) and accessibility to select study sites.

Bachman's Sparrow habitat within study sites primarily was composed of mesic longleaf pine woodlands, as use of other habitat types is rare in North Carolina (Taillie et al. 2016). Wet pine woodlands were characterized by an open canopy, seasonally saturated soils, and a diverse groundcover layer. In addition to longleaf pine, less abundant tree species included loblolly and pond pine (*Pinus serotina*). Prescribed fire in our study area typically was applied in the dormant and early growing seasons on a 1- to 5-yr return interval, but sometimes exceeded 5 yr on privately owned sites where groundcover management and restoration were not the primary objectives.

Field data collection

Reproductive status and territory mapping.—We captured adult male Bachman's Sparrows at the beginning of each breeding season in 2014 and 2015. Female Bachman's Sparrows are not easily observed or captured (Tucker et al. 2006), so we focused on the reproductive behaviors of male sparrows. We lured males into mist nests using playback of conspecific vocalizations and by placing nets in frequently used flight paths. Once captured, we determined sex (i.e., presence of a cloacal protuberance) and fitted individuals with a unique combination of three colored leg bands and a U.S. Geological Survey aluminum band to allow for visual identification of individual sparrows. In addition to the banded population, we studied a small subset of singing males that we were unable to capture, but these individuals were always bordered by color-banded males and their identity was confirmed through weekly territory mapping.

Fragmentation is likely to impact several breeding demographic components (Lampila et al. 2005), and quantifying reproductive success via nest survival alone can be logistically impractical for cryptically nesting species like Bachman's Sparrow (Vickery et al. 1992, Dunning 2006, Tucker et al. 2006). Therefore, we evaluated multiple components of reproductive success using a modified reproductive index (Vickery et al. 1992, Tucker et al. 2006) that relied on behavioral observations and reduced the need to intensively monitor nests. We collected behavioral data on individual males at one-week intervals from mid-April until the end of July to determine reproductive success (hereafter, a reproductive visit). Reproductive visits were conducted from 05:30 and 13:00, and we varied visit times and observers every week for each male. For each reproductive visit, an observer spent 60 min in the focal male's territory recording behaviors that indicated territoriality (i.e., male on territory for ≥4 weeks) and reproductive status. In particular, we looked for signs of successful pairing (e.g., a male in close proximity to a female, copulation, or nest building) and successful fledging of offspring (e.g., adults carrying food to fledglings; Vickery et al. 1992). When active nests were located in a male's territory, they also were monitored to aid in our determination of reproductive success. Nests were monitored every 1–4 d until young fledged or the nest failed, and were considered to have failed if they were depredated, abandoned, destroyed by prescribed fire, or lost to unknown causes. Bachman's Sparrows are able to raise multiple broods per season (Dunning 2006), so we recorded the number of successful broods observed and fate of nesting attempts per territory. Because nests and fledglings are difficult to locate and observe for this species (Dunning 2006), we were not able to precisely estimate productivity (i.e., number of offspring fledged) for each male. At the end of each breeding season, we determined three components of reproductive success for each individual based on weekly reproductive visits and nest fates: (1) pairing success (i.e., paired vs. unpaired), (2) success at fledging ≥1 offspring, and (3) the number of successful broods raised.

While conducting reproductive visits, observers also mapped individual male territories by marking their locations with a GPS unit (5-m precision) and flagging. We defined a territory as the entire area used during the breeding season, and recorded locations where males were observed foraging, singing, following mates, and feeding fledglings. We followed males from a distance to avoid influencing routine behaviors, and recorded 1–5 GPS points of male locations during each reproductive visit (20 ± 12 SD points/territory/season). GPS locations were collected when a bird had traveled a substantial distance (>15 m) between subsequent locations to avoid taking GPS points repeatedly within the same area. To delineate territory boundaries for each male, we used the adehabitatHR package (Calenge 2006) to create 95% minimum convex polygons (MCP) from territory mapping locations.

Territory-scale measurements.— Territory-scale vegetation structure was quantified for each male from five randomly selected territory locations that were collected during weekly reproductive visits. Groundcover vegetation structure was measured at 1-m increments along two perpendicular 10-m transects centered on territory locations. At each transect point, vegetation structure was quantified by recording the presence of each vegetation category (i.e., "hits" or vegetation contacts) on 0.1-m sections of a 1.5-m vertical pole placed flush with the ground. Vegetation categories included grass, woody vine–shrub (hereafter "woody vegetation"), and forb–fern following Taillie et al. (2015). Using this sampling protocol, we obtained indices of density and height for each vegetation category: (1) vertical density, which included the number of vegetation hits along the entire length of the pole, and (2) maximum height, recorded as the tallest 0.1-m section of the pole with a vegetation contact (Wiens and Rotenberry 1981, Moorman and Guynn 2001, Taillie et al. 2015). Groundcover vegetation structure measurements then were averaged across the 21 sampling points for each territory location. Finally, we estimated the total basal area of pines using a 10-factor prism at each territory location.

We obtained time since fire for each male's territory from Geographic Information System data layers (NCWRC, NCPCP, and TNC, *unpublished data*) or by communicating with private land managers. Data substitution was necessary for 3% of territories with missing fire data. For a single male monitored in 2014 and 2015, time since fire was unknown, but to our knowledge prescribed fire had not occurred in ≥10 yr. Therefore, time since fire was recorded as 10 yr for that individual to reduce the influence of outliers in our models. For another two territories, the most recent fire occurred 7–10 yr prior, so we selected the median burn date. Several territories also encompassed multiple management units with differing burn histories, and for those males, we used the average time since fire across units within each territory. Averaging time since fire across units was necessary for 29% (n = 28) of males included in the analyses.

Statistical analyses

All statistical analyses were carried out using program R, version 3.2.2 (R Development Core Team 2016), and we report mean ± SD unless noted otherwise.

Landscape-scale habitat amount.— We used landscape-scale habitat amount (hereafter "habitat amount") surrounding male territories as a metric to assess the effects of habitat loss and fragmentation on Bachman's Sparrow reproductive success. We chose this metric because it offers a simple interpretation of both patch size and isolation (Fahrig 2013), and habitat amount has been shown to be an important predictor of Bachman's Sparrow occupancy (Taillie et al. 2015). To quantify habitat amount surrounding each male Bachman's Sparrow territory, we adopted a "species-centered" approach (Shirley et al. 2013, Betts et al. 2014). Most landscape studies rely on human-defined land cover types to quantify habitat amount, which may be inaccurate or fail to accommodate a focal species' perception of a landscape (Betts et al. 2014). For example, longleaf pine forest classified by the Southeast GAP analysis was often incorrect in the study area (J. M. Winiarski, *personal observation*), and Bachman's Sparrow can use other habitat types such as open pine woodlands, clearcuts, and powerline right-of-ways (Dunning 2006). Alternatively, it is possible to accurately quantify habitat amount using species occurrences and unclassified Landsat reflectance bands (Shirley et al. 2013) that do not suffer from such biases. This species-centered approach is a promising method that has been used to reveal the effects of landscape-scale habitat loss and fragmentation on species occupancy and vital rates (reviewed in Betts et al. 2014).

To quantify Bachman's Sparrow habitat amount within the study area, we constructed a species distribution model (SDM) using maximum entropy modeling (Maxent; Phillips et al. 2006). Maxent generally performs well and is considered to be one of the most effective approaches to creating SDMs with presence-only data (Elith et al. 2011). Maxent uses environmental data and species occurrence locations to produce a raster map of the predicted habitat suitability (Elith et al. 2011). We used Bachman's Sparrow occurrence data obtained from 119 point counts conducted across the Coastal Plain during April–July, 2007–2014 (NCWRC and NCSU, *unpublished data*; Appendix S1: Fig. S1), and Landsat reflectance bands and normalized difference vegetation index calculated from an April 2014 Landsat image of the study region (Shirley et al. 2013, Betts et al. 2014). We used 2014 because it closely represented the landscape conditions that existed during the study period. To assess model performance, we performed 10-fold cross-validation and evaluated the area under the curve of the receiver–operator plot (Phillips et al. 2006; Appendix S2: Fig. S2). The resulting SDM was converted to a binary habitat model by classifying values ≥0.5 to a value of 1 (habitat) and values <0.5 to a value of 0 (non-habitat; Betts et al. 2014).

To obtain habitat amount from the binary habitat model, we first used the rgeos package (Bivand and Rundel 2015) and the "gCentroid" function to extract coordinates of each male's territory centroid from its 95% MCP. Finally, we used the "land.metrics" function in the spatialEco package (Evans 2016) and the binary habitat model to derive percent habitat amount within a 3-km buffer around each male's territory centroid. This 3-km scale was important for predicting the effects of habitat amount on Bachman's Sparrow occupancy in North Carolina (Taillie et al. 2015), and reflects the estimated dispersal distance for this species based on home range size (Cox and Jones 2007, Brown 2012; J. M. Winiarski, C. E. Moorman, and J. P. Carpenter, *unpublished manuscript*) and the proportional relationship between territory size and median dispersal of songbirds described by Bowman (2003).

Reproductive success.—We analyzed reproductive success of monitored Bachman's Sparrows (Table 1) using generalized linear mixed-effects models (GLMM) with the lme4 package (Bates et al. 2015). We included "site" as a random effect in all models to account for variation among study sites. For each component of reproductive success, we built models to evaluate the effects of vegetation structure variables, time since fire, and habitat amount (Table 2). We used grass vertical density as a variable because it is an important predictor of Bachman's Sparrow habitat selection (Dunning and Watts 1990, Brooks and Stouffer 2010, Taillie et al. 2015).

Table 1. Summary of Bachman's Sparrow territories monitored by site in the Coastal Plain of North Carolina, USA, 2014–2015.

			No. males				
Study site	County	Year	B	UB	RT	Paired (%)	Fledged (%)
Holly Shelter	Pender	2014	31	3	8	32/34 (94)	24/32 (75)
Holly Shelter	Pender	2015	28†	0	13	24/28 (86)	19/24 (79)
Compass Pointe	Brunswick	2014	1	0	0	1/1 (100)	1/1 (100)
Compass Pointe	Brunswick	2015	1‡	0	0	0/1 (0)	0/0 (0)
Sleepy Creek	Bladen	2014	4	0	2	1/4 (25)	0/1 (0)
Shaken Creek	Pender	2015	1	1	0	1/2 (50)	1/1 (100)
Molpus	Brunswick	2014	2	0	0	1/2 (50)	0/1 (0)
Green Swamp	Brunswick	2015	13	3	9	6/16 (38)	6/6 (100)
Pinch Gut	Brunswick	2015	2	0	0	0/2 (0)	0/2 (0)
Boiling Spring	Brunswick	2015	6	0	5	0/6 (0)	0/6 (0)

Notes: B, number of color-banded males; UB, number of unbanded males; RT, number of males affixed with a radio transmitter for concurrent home range study. Percent of males that fledged young included paired males only. Note that eight banded males were monitored in both years.

† Includes seven color-banded males monitored in both 2014 and 2015.

‡ Same color-banded male monitored in both 2014 and 2015.

Table 2. Summary statistics (means ± SD) by study site for all landscape- and territory-level habitat variables used to model Bachman's Sparrow reproductive success in the Coastal Plain, North Carolina, USA, 2014–2015.

	Study sites			
Variable	BSLP	COPO	GSPR	HSGL
Habitat within 3 km (%)	3.34 ± 0.09	8.63 ± 0.04	5.02 ± 1.06	20.86 ± 2.60
Time since fire (yr)	2.19 ± 0.52	10.00 ± 0.00	2.09 ± 2.42	1.32 ± 0.56
Grass density (hits)	1.88 ± 0.31	0.61 ± 0.15	1.72 ± 0.74	2.72 ± 0.80
Woody height (dm)	2.50 ± 0.54	2.51 ± 0.31	1.96 ± 0.46	1.89 ± 0.66
Pine basal area (m^2/ha)	5.24 ± 2.19	3.10 ± 0.50	9.63 ± 6.20	10.02 ± 3.39
	MOLP	PGGL	SCFA	SCPR
Habitat within 3 km (%)	16.61 ± 0.28	5.11 ± 0.70	10.01 ± 0.66	17.07 ± 0.57
Time since fire (yr)	8.29 ± 0.00	1.22 ± 0.00	4.00 ± 0.00	1.66 ± 0.00
Grass density (hits)	0.54 ± 0.14	2.10 ± 0.58	2.15 ± 0.44	1.72 ± 0.39
Woody height (dm)	4.40 ± 3.04	1.94 ± 0.43	2.60 ± 0.95	1.89 ± 0.70
Pine basal area (m^2/ha)	7.12 ± 1.95	1.78 ± 1.07	2.30 ± 1.16	12.28 ± 3.73

Note: Study site codes: BSLP (Boiling Spring), COPO (Compass Pointe), GSPR (Green Swamp), HSGL (Holly Shelter), MOLP (Molpus), PGGL (Pinch Gut), SCFA (Sleepy Creek), and SCPR (Shaken Creek).

Additionally, we included basal area and shrub height as covariates because higher levels of these vegetation characteristics are associated with low quality or unoccupied habitat patches (Haggerty 1998, Dunning 2006, Brooks and Stouffer 2010, Taillie et al. 2015; Table 2). In a concurrent study investigating Bachman's Sparrow microhabitat selection and home range size (J. M. Winiarski, C. E. Moorman, and J. P. Carpenter, *unpublished manuscript*), we affixed radio transmitters to a subset of males in the current study (n = 37). Because transmitters and other devices can negatively affect productivity in birds (Barron et al. 2010), we also included a dummy variable indicating whether a male was fitted with a radio transmitter (Table 1). More isolated sites were sampled in 2015 than in 2014, so we did not include year as a predictor variable in the models. While we acknowledge that reproductive success may vary annually in response to fluctuating weather conditions and predator abundance, we did not detect a difference in the number of males that paired ($\chi^2 = 1.14$, df = 1, $P = 0.29$) or fledged young ($\chi^2 = 0.00$, df = 1, $P = 1.00$) at sites that we were able to sample in both years of the study (n = 64 territories).

Pairing (0 = unpaired, 1 = paired) and fledging success (0 = no offspring fledged, 1 = at least one offspring fledged) were fitted to binomial distributions with a logit link. Only territorial males (i.e., males present ≥4 weeks) were used in both analyses, and only paired males were included in the fledging success analysis. We also repeated the GLMM analyses considering the number of successful broods fledged per male (fitted to a Poisson distribution), and examined the effects of temporal-, local-, and landscape-scale covariates on daily nest survival in a concurrent study (Winiarski et al. 2017). Because these two additional analyses resulted in similar findings to the fledging success GLMM analysis, we do not present them here. We ran univariate models for each of the GLMM analyses, and the top pairing and fledging success models were selected using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) using the "MuMIn" package (Bartoń 2016). Models were ranked according to their AIC_c values, and we considered models with $\Delta AIC_c \leq 2$ to be competitive (Burnham and Anderson 2002). Variables were considered important if the 85% confidence interval did not include zero, and were considered to have no effect on the response variable if the 85% confidence interval overlapped zero (Arnold 2010). We used 85% confidence intervals because they are more appropriate than 95% intervals when using AIC for model selection (Arnold 2010).

RESULTS

Territory and landscape attributes

We monitored 112 Bachman's Sparrow territories, and were able to evaluate reproductive success for 96 Bachman's Sparrow territories where males were present for ≥4 weeks: 43 males at five sites in 2014 and 53 males at five sites in 2015 (Table 1). Of the 96 males, 89 (93%) were color-banded, and eight of these banded males were monitored in both years of the study (Table 1). Territory-level vegetation conditions were comparable across study sites, but burn histories varied considerably (Table 2). Habitat amount within 3 km of male territories was variable by study site (Table 2) and ranged from 3% to 25% of the surrounding landscape.

Reproductive success

Pairing success.—Approximately 69% of males were paired across all years and sites combined, and pairing success ranged from 0% to 100% per site (Table 1). Territory-scale vegetation variables and time since fire were not significant predictors of pairing success for male Bachman's Sparrows (Table 3). Also, radio transmitters did not affect the probability of males to pair with females (Table 3). However, pairing success was negatively related to percent habitat amount within 3 km of a male's territory (standardized β = 0.20 ± 0.04 SE, 85% CI = 0.12, 0.26; Table 3, Fig. 2).

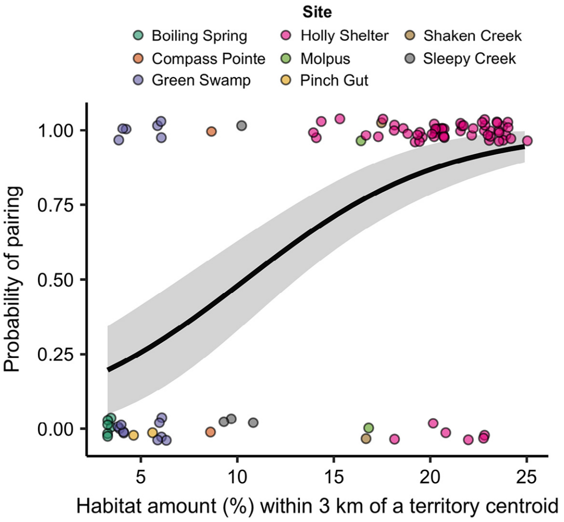

Fig. 2. Predicted probability of pairing for male Bachman's Sparrows in relation to percent habitat within 3 km of a territory. Shaded regions are 95% confidence intervals, and colored points indicate pairing success (paired = 1, unpaired = 0) of males by study site. Points are slightly jittered for clarity.

Fledging success.—Sixty-six paired males were included in the fledging success GLMM analysis, and fledging success ranged from 0% to 100% per site (Table 1). Of these 66 males, approximately 23% produced zero offspring, 64% fledged a single brood, and 13% raised two broods. Although Bachman's Sparrows can attempt three broods per season, we documented no evidence of males successfully fledging more than two broods in a single season. No variables predicted the probability of males fledging ≥1 offspring (Table 3).

Table 3. Top five mixed-effects logistic regression models of pairing and fledging success for Bachman's Sparrows in the Coastal Plain region of North Carolina, USA, 2014–2015.

Model	K	Loglik	AIC_c	$\Delta\mathrm{AIC}_c$	w_i
Pairing success					
Percent habitat amount	3	−41.69	89.63	0.00	0.75
Null	2	−45.10	94.32	4.69	0.07
Radio transmitter	3	−44.21	94.68	5.05	0.06
Pine basal area	3	−44.69	95.64	6.01	0.04
Time since fire	3	−44.85	95.96	6.33	0.03
Fledging success					
Null	2	−35.37	74.94	0.00	0.24
Time since fire	3	−34.33	75.05	0.11	0.22
Woody maximum height	3	−34.65	75.68	0.74	0.16
Percent habitat amount	3	−35.08	76.54	1.60	0.11
Grass vertical density	3	−35.25	76.89	1.95	0.09

Notes: K, degrees of freedom; Loglik, log likelihood; $\Delta\mathrm{AIC}_c$, change in AIC_c in relation to the highest-ranked model; w_i, AIC_c weight. Site was used as a random effect in all models. Models were compared using Akaike's information criterion corrected for small sample size (AIC_c).

DISCUSSION

Our study of male Bachman's Sparrows in southeastern North Carolina revealed differences for key breeding demographic parameters in response to habitat loss and fragmentation. Male sparrows that occupied relatively isolated habitat patches were unlikely to acquire a mate during the breeding season, regardless of habitat quality at the local scale (i.e., vegetation structure and time since fire). In contrast, the probability of fledging offspring was not influenced by either local- or landscape-scale factors, despite the importance of vegetation conditions and frequent fire emphasized by previous studies (Haggerty 1998, Tucker et al. 2004, 2006), or the negative effects of habitat fragmentation for other nesting passerines (Robinson et al. 1995). We suggest that fragmentation leading to reduced pairing success may be a potential driver of the low occupancy rate and range contraction of Bachman's Sparrows recently observed in the same landscape (Taillie et al. 2015, 2016). Our work also builds upon an increasing number of studies demonstrating that habitat amount is the strongest predictor explaining patterns of avian richness, occupancy, and abundance (Smith et al. 2011, Davis et al. 2013, Carrara et al. 2015, Taillie et al. 2015).

Reduced pairing success for males in isolated habitat patches has been observed in migratory (Gibbs and Faaborg 1990, Burke and Nol 1998, Bayne and Hobson 2001) and resident birds (Cooper and Walters 2002, Robles et al. 2008) in a variety of fragmented ecosystems. Males in isolated patches may fail to acquire a mate because these areas are rarely encountered by dispersing females (the "disrupted dispersal" hypothesis; Dale 2001, Cooper and Walters 2002, Lampila et al. 2005, Robles et al. 2008). Female-biased natal dispersal is common in birds (Greenwood 1980), and females in fragmented landscapes may have difficulty undertaking natal movements and become "lost" from the breeding population when dispersal is unsuccessful (i.e., dispersal into areas lacking conspecifics; Dale 2001). This disruption of female dispersal may result in male-biased populations, which often occurs in small populations in decline (Dale 2001, Donald 2007, Morrison et al. 2016). In agreement with this hypothesis, we observed no females at two sites and only one female at four sites, all of which were small and isolated. Disrupted dispersal seems a plausible explanation for low pairing success of Bachman's Sparrows in our study, and such movements have been negatively impacted by fragmentation in a more mobile longleaf pine specialist, the Red-cockaded Woodpecker (*Picoides borealis;* Kesler and Walters 2012). We propose that future studies experimentally translocate females to unpaired males in isolated and continuous landscapes (Cooper and Walters 2002) to assess whether disrupted dispersal is a possible explanation for low pairing success in Bachman's Sparrows. Additionally, translocating territorial males (Jones et al. 2017) would help to determine which matrix types are limiting Bachman's Sparrow dispersal.

Females also might not choose to settle and pair with males in isolated patches due to the potentially lower quality of these areas (Cooper and Walters 2002). However, we accounted for several measures of habitat quality (i.e., territory-level vegetation variables and time since fire) in the pairing success analysis and did not find support for these factors. Earlier work showed that breeding productivity was greatest for Bachman's Sparrows in areas burned within 1–3 yr and declined significantly after 3 yr (Tucker et al. 2006). Although time since fire exceeded 3 yr for ~30% of unpaired males and was longer on average for unpaired males (2.71 ± 2.60 yr) than paired males (1.60 ± 1.49 yr), differences were not significant. Three of the sites containing mostly unpaired males and lacking frequent prescribed fire had groundcover vegetation maintained by other means (e.g., recent mowing or clearcutting), which might explain why time since fire and vegetation variables were not significant in the current study.

Male quality (Cooper and Walters 2002) and breeding experience (i.e., male age; Bayne and Hobson 2001, Dale 2011) also can be important determinants of pairing success. However, we did not consider the influence of male quality in this study, and evaluating the effect of male age was not possible because adult Bachman's Sparrows can be classified only as after-hatch-year (Pyle 1997). Nevertheless, data from several males monitored in successive years did not indicate that breeding experience was related to pairing success in this study; two males banded as nestlings in 2014 bred successfully as adults the following breeding season, and six males banded in 2014 and subsequently monitored in 2015 were unpaired and at least 3 yr old.

We documented no evidence for an effect of habitat amount on fledging success, which was consistent with previous work that showed daily nest survival was similar in fragmented and relatively continuous landscapes in the Coastal Plain of North Carolina (Winiarski et al. 2017). Additionally, Brown-headed Cowbirds (*Molothrus ater*) parasitized only ~11% of Bachman's Sparrow nests in the Coastal Plain (J. M. Winiarski, *personal observation*), and low levels of brood parasitism have been reported elsewhere for the species (Haggerty 1988, Stober and Krementz 2000, Tucker et al. 2006). Further, the probability of fledging ≥1 offspring was high for paired males in the current study, regardless of habitat amount in the surrounding landscape. Therefore, our findings suggest that mechanisms contributing to the decline of some passerines (i.e., higher rates of nest predation and brood parasitism; Robinson et al. 1995) may not pose the most significant threats to Bachman's Sparrow populations. It is unclear whether this difference owes to the species' well-hidden nests and cryptic breeding behavior, or whether nest predators are more sensitive to habitat fragmentation than Bachman's Sparrows. However, we also acknowledge that low pairing success leads to the discovery of few nests in the most isolated study sites, which may have limited our ability to detect whether fledging success was lower in these locations.

For Bachman's Sparrow, it remains uncertain which demographic parameters are contributing the most to population change and how they are affected by landscape continuity. For Willow Warblers in Britain, fragmentation leading to small and declining populations with male-skewed sex ratios (and consequently low pairing success) could be driving reduced productivity and population declines (Morrison et al. 2016). Although reduced pairing success may be a potential driver of Bachman's Sparrow declines in our fragmented study system in North Carolina, population growth in a variety of bird species is generally most sensitive to changes in adult survival (Sæther and Bakke 2000), and previous work suggests this pattern may apply to Bachman's Sparrow populations. Pulliam et al. (1992) reported that adult survival and juvenile survival were the most important vital rates for Bachman's Sparrow population growth from a spatially explicit simulation model, and adult survival had a stronger influence on population growth than annual productivity for Bachman's Sparrows in an old-growth longleaf forest in Georgia (Cox and Jones 2010). However, both studies selected reproductive rates from the literature and assumed that juvenile survival maintained constant population growth ($\lambda = 1.0$). Therefore, obtaining accurate estimates of reproductive success and other demographic rates (i.e., adult and juvenile survival) is necessary to gain a better understanding of Bachman's Sparrow population dynamics and to implement effective conservation strategies. Alternatively, it is plausible that Bachman's Sparrow declines in this region could simply be the product of extensive habitat loss rather than altered demographic processes within remnant longleaf pine patches.

Conservation implications

In the rapidly urbanizing southeastern United States, wildlife species associated with open pine woodlands, such as Bachman's Sparrow, are likely to experience among the highest rates of habitat loss under future land-use scenarios (Martinuzzi et al. 2015). Urban sprawl in this region is expected to double or triple within the next 50 yr, placing already vulnerable species at further risk by decreasing habitat amount and hindering management actions (i.e., prescribed fire) that are necessary to maintain open pine ecosystems (Terando et al. 2014). In light of these recent studies, understanding the effects of landscape transformation on Bachman's Sparrow demographics will become increasingly critical. Promoting breeding opportunities, and perhaps long-term persistence of this species, depends on the conservation and management of all remnant patches of longleaf pine communities (particularly with frequent prescribed fire; Tucker et al. 2004, 2006), and—more importantly—increasing landscape-scale habitat amount. Our results suggest that managers should focus restoration and management activities in landscapes comprised of ≥20% habitat (~560 ha) within 3 km to ensure high pairing success (~100%) for male Bachman's Sparrows. This threshold in habitat amount is also important in determining Bachman's Sparrow occurrence on the landscape (Taillie et al. 2016). Without such a regional approach to Bachman's Sparrow conservation, efforts may fail to accommodate the species and other longleaf pine inhabitants despite suitable conditions at the local scale.

ACKNOWLEDGMENTS

Funding for our research was provided through the Wildlife Restoration Act and the North Carolina Wildlife Resources Commission with matching funds from the Fisheries, Wildlife, and Conservation Biology Program at North Carolina State University. We thank A. Bartelt, D. Bernasconi, A. Bledsoe, S. Masecar, M. McAlister, T. Root, M. Seamster, and M. Wallgren for assistance in the field. A. Carl, R. Hudson,

H. McIver, and L. Starke granted site access and provided valuable fire data and logistical assistance. We thank the North Carolina Wildlife Resources Commission for providing access to Bachman's Sparrow presence data. Comments by C. Lepczyk, C. DePerno, and two anonymous reviewers greatly improved an earlier version of the manuscript.

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