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Research Paper

Bachman's Sparrow (*Peucaea aestivalis*) response to variation in the extent of burns conducted during the nesting season

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ABSTRACT. Bachman's Sparrow (*Peucaea aestivalis*), an endemic North American passerine, requires frequent (≤ 3 yr) prescribed fires to maintain preferred habitat conditions. Prescribed fires that coincide with the sparrow's nesting season are increasingly used to manage sparrow habitat, but concerns exist regarding the effects that nesting-season fires may pose to this understory-dwelling species. Previous studies suggested that threats posed by fires might be lessened by reducing the extent of prescribed fires, thereby providing unburned areas close to the areas where fires eliminate ground-cover vegetation. To assess this hypothesis, we monitored color-marked male Bachman's Sparrows on 2 sites where the extent of nesting-season fires differed 5-fold (> 70 ha vs. < 15 ha). Monthly survival for males did not differ between the large- and small-extent treatments, and survival rates exceeded 90% for all months except one during the second year of our study when fires were applied later in the season. Male densities also did not differ between treatments, but treatment-by-year interactions pointed to effects relating to the specific time that fires were applied. The distances separating observations of marked males before and after burns were smaller on small-extent treatments in the first year of study but larger on the small-extent treatments in the second year of study. Burn extents also had no consistent effect on postburn reproductive status. The largest extent we examined could have been too small to affect sparrow populations, but responses may also reflect sustainable metapopulation dynamics in a setting where a large sparrow population is maintained at a regional scale ($> 100,000$ ha) using frequent prescribed fire (≤ 2 -yr return intervals). Additional research is needed regarding the effects that nesting-season fires may have on small, isolated populations as well as sites where much larger burn extents (> 100 ha) or longer burn intervals (> 2 yr) are used.

Réaction du Bruant des pinèdes (*Peucaea aestivalis*) aux variations de l'étendue des brûlis effectués durant la saison de nidification

RÉSUMÉ. Le Bruant des pinèdes (*Peucaea aestivalis*), un passereau endémique de l'Amérique du Nord, a besoin de feux fréquents (≤ 3 années) prescrits pour le maintien des caractéristiques préférées de son habitat. Les feux prescrits pendant la saison de nidification de ce bruant sont utilisés de plus en plus souvent pour l'aménagement de son habitat, mais leurs effets à cette période pourraient être préoccupants pour cette espèce des sous-étages. Des études antérieures ont indiqué que la menace posée par ces feux pourrait être amoindrie en réduisant leur étendue, fournissant ainsi des secteurs non brûlés près des secteurs où le feu a éliminé la végétation au sol. Afin d'évaluer cette hypothèse, nous avons suivi des Bruants des pinèdes mâles, marqués à l'aide de bagues de couleur, sur deux sites pour lesquels l'étendue des feux effectués durant la saison de nidification différait par un facteur de 5 (> 70 ha contre < 15 ha). La survie mensuelle des mâles n'a pas été différente entre les traitements de grande ou de faible étendue, et les taux de survie étaient supérieurs à 90 % pour tous les mois sauf un durant la seconde année de notre étude, lorsque les feux ont été allumés plus tard en saison. Les densités de mâles ont également été les mêmes entre les traitements, mais les interactions traitement-par-année ont montré des effets attribuables au moment précis où les feux ont été effectués. Les distances séparant les observations des mâles avant et après les brûlis étaient plus courtes dans les traitements de faible étendue lors de la première année de l'étude, mais plus grandes dans ces mêmes traitements lors de la seconde année. L'étendue des brûlis n'avait pas d'effet important sur le statut de reproduction post-brûlis. L'étendue de brûlis la plus grande que nous avons examinée était peut-être trop petite pour qu'elle ait affecté les populations de bruants, mais les réactions des oiseaux reflètent peut-être aussi des dynamiques stables de métapopulations permettant le maintien d'une grande population de bruants à l'échelle régionale ($> 100\,000$ ha) au moyen de feux prescrits fréquents (tous les deux ans ou moins). Davantage de recherches sont requises pour évaluer les effets que les feux en saison de nidification peuvent avoir sur des petites populations isolées, de même que sur des sites dans lesquels de plus grandes étendues sont brûlées (> 100 ha) ou encore des intervalles plus longs (> 2 années) sont privilégiés.

Key Words: *Bachman's Sparrow*; *longleaf pine*; *nesting season*; *Peucaea aestivalis*; *Pinus palustris*; *prescribed fire*; *site fidelity*; *survival*

INTRODUCTION

Longleaf pine (*Pinus palustris*) forests of the southeastern United States support some of the highest levels of species diversity in North America (Walker and Peet 1984, Clewell 1985, Hardin and White 1989, Drew et al. 1998). The diversity of longleaf forests is associated with a diverse ground-cover community maintained by frequent fires that occurred every 2-5 yr during seasonal periods of increased lightning activity (Bartram 1791 [1955], Ware et al. 1993, Glitzenstein et al. 2003, Huffman 2006). Prescribed fires now serve as surrogates for natural fires, and many prescribed fires are set during periods of peak lightning activity in an attempt to mimic the seasonal timing of historical fires (Seaman and Krementz 2000, Cox and Widener 2008).

Bachman's Sparrow (*Peucaea aestivalis*) is one of several species that is closely associated with the ground-cover community found in longleaf forests and consequently has life-history traits linked to frequent fire (Dunning 2006). Bachman's Sparrows forage and nest exclusively on the ground and typically do not occupy pine forests where fire has been excluded > 3 yr (Engstrom et al. 1984). Loss of open conditions at ground level, coupled with increases in woody shrubs, reduces habitat suitability for sparrows as postfire succession progresses, and suitable conditions may disappear \leq 18 mo following the application of prescribed fire (Jones et al. 2013). Frequent prescribed fire may also enhance food resources once vegetation has recovered (Cox and Jones 2009) as well as alter nest-predator communities (Jones et al. 2004). Fire suppression over the past 150+ yr has led to degradation of longleaf forests and range-wide population declines for Bachman's Sparrow; thus the Bachman's Sparrow is now listed as a species of conservation concern in every state in which it breeds (Dunning 2006).

Although preferred habitat conditions for this ground-nesting sparrow are best maintained using prescribed fire (Dunning 2006), the breeding season for Bachman's Sparrow overlaps broadly with the time when lightning-season fires occurred historically, ca. April-June in many areas (Cox and Widener 2008). This overlap has led to concerns about the effects that increased use of nesting-season fires may have on sparrow populations. Seaman and Krementz (2000) reported that all radio-tagged Bachman's Sparrows dispersed and never returned to a site where a nesting-season burn was applied. They also documented lower sparrow abundances following the application of the nesting-season fire. In contrast, Cox and Jones (2007) found that color-marked males whose territories were burned by nesting-season fires did not abandon territories at an accelerated rate when compared to marked males residing on unburned areas. Cox and Jones (2007) also found home-range extents before and after nesting-season fires to be similar for color-marked males monitored on burned and unburned areas.

The threat that nesting-season fires may pose to Bachman's Sparrows could vary in relation to multiple factors including (1) the extent of the area burned (Lyon et al. 2000), (2) the intensity of the fire (Lyon and Marzluff 1985), (3) the specific time within the nesting season that fires are applied (Shriver et al. 1999, Tucker et al. 2006), and (4) the burning conducted on adjacent areas (Seaman and Krementz 2000). Nesting-season burns likely affected large areas over evolutionary time periods (Huffman 2006), but a reduction in the extent of areas burned might offset

potential short-term impacts associated with burning because it would decrease the distance to unburned ground-cover vegetation. This hypothesis has been used to recommend small-extent burns in the management of some pine-grassland species (Wellendorf and Palmer 2009), but it has not been evaluated experimentally for Bachman's Sparrow.

We assessed the effects that the extent of nesting-season fires might have on Bachman's Sparrows by monitoring color-marked sparrow populations on 2 study areas where the extent of burns varied 5-fold. Both sites were dominated by mature longleaf pines and contained diverse, natural ground cover, but the prescribed fires conducted on one site averaged 10-15 ha in extent, whereas the fires on the second site were \sim 5 times larger and averaged 70-100 ha in extent. If small-extent burns lessen the effects of burns by providing greater heterogeneity of burned and unburned habitat, we predicted that Bachman's Sparrows associated with small-extent fires should have (1) higher survivorship; (2) greater reproductive potential, i.e., more evidence of breeding activity; (3) greater densities; and (4) higher site fidelity when compared to sparrows associated with large-extent burns. If these predictions hold, reductions in the extent of burns might help stabilize or reverse the population declines evident for some managed populations. On the other hand, a reduction in the area burned also has the potential to increase the time and resources needed to conduct prescribed fires and could reduce the area burned each year (Lyon et al. 2000). If so, the extra time needed to conduct small-extent burns could reduce the acreage treated annually and lead to a decrease in population sizes and stability. A better understanding of the impacts that fire extent may have on Bachman's Sparrow populations could help land managers evaluate trade-offs surrounding the manner in which prescribed fires are applied.

METHODS

Study areas

Our study was conducted on Pebble Hill Plantation (30°45' N, 84°0' W; Grady County, Georgia) and the Wade Tract (30°46' N, 84°5' W; Thomas County, Georgia). The study areas were managed by Tall Timbers Research Station, < 7 km apart, and dominated by mature (> 90-yr-old) longleaf pine woodlands. Ground cover across the study areas was dominated by wiregrass (*Aristida* spp.), runner oak (*Quercus pumila*), goat's rue (*Tephrosia* spp.), and other plants that can be eliminated by mechanical disturbance (Ambrose 2001), and this type of ground cover supports large sparrow populations (Rutledge and Conner 2002). Both study areas have also been maintained for decades using frequent prescribed fires, i.e., \leq 2-yr return intervals (Tall Timbers Research Station, unpublished data) and coincide with territories of the imperiled Red-cockaded Woodpecker (*Picoides borealis*), which is widely regarded as an indicator of mature pine forests in the southeastern United States (Jackson 1994). Management for mature timber, large areas of undisturbed ground cover, and the regular application of prescribed fires sustain large Bachman's Sparrow populations on both areas (Jones 2008).

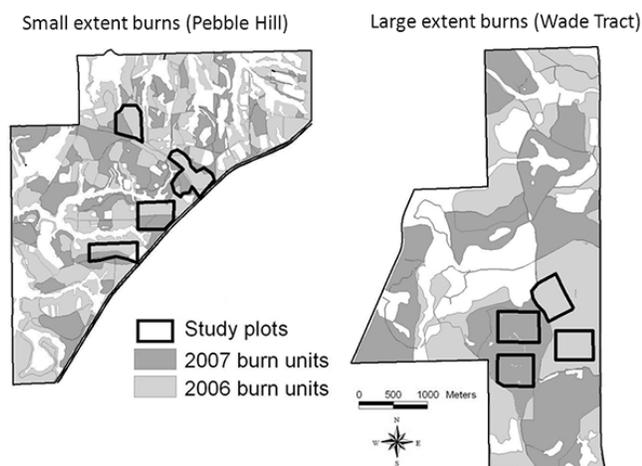
Fire treatments

Nesting-season prescribed fires were applied in 2006 and 2007. The earliest nest recorded in the region had eggs on March 26,

whereas the latest nest fledged young on September 22 (J. Cox, unpublished data). Fires were set on both study areas during a 10-d period spanning the last week of April and the first week of May in 2006. Drought conditions during 2007 delayed the application of fire until June, but all burns in 2007 were also conducted during a 10-d period on both study areas. This type of annual variation is common on managed lands in the southeastern United States, and, because of the biennial burn regimes used, areas treated with prescribed fires in 2006 were previously burned in 2004, and areas treated in 2007 were previously burned in 2005 (Tall Timbers Research Station, unpublished data).

Large burn compartments (70-100 ha) were located in and around the large-extent study area on the Wade Tract, and smaller burn compartments that ranged 10-15 ha in extent were located on Pebble Hill (Fig. 1). Prescribed fires typically remove > 85% of the ground cover (Tall Timbers Research Station, unpublished data), and the smaller burn extents used on Pebble Hill provided unburned ground-cover vegetation within 150 m of all areas burned. In contrast, the larger burn units used on the Wade Tract created > 50 ha of cleared ground \geq 150 m from unburned vegetation. A large sparrow territory in this region typically spans ~150 m (Cox and Jones 2009).

Fig. 1. Study plots and burn units for small-extent burns and large-extent burns. Large burn units (70 - 100 ha) were located in and around the large-extent study area on the Wade Tract, and smaller burn compartments that ranged 10 - 15 ha in extent were located on Pebble Hill. Plots on the large-extent study area were either burned or not burned during the 2-yr study, whereas plots on the small-extent study area were only partially burned each year.



On each of the 2 study areas, sparrows were monitored on 4 plots that each encompassed 15-24 ha (N = 8). Each plot was capable of supporting 15-25 territories (Cox and Jones 2007). Plots on the large-extent study area were either burned or not burned during the 2-yr study, whereas plots on the small-extent study area were partially burned (ca. 50%) each year (Fig. 1). The experimental design could have been improved by randomly assigning burn treatments to plots; however, the property-based treatments were dictated by the management goals in effect and use of established trails as fire breaks.

Mark-resighting and density estimations

Target netting (Jones and Cox 2007) was used to mark males using a unique combination of 3 plastic color bands and a single federal band. Marked individuals were resighted during weekly surveys of each plot conducted from late March through September. We also searched a 200-m area surrounding each plot to resight males whose territories fell along plot boundaries. Color-band combinations were determined using spotting scopes, and locations of marked males were recorded using a handheld Trimble Geo XM global positioning system (GPS) accurate to within 5 m. Locations (N = 2161 in 2006; N = 1738 in 2007) were processed for analysis using a geographic information system (GIS; ESRI 2006). Individual surveys typically lasted 5-6 h and were conducted on a rotational basis among plots. We also tallied observations at the end of each month and conducted additional surveys to locate color-marked individuals not yet sighted that month. Following Cox and Jones (2010), additional surveys (2-3 per month) were also performed 0.2-2 km outside study plots to locate dispersed individuals, hereafter called off-plot surveys. Off-plot surveys were performed by walking through suitable habitat, playing Bachman's Sparrow vocalizations intermittently, and recording locations of marked and unmarked males using a GPS.

Sparrow abundances were estimated for each plot using spot-mapping techniques similar to those used elsewhere for Bachman's Sparrow (Shriver and Vickery 2001). We walked transects spaced 100-150 m within each plot each month and played recordings of male songs to solicit territorial behavior. Most (> 90%) individuals encountered during these surveys were identified using their color bands to avoid double counting. Locations were georeferenced using GPS and entered into GIS so that density estimates could be made for each month based on the number of individuals observed in each plot and the total area surveyed. Because of differences in the months in which fires were applied during the 2-yr study, density estimates were pooled by study site and treatment and averaged for all months prior to and after burn treatments. Two months of observations preceded treatments, and 3 mo of observations followed treatments in 2006. In 2007, 4 mo of observations preceded treatments, and 2 mo followed treatments.

Movement and reproductive status

We used two procedures to assess the potential effects that nesting-season burns had on male movements. First, we used GPS to georeference all observations of marked birds and then calculated the average x,y coordinates for locations recorded prior to burns and locations recorded after burns, hereafter called pre- and postburn centroids, respectively. The minimum distances separating pre- and postburn centroids were determined using GIS (Cox and Jones 2007). We also used GIS to calculate the maximum distance among all recorded observations in a given year in an attempt to identify long-distance movements that might have been induced by burns. Following Cox and Jones (2007), we used maximum movements > 300 m to identify potential long-distance movements attributable to the burns. A causal relationship between long-distance moves and burns was inferred when a marked individual held a stable territory prior to burns but then moved > 300 m within 2 wk following the burn and remained for the rest of the breeding season. Otherwise, the long-distance moves we observed were attributed to factors other than burning.

The territories held by some marked individuals were not completely burned. Variation in the vegetation retained could influence responses independent of burn extent treatments. To assess the effects that fires had on individual territories, we created home-range polygons using the locations recorded for marked males observed ≥ 10 times prior to burns and 95% fixed kernel procedures provided by Hooge and Eichenlaub (1997). Areas of ground-cover vegetation that did not burn were digitized after each burn using GPS and entered into GIS (minimum patch size = 0.05 ha). Unburned patches were cross-tabulated with home-range polygons to quantify the extent to which the ground-cover vegetation within each territory had been removed by fire treatments. We classified territories as burned when $> 75\%$ of the ground-cover vegetation was removed and unburned when $\leq 25\%$ of the vegetation was removed. The number of observations used to create home-range polygons (≥ 10) was less than the number generally recommended for home-range studies (Ackerman et al. 1990); however, this minimum appeared to provide unbiased home-range estimations and enabled us to evaluate the effects that burns had on 59 individuals. An additional 17 individuals met our selection criteria in both years of our study. Therefore, to avoid pseudoreplication, we randomly selected only 1 yr of observations for these individuals.

We assessed reproductive potential for this same group of 59 males by monitoring each individual ≥ 10 min each week before and after burns to determine whether the individual was engaged in nesting activities. Although nests of Bachman's Sparrows are difficult to observe, unpaired males sing more frequently than males engaged in nesting activities (Sirman and Cox 2010), and the time allowed for observing each individual enabled us to observe the presence of females, males feeding young, and other behaviors associated with nesting (Sirman and Cox 2010). Based on the total observations accumulated for each individual before and after burns, we used a simple dichotomous classification to quantify the reproductive potential for individual males: (1) unpaired throughout the survey period or (2) engaged in nesting activities at some point during the survey period.

Statistical and survival analysis

Summary statistics and statistical tests were calculated using Systat (version 12.0) and program R (R Core Team 2012). ANOVA was used to assess changes in sparrow density by treatment across both years of study. This analysis was based on a 2-period crossover design (Grizzle 1965) because 2 treatments, i.e., prescribed fire and no fire, were applied to each study plot in alternating years. The approach has the advantage of allowing each study site to serve as its own control because each plot, or portion of the plot for the small-extent burns, receives both treatments. Potential carryover effects were minimal in this setting because (1) nest-site suitability for Bachman's Sparrow changes markedly within the first 12 mo following a burn (Jones et al. 2013) and (2) similar burn treatments were applied consistently for > 10 yr prior to this study.

Reproductive status, i.e., unpaired versus nesting, following burns was assessed using logistic regression. The 6-wk difference in the specific time that burns were conducted created variation in reproductive status by year with only 35% of males remaining unpaired following burns in 2006 compared with 48% in 2007. For this reason, we analyzed reproductive potential separately for each year and examined the influence of variables for the burn

extent of treatments, i.e., large or small; the amount of vegetation retained in a territory following a burn ($> 75\%$ or $< 25\%$), noting that some territories overlapped burned and unburned portions of the plot; and the reproductive status prior to burns, i.e., the success of individuals in securing mates, on whether an individual exhibited breeding evidence following burns.

A global model containing all predictors was created, and then subsets of the variables were used to construct candidate models. An information-theoretic approach (Burnham and Anderson 2002) was used to create and assess the relative fit of each model. The fit of each model was determined using Akaike's information criterion (AIC; Akaike 1973) with the small sample bias adjustment (AICc; Hurvich and Tsai 1989). Model averaging was used to incorporate uncertainty in model selection into the parameter estimates. Model-averaged estimates of the coefficients, standard errors, and 95% confidence intervals were calculated according to Burnham and Anderson (2002). Estimates of the regression coefficients and standard errors were weighted for each model according to their corresponding AICc weight and then used to compute a composite model. The composite model was composed only of parameters contained within the confidence set of models ($\Delta\text{AICc} < 2$).

ANOVA was used to test whether the distances that individuals moved following burns differed by burn extent treatments. Distance measures were log-transformed to satisfy normality assumptions, based on the Shapiro-Wilk test in Systat, and distances were then compared with three factors: large- or small-extent burn treatments, burned or unburned territories, and the year of the observations. Chi-square statistics were used to assess variation in the number of long-distance movements observed.

Cormack-Jolly-Seber (CJS) models within program MARK (White and Burnham 1999) were used to estimate monthly apparent survival for treatment groups and to assess the effects of fire extent on survival. CJS models allowed apparent survival estimates to be generated across all sampling periods without being constrained by the detection probabilities of individuals during a single sampling period. We analyzed each year separately because of the difference in the timing of the application of the fire between years. Models estimating survival were created based on a priori knowledge of habitat and demographic relationships suspected to be driving differences in survival and detection. The model with the lowest AICc value of all candidate models was selected as the most parsimonious model with the best fit. To account for overdispersion, 1000 bootstrap simulations were conducted to assess model deviance for the global model and estimate \hat{c} , the variance inflation factor that would be applied to AIC values (QAICc; Burnham and Anderson 2002) for those data showing evidence of overdispersion (i.e., $\hat{c} > 1$). No adjustments were made for data lacking evidence of overdispersion. All models with a $\Delta\text{QAICc} \leq 2$ of the best fitting model were considered part of the confidence set of models (Burnham and Anderson 2002); however, we reported the top 4 models.

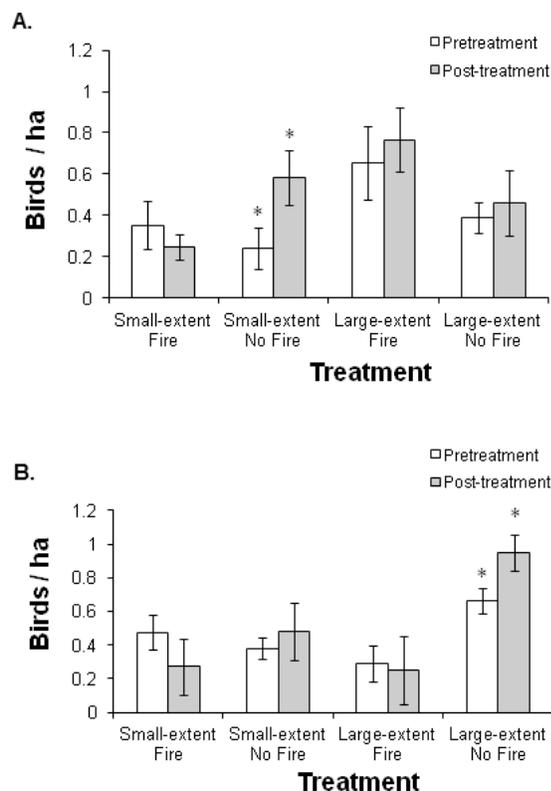
RESULTS

Density of males and reproductive status

The average density (ha^{-1}) of male Bachman's Sparrows prior to application of prescribed burns on small-extent plots was 0.36 (SE = 0.08) and 0.41 (SE = 0.05) in 2006 and 2007, respectively.

Baseline densities on large-extent plots generally were higher in both years with 0.57 (SE = 0.09) and 0.54 (SE = 0.15) males in 2006 and 2007, respectively. Changes in the densities of males following the application of prescribed fire differed by year and by fire extent (Fig. 2). In 2006 (Fig. 2A), densities on large-extent burns increased by 0.11 (SE = 0.09) males following burns, whereas densities on small-extent burns decreased by 0.11 (SE = 0.03) males. In 2007 (Fig. 2B), sparrow density on both large- and small-extent burns declined following fires. However, small-extent fires exhibited larger decreases (averaging 0.2 males; SE = 0.09), whereas large-extent fires decreased less (averaging 0.04 males; SE = 0.1). Changes in male densities observed on the large-extent plots were not significant ($F_{1,2} = 3.55$; $P = 0.21$); however, changes in density on the small-extent plots were significant ($F_{1,4} = 26.42$; $P = 0.01$). When the overall effect of fire extent was examined, significant changes in male densities occurred ($F_{1,8} = 20.84$; $P = 0.002$) relating to the lower densities observed after burns; however, a significant treatment-by-year interaction was also evident ($F_{1,8} = 5.6$; $P = 0.05$), indicating that the effect varied by year. Postburn densities were higher in 2006 but lower in 2007 (Fig. 2).

Fig. 2. Changes in density of male Bachman's Sparrows (*Peucaea aestivalis*) in 2006 (A) and 2007 (B) in response to large- or small-extent plots, pre- and postburn time periods, and burned and unburned fire treatments. Density estimates were pooled for months preceding application of prescribed fire and those following application. Error bars are 95% confidence intervals (*, significance at the 0.05 level).



The proportion of males observed engaged in reproductive activities following burns averaged 0.49 (± 0.34) over the course of this study. The average proportions observed on large-extent plots following burns were 0.52 (± 0.10) and 0.42 (± 0.83) in 2006 and 2007, respectively; whereas proportions on the small-extent treatments averaged 0.61 (± 0.17) and 0.52 (± 0.58) for the same time periods. The null model was present in the top models for the logistic regression analyses for reproductive evidence before and after the application of the burns (Table 1). The null model is an intercept-only model containing no predictor variables. Its presence in the top models indicates that it had a similar likelihood as the other models present in the confidence set. Model averaged parameter estimates for all parameters during both years were not significant (Table 2).

Table 1. Top models for predicting reproductive status of Bachman's Sparrows (*Peucaea aestivalis*) following the application of breeding-season prescribed fire. EXTENT distinguishes males associated with large-extent (70 - 100 ha burn blocks) or small-extent (< 15 ha) burn treatments. TERBURN (territory burned) distinguishes males that occupied home ranges where most ($\geq 75\%$) ground cover was removed by fires versus males that occupied home ranges where most ground cover was not removed by fires (at least 75% retained). PREPAIR males were those individuals that were paired or showed other evidence of breeding prior to burns.

Model	AICc	Δ AICc	AICcWt
2006			
null	51.02	0	0.33
EXTENT	52.23	1.21	0.18
PREPAIR	52.63	1.61	0.15
2007			
TERBURN	32.80	0	0.25
null	32.98	0.18	0.23
TERBURN + EXTENT	33.48	0.68	0.18
EXTENT	34.33	1.53	0.12

Male survival

Monthly survival estimates were based on 96 males monitored in 2006 and 115 males monitored in 2007. In 2006, the best model for male survival had constant survival, whereas detection probabilities varied by month (Table 3). This model was > 1.5 times more likely than other models that included burn extent and month-dependent survival and detection probabilities (Table 3). Based on the top model for 2006, the overall probability of monthly survival for all the males monitored was 0.93 (Table 4), and monthly detection probabilities varied from 0.48 during May-June to 0.81 during June-July. The May-June interval immediately followed the 2006 burns.

In 2007, the most parsimonious model indicated that survival varied by month and that detection probabilities varied by burn treatment (Table 3). This model was 8 times more likely than the next best model that contained monthly survival probabilities and constant detection probabilities. Estimates for monthly survival derived from this model were highest prior to burns in April-May (0.98, SE = 0.04) and lowest after burns from July to August (0.77, SE = 0.07) (Table 4). The probability of resighting differed

Table 2. Model-averaged parameter estimates from top models for predicting reproductive status of Bachman's Sparrows (*Peucaea aestivalis*) following the application of breeding-season prescribed fire. EXTENT distinguishes males associated with large-extent (70 - 100 ha burn blocks) or small-extent (< 15 ha) burn treatments. TERBURN (territory burned) distinguishes males that occupied home ranges where most ($\geq 75\%$) ground cover was removed by fires versus males that occupied home ranges where most ground cover was not removed by fires (at least 75% retained). PREPAIR males were those individuals that were paired or showed other evidence of breeding prior to burns.

	Estimate	Lower 95% CI	Upper 95% CI
2006			
EXTENT	0.693	-0.665	2.051
PREPAIR	0.709	-1.086	2.504
2007			
TERBURN	-2.094	-4.775	0.587
EXTENT	1.531	-0.821	3.883

Table 3. Model selection for the effects of nesting-season prescribed fire (BURN) and extent of fire (EXTENT) on male Bachman's Sparrows (*Peucaea aestivalis*) monthly survival during 2006 and 2007. The top five models are shown for each year, but the confidence set included only those models with a $\Delta\text{QAICc} < 2.0$. ϕ , probability of survival; p, probability of resighting; t, time dependence; •, constant.

Model	QAICc	ΔQAICc	QAICcWt
2006			
$\phi(\bullet)p(t)$	420.13	0	0.29
$\phi(\text{BURN})p(t)$	420.87	0.74	0.19
$\phi(\text{EXTENT})p(t)$	422.12	1.98	0.11
$\phi(t)p(t)$	422.14	2.01	0.11
2007			
$\phi(t)p(\text{BURN})$	555.37	0	0.64
$\phi(t)p(\bullet)$	559.53	4.17	0.08
$\phi(\bullet)p(t)$	559.95	5.58	0.07
$\phi(\text{EXTENT})p(t)$	560.29	4.92	0.06
$\phi(t)p(\text{EXTENT})$	561.34	5.94	0.03

between burned and unburned treatments with burned plots having a lower resighting probability (0.51, SE = 0.05) than unburned plots (0.67, SE = 0.04).

Male movement

The median displacement of pre- and postburn centroids across all years was 104 m ($\mu = 124$, SD = 132; N = 59). The median displacement on large-extent treatments was 112 m ($\mu = 122$, SD = 52; N = 18) in 2006 and 103 m ($\mu = 115$, SD = 84; N = 15) in 2007. The median displacement on small-extent treatments was 81 m ($\mu = 87$, SD = 38; N = 18) in 2006 and 116 m ($\mu = 235$, SD = 321; N = 8) in 2007. An ANOVA using the log-transformed distances separating pre- and postburn centroids indicated that significantly shorter postburn distances occurred on small-extent

Table 4. Estimated monthly survival for male Bachman's Sparrows (*Peucaea aestivalis*) in 2006 and 2007 based on the most parsimonious models provided in Table 3.

Year	Months	Survival probability	95% CI
2006	(constant)	0.93	0.87 - 0.96
2007	Apr - May	0.98	0.57 - 0.99
	May - June	0.94	0.74 - 0.99
	June - July	0.97	0.39 - 0.99
	July - Aug	0.77	0.59 - 0.88
	Aug - Sept	0.94	0.23 - 0.99

Table 5. Analysis of variance comparing the log-transformed distances separating pre- and postburn centroids calculated for color-banded males (n = 59) monitored in 2006 and 2007. Centroids represent the average x, y coordinates for observations collected for marked Bachman's Sparrows (*Peucaea aestivalis*) during each year of study. EXTENT distinguishes males associated with large-extent (70 - 100 ha burn blocks) or small-extent (< 15 ha) burn treatments. TERBURN (territory burned) distinguishes males that occupied home ranges where most ($\geq 75\%$) ground cover was removed by fires versus males that occupied home ranges where most ground cover was not removed by fires (at least 75% retained).

Year	Factor	SS	df	F-ratio	p-value
2006	Extent	0.334	1	7.838	0.009
	TERBURN	0.008	1	0.199	0.659
	Extent*TERBURN	0.109	1	2.560	0.119
	Error	1.376	32		
2007	Extent	0.408	1	6.002	0.024
	TERBURN	0.437	1	6.432	0.020
	Extent*TERBURN	0.380	1	5.587	0.029
	Error	1.291	19		

plots in 2006 (Table 5); however, postburn movements were significantly larger on small-extent plots in 2007. The vegetation not burned within a territory also influenced movements in 2007 (Table 5). Males on the small-extent plots whose territories were extensively burned in 2007 had the largest postburn movements of any category (Table 5).

Approximately 25% (N = 36) of the maximum within-year movements were long-distance moves (> 300 m). Although the number of long-distance moves was consistent from year to year ($X^2 = 1.092$; P = 0.296), more of the long-distance moves recorded on small-scale plots appeared to bear some relationship to burns ($X^2 = 8.916$; P = 0.003). For example, the percentage of long-distance moves observed on the small-extent plots within 2 wk of burns ranged from 57% (4 of 7) in 2006 to 89% (8 of 9) in 2007. In contrast, only 2 of the 11 (18%) long-distance moves recorded on large-scale burn plots in 2006 and only 3 of the 11 moves recorded in 2007 (27%) occurred within 2 wk after burns. Most (77%) long-distance movements recorded on the large-extent plots took place prior to burning. Differences in the total number of marked males encountered during off-plot surveys might bias

these results, but such encounters were equally distributed between small- and large-extent study areas ($N = 3$ on both study areas).

DISCUSSION

Although a reduction in the extent to which prescribed fires are applied might improve the retention and survival of Bachman's Sparrows after burns are completed, we failed to detect significant changes in the retention, breeding potential, and other response variables when burn extent was reduced from 70 ha to 15 ha. Male abundances generally were higher on areas where large-extent burns were used, and male survival and breeding status were also similar under different burn-extent treatments. There were differences in the postburn movements recorded for males, but the results were inconsistent across years. The smallest and largest postburn movements occurred on the small-extent plots. These results likely reflect the complex relationship among fire frequency, habitat quality, territoriality, metapopulation dynamics, and the life-history traits of a species that evolved in a setting where large-extent burns occurred frequently.

Vegetation features associated with Bachman's Sparrow nest sites are highly ephemeral as postburn vegetation succession proceeds (Jones et al. 2013). Open ground is an important structural feature that enables sparrows to move freely at ground level and also find food. Suitable ground-level conditions become scarce in the setting studied within 18 mo following a burn as vegetation grows and accumulates (Jones et al. 2013). As a result, the areas that were burned each year in this study had less suitable nest-site conditions at the outset of the breeding season because those areas had been burned ~2 yr previously. This difference likely accounted for the long-distance movements observed prior to burns on some of our plots. Conversely, the areas that were not burned during our study had preferred nest-site conditions because those areas had been burned ~10-12 mo earlier. This recurring and rapid shift in habitat suitability has implications for the areas that sparrows might use because an implicit assumption underlying the potential advantages of small-extent burns is that unburned areas proximate to the areas burned are available to individuals displaced by burns. As noted by Seaman and Krementz (2000), this assumption will not hold in areas where territorial male Bachman's Sparrows actively defend space against intruders. We did not quantify territorial interactions following burns, but territorial defense is expected to be more intense on areas with higher quality nest-site conditions (Koronkiewicz et al. 2006). In addition, the largest postburn movements we observed occurred on the small-extent burn treatments in 2007 and frequently involved dispersal to other study plots (75% of observations), not movement into the nearest block of unburned vegetation (25% of observations).

On sites where longer burn intervals are used to manage sparrow habitat, e.g., ≥ 3 -yr return intervals, we hypothesize that sparrow responses could differ because the juxtaposition of preferred and less preferred ground-cover characteristics would be more complex. In these settings, prescribed fire would be applied to areas with 3 yr of postfire growth, i.e., lowest quality; whereas areas with 1 yr, i.e., highest quality, and 2 yr, i.e., medium quality, would exist nearby. Sparrow densities and territorial interactions should be lower in the 2-yr patches and thus provide better refuge for individuals displaced by fire. In addition, because Bachman's

Sparrows appear to maintain year-round territories (Cox and Jones 2009), territorial exclusion could affect postburn settling patterns when prescribed fires are conducted outside the breeding season.

Reduced reproductive potential is frequently cited as a drawback associated with nesting-season burns (Seaman and Krementz 2000). We quantified indirect measures of productivity and found no differences attributable to the extent to which nesting-season fires were applied. In 2006, the proportions of males observed engaged in nesting activities were similar across extent treatments, and most males failed to engage in nesting activities until after the burns were conducted early in the breeding season. In 2007, the proportions of males engaged in nesting activities again were similar across treatments, but most males secured mates prior to the burns conducted. The proportions of males we observed engaged in breeding attempts were similar to those reported elsewhere (Tucker et al. 2006, Sirman and Cox 2010). Furthermore, Jones et al. (2013) found that the vast majority of the sparrow nests constructed in this region occurred on areas with 1 yr of postburn growth rather than areas that had 2 yr of postburn growth. Rapid postburn plant succession creates dense ground-cover conditions that reduce foraging and nest-site suitability (Jones et al. 2013). Fires thus effectively increased the reproductive potential of the areas that were burned and likely improved nesting conditions for the following year.

Bachman's Sparrows exhibit several life-history traits that appear to be shaped by the frequent, large-extent fires that have been prevalent in longleaf ecosystems over evolutionary time periods (Huffman 2006). One such trait is the capacity to track the shifting and ephemeral resources created by fire. Several marked males ($N = 6$) that were holding territories on sites scheduled for burns abandoned the territories before burns were applied, whereas others moved into burned areas soon after treatments were applied. As is the case with the vegetation associated with nest sites, food items sought by Bachman's Sparrows can vary markedly in relation to application of prescribed fires (Clewell 1989, Duever 1989, Platt et al. 1991), so these pre- and postburn movements likely were associated with attempts to find new areas with better nest-site conditions and/or food resources. Bachman's Sparrows also have been observed establishing territories within days following a nesting-season burn and remaining on these areas throughout the remainder of the breeding season (Shriver and Vickery 2001, Tucker et al. 2006). Although frequent movement may be equated with lowered habitat quality in some species (Winker et al. 1995), for species that reside in ephemeral habitats, movement is essential for tracking shifting resources and may be an imprecise gauge of habitat quality and responses to ecological disturbances.

Additional life-history traits associated with frequent fire include high survival, an extended nesting season, i.e., March to September in this area, and multiple broods (Haggerty 1994). The monthly survival rates we observed were similar to the values reported for sites that were not subjected to burns (Krementz and Christie 1999, Stober and Krementz 2000). We also recorded postburn reproductive activity across both sites in both years of study. Collectively, high survival and mobility can combine to form a stable metapopulation provided that subpopulations intermittently function as sources (Hanski et al. 1996). Adult

survival also has a larger influence on population growth rates in Bachman's Sparrow than does annual productivity (Cox and Jones 2010), so a loss in productivity could be offset by enhanced productivity or survival in months or years following prescribed fire (Tucker et al. 2004).

Interaction effects between extent of treatments and year were observed in comparisons of male densities and postburn movements. The lower male densities, monthly differences in survival, and greater postburn movements observed in 2007 suggested that the specific time that nesting-season fires were applied, which was later in the season because of drought delaying initiation of fire, probably influenced sparrows more so than the extent to which fires were applied. The higher preburn reproductive indices recorded in 2007 also suggested that the later timing of fires likely enabled many males to complete initial nesting attempts. Based on observations of nest success (Jones et al. 2013), we do not think that the drought influenced nest success or other reproductive activity on our study areas. However, our study only took place over the course of 2 yr, and additional investigation of the influences of drought on Bachman's Sparrow demographics and habitat management is warranted. Historically, fires likely occurred under a great range of weather conditions and burned for several days or weeks, including nighttime periods when higher relative humidity and lower wind speeds would lower fire intensity and likely create a greater patchwork of burned and unburned ground-cover vegetation relative to areas burned during daylight hours with lower relative humidity. Variation in bird responses to such subtleties will be difficult to assess, but these factors may have greater importance than the extent to which fires are applied.

The burn extents used in this study may have been too small to have an effect (Wiens et al. 1986); however, other studies have reported extent-related effects in situations where much smaller differences in burn blocks were used (Wellendorf and Palmer 2009). Martin (2009) studied the effects of fire extent on the nesting success and survival of the Northern Bobwhite (*Colinus virginianus*) using burn extents similar to those we used. Martin (2009) found that fire extent had some bearing on quail demographics but that it was inconsistent and generally less important than weather and other factors. Management for the Northern Bobwhite often strives for small improvements in demographic parameters to help improve recreational hunting. Management for the maintenance of sustainable populations is the common goal for Bachman's Sparrows, and this goal can be achieved using burn blocks much larger than those needed to improve quail numbers.

The amount of unburned vegetation remaining in a territory did not influence reproductive success in our study; however, male displacement distances were shorter on small-extent plots during 2006 and longer during 2007. Additionally, there was an interaction between the extent of burns and proportion of territory burned during the second year of our study in 2007. We suspect that drought conditions, which delayed the application of prescribed fires in 2007, likely resulted in the increased distances we observed on the small-extent plots. Those territories with little or no unburned patches remaining resulted in large movements. In drought years especially, applying prescribed fire in a manner that leaves some unburned patches behind, i.e., applying fire when

relative humidity is high, may decrease displacement distances, but further study is needed.

The relationships between prescribed fire and Bachman's Sparrow population dynamics are complex and require comprehensive assessments of survival, reproduction, and other demographic variables over multiple years. The abandonment of territories monitored by Seaman and Krementz (2000) led them to conclude that nesting-season fires had negative effects. We observed several males (N = 5) abandoning territories both before and after fires were conducted, and we suggest that these males may have abandoned territories for different reasons. Preburn abandonment likely occurred in response to the loss of suitable nest-site conditions as postburn succession progressed (Jones et al. 2013), whereas postburn abandonment likely occurred because of the vegetation removed by fires. Additional study is also needed in situations where small, isolated populations occur. The region we studied supported a large regional sparrow population that extended over > 100,000 ha (Cox et al. 2001). The effects of large-extent burns likely will differ in areas with longer burn rotations, less productive soils, and/or small, isolated sparrow populations. Even so, nesting-season burns will not likely threaten Bachman's Sparrow populations if the burns make up part of a comprehensive burn program that strives to achieve frequent burn intervals. Nesting-season fires can help to increase the acreage burned each year, and because small-extent fires can increase the time and effort needed to complete a burn (Lyon et al. 2000), we recommend that land managers conduct burns to the extent needed to achieve \leq 3-yr fire-return intervals but also monitor their sparrow populations to ensure population growth and persistence under these treatments.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/632>

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