Bachman’s Sparrow survival and nest predation response to a hardwood canopy reduction experiment

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Citation: Malone, K. M., T. M. Terhune II, and K. E. Sieving. 2021. Bachman’s Sparrow survival and nest predation response to a hardwood canopy reduction experiment. Ecosphere 12(5):e03389. 10.1002/ecs2.3389

Abstract. Where historical fire regimes have been disrupted, reduction in woody vegetation is often used to maintain or restore habitat for grassland and early successional birds. In pine savanna ecosystems of the southeastern USA, mechanical hardwood canopy reduction can restore pine savanna communities and is often employed on privately owned lands to improve habitat for the Northern Bobwhite (Colinus virginianus), although scant empirical evidence exists of its effects on target or non-target species. We measured the response of a pine savanna specialist, the Bachman’s Sparrow (Peucaea aestivalis), to large-scale hardwood reduction in a before–after–control–impact design on two properties where two-year fire-return intervals were established and the Bachman’s Sparrow population was stable. We investigated the effects of mechanical hardwood reduction on Bachman’s Sparrow daily nest survival, cause-specific nest mortality and adult male annual survival. During the four-year study, we monitored 107 Bachman’s Sparrow nests, recorded 49 nest predation events, and banded 113 adult male Bachman’s Sparrows. We found Bachman’s Sparrow nest and adult survival were resilient to changes in the hardwood canopy and did not differ significantly between treatment and control sites. Average annual adult male survival was 0.41 (0.32–0.52) and daily survival rate of nests with surveillance declined annually from 0.94 (0.92–0.96) to 0.88 (0.83-0.92). The identity of predators at nests was dominated by two snake species, black racer (Coluber constrictor) and corn snake (Pantherophis guttata). We found evidence for opposing treatment effects on the frequency of nest depredations by the dominant species; racers responded positively and corn snakes responded negatively. Our results suggest a moderate midstory canopy does not limit Bachman’s Sparrow vital rates when management includes frequent prescribed fire. Our results also suggest hardwood reduction to mitigate nest predation may be complicated with a diverse predator suite.

Key words: black racer; corn snake; mechanical hardwood reduction; nest survival; non-target species; Peucaea aestivalis; pine savanna; predator identity.

Received 14 January 2020; accepted 2 October 2020; final version received 8 December 2020. Corresponding Editor: Paige S. Warren.

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INTRODUCTION

Land management activities can have diverse effects on associated wildlife communities and populations (Van Lear et al. 2005). When management actions, including habitat manipulation, target a focal species, it is critical to assess the impacts on other native species (Gallo and Pejchar 2016). This information could provide insight to the response of target species (i.e., predator–prey interactions), elucidate potential unintended consequences for non-target species (Powell et al. 2000, Zarnetske et al. 2010), and provide better understanding of the overall community response to management actions. In pine savanna ecosystems of the southeastern United States,
management actions on private lands often aim to improve habitat for the Northern Bobwhite (Colinus virginianus), yet scant empirical evidence exists for the effects on non-target species.

Pine savanna ecosystems of the southeastern USA are extremely biodiverse (Engstrom 1993, Lubertazzi and Tscharnka 2003, Means 2007, Noss 2013, Peet et al. 2014), yet extremely threatened (Frost 2007). In much of the remaining southeastern pine savanna, the canopy and understory vegetation have been greatly altered since European settlement, largely from fire suppression, plowing, and hardwood encroachment (Van Lear et al. 2005). Frequent fire impedes hardwood encroachment, maintains an open, herbaceous understory, and is fundamental for the diversity of species and functions historically found in southeastern pine savanna (Mitchell et al. 2006, Noss 2013). Where short fire-return intervals (1–3 yr) have been maintained, mature hardwoods are mostly confined to riparian areas (Kirkman et al. 2004). During sustained periods of fire suppression, hardwoods reach mature stages and are no longer susceptible to low-intensity fire (Provencher et al. 2001). Some mesophytic hardwood species also create less pyric conditions in the understory (Kane et al. 2008). Management strategies aimed at reducing mature mesophytic hardwoods in previously fire-suppressed pine savanna may help to restore understory habitat for native fauna (Cram et al. 2002, Askins et al. 2007, Hiers et al. 2014, McIntyre et al. 2019). Avian and herpetological communities respond positively to restoring southeastern pine savanna by reintroducing fire and reducing hardwood canopy (Provencher et al. 2002, Steen et al. 2013a, b). However, where frequent fire is already established, the unique impacts of hardwood canopy reduction on population vital rates (survival and reproduction) of pine savanna specialists are largely unknown (but see McIver et al. 2012).

Hardwood encroachment can inhibit grassland bird populations (Bakker 2003, Thompson et al. 2016), often through increased predation (Winter et al. 2000, Blouin-Demers and Weatherhead 2001, Davis et al. 2019). In turn, hardwood reduction in pine savanna is considered a means to alter the community of adult and nest predators via changes in habitat use by predators or prey (Whittingham and Evans 2004, Kirby et al. 2016a, Jacques et al. 2017, Stevenson et al. 2018). Indeed, habitat management can be used to reduce predation by either increasing cover for prey (Schranck 1972), reducing breeding or perching sites for predators (Gibbons 2007, Kirby et al. 2016b), reducing edge habitat used by predators (Chalfoun and Martin 2009, Ellison et al. 2013), or increasing food resources for prey (Martin 1993). Predator responses to manipulations of habitat structure can include both functional (e.g., altered foraging patterns) or numerical shifts (e.g., emigration to higher quality habitat; Klug et al. 2010, Kirby et al. 2016a). Given that predation is the dominant cause of nest mortality for Bachman’s Sparrow (Malone et al. 2019), structural changes that modify nest predator encounter patterns are likely to influence nest predation rates and could, in turn, influence population trajectories (Lyons et al. 2015, Sedinger et al. 2016, Palmer et al. 2019).

In the Red Hills region of northern Florida and southern Georgia (Fig. 1), Bachman’s Sparrow (Peevace aestivalis) has been extensively studied in longleaf pine savanna with native ground cover dominated by wiregrass (Aristida beyrichiana; Cox and Jones 2007, 2009, Jones et al. 2013). Yet most of their remaining habitat in the Red Hills region consist of old-field ground cover on private lands that are intensively managed for the Northern Bobwhite (hereafter bobwhite) using frequent prescribed fire, year-round supplemental feeding, mechanical hardwood reduction, and mesomammal trapping. Management for bobwhites is thought to benefit Bachman’s Sparrow by creating and maintaining an open canopy and herbaceous ground cover and reducing mesomammalian nest predators. On private lands in the Southeast managed for bobwhites, mechanical hardwood reduction is often employed to increase bobwhite population density by (1) increasing the amount of habitat (Provencher et al. 2002) and (2) decreasing predation risk by removing habitat of common predator species such as arboreal snakes, raccoons (Procyon lotor), and avian predators that use dense canopy to stalk prey (Palmer and Sisson 2017). Mechanical hardwood reduction is costly, yet broadly applied; however, scant empirical evidence exists of its effects on target species (bobwhite) and non-target species.

We measured the response of Bachman’s Sparrow daily nest survival, cause-specific nest
mortality, and adult male annual survival to a large-scale hardwood reduction in a before–after–control–impact (BACI) study design. A manipulative study like this one is necessary to evaluate the outcomes of management, particularly for non-target species that are not regularly assessed. We hypothesized that changes in nest survival would be dependent on the predator species most common at nests during the study. Thus, we predicted that if semi-arboreal snakes such as corn snakes (*Pantherophis guttata*) and gray rat snakes (*Pantherophis spiloides*) or hardwood-associated mammals, such as raccoons (Kirby et al. 2016a, b), dominated as nest predators, then nest survival would increase following hardwood reduction. If grass-associated snakes and mammals like the eastern coachwhip (*Masticophis flagellem*), black racer (*Coluber constrictor*),
and hispid cotton rat (*Sigmoidon hispidus*) dominated as nest predators, we predicted that nest survival would decrease with hardwood reduction. Accordingly, we hypothesized that the species identity of nest predators would shift relative to hardwood reduction. Additionally, our demographic estimates for Bachman’s Sparrow represent the first reported on sites managed intensively for bobwhite, and we compare our estimates to those from studies outside of this management context.

**METHODS**

**Study site and experimental design**

The study took place on two properties owned and managed by Tall Timbers, located in northern Florida in the Red Hills physiographic region (Fig. 1). This region includes ~405,000 ha (approximately the area of Switzerland) and was historically dominated by longleaf (*Pinus palustris*) and shortleaf pine (*Pinus echinata*) savanna. Two study sites (one treatment, one control; each 400 ha) are on the Dixie Plantation property (Dixie hereafter; 3682 ha total) located in Jefferson County, Florida, and another treatment and control site (each ~300 ha) are located on Tall Timbers Research Station (TT hereafter; 1300 ha total) in Leon County, Florida. All study sites are predominately upland pine savanna with associated old-field understory vegetation maintained with frequent prescribed fire (1–2-yr fire-return interval) and comprised of hardwood saplings and herbaceous plants including native species and agricultural weeds. The upland canopy is dominated by loblolly pine (*Pinus taeda*) and shortleaf pine and includes longleaf pine along with a variety of oak species (*Quercus virginiana*, *Q. hemisphaerica*, *Q. nigra*, *Q. falcata*, *Q. alba*). Management activities conducted similarly throughout the study period across TT and Dixie properties included burning approximately half of the uplands in March–April, roller-chopping and mowing in the fall, and supplemental feeding for bobwhites every few weeks throughout the year. Frequent fire had been applied at both sites for >4 decades. Mesomammals including raccoons, nine-banded armadillos (*Dasypus novemcinctus*), Virginia opossums (*Didelphis virginiana*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) were trapped and killed from May to September during each year to relieve predation pressure on bobwhite nests. Traps were spaced at ~1 per 21 ha at TT and ~1 per 17 ha at Dixie and distributed evenly throughout the study sites, with equal effort between control and treatment sites. However, these trapping efforts reduce rather than eliminate mesomammalian activity (Jackson et al. 2018, Palmer et al. 2019). Raccoons were still the most common predator species at bobwhite nests (23% of depredations, *n = 30*) and mesomammals were the most common predator type at bobwhite nests during a concurrent video-surveillance study at TT and Dixie (K. M. Malone, personal observation).

We randomly assigned the treatment to one site at each property (Fig. 1). Hardwood trees were mechanically removed using a bulldozer from the 400-ha treatment site at Dixie in April 2016 and from the 300-ha treatment site at TT in April 2017. The other site at each property served as a control. On treatment sites, trees were knocked down, pushed into piles using a rubber-tired frontend loader, and then burned. Mature hardwoods were reduced to ~1 tree per 3 ha, which reduced the hardwood canopy at the Dixie treatment site by ~45.5%. At the TT treatment site, pine trees were also moderately thinned and harvested at the same time hardwoods were reduced, reducing the canopy at the TT treatment site by ~62%. Immediately following application of the treatment, sorghum, pearl millet, and browntop millet seed were broadcast over patches of bare ground that resulted from mechanical disturbance and the removal of trees. This was done to quickly restore vegetative cover to bare patches. Damage to the understory vegetation was localized, and most of the understory cover in the treatment sites remained intact. Native vegetation in the bare patches recovered by the following breeding season. Prescribed fire and other management practices were applied equally in control and treatment sites and throughout the duration of the study. We collected data on Bachman’s Sparrow in April–August each year from 2015 to 2018. Thus, data include one year of pre-treatment and three years of post-treatment at Dixie and two years of pre-treatment and two years of post-treatment at TT. We also collected data during all four years in both control sites.
Data collection

We searched for nests on four, 15-ha plots randomly placed in each treatment and control site at TT and Dixie (16 plots total; Fig. 1). We searched throughout the day, starting in mid-April and continuing through the end of August during each year of the study. We found nests using behavioral cues given by the parents and systematic searches by walking through vegetation to flush an attending parent. Nesting adults exhibit cryptic behavior but can be seen provisioning either nestlings or incubating females. We spent equal time and effort searching in treatment and control sites. We flagged nests with two small, pink flags tied close to the ground, each 2.5 m from the nest. We used video surveillance to monitor nest fate for a subset of nests. An observer checked nests every 1–5 d regardless of whether the nest was under video surveillance. We carefully avoided disturbing vegetation surrounding nests and creating paths leading to nests, and we minimized the time spent at or near nests. We considered a nest successful if at least one chick fledged. For most nests, we used video to determine the fate. For nests that were not monitored with video surveillance, we used the age of the nestlings, signs at the nest (fecal sacs present, nest intact) and in the surrounding area (i.e., parents provisioning fledglings or fledgling vocalizations) to determine nest fate. We visited nests without video surveillance more frequently during the late nestling stage to better determine their fate.

Video-surveillance systems were user-built and generally followed the recommendations of Cox et al. (2012). Cameras were small (10 cm long x 6 cm in diameter) and camouflaged and were placed 2–10 cm above the ground, a minimum of 30 cm from the nest entrance, and at an angle to the nest entrance. We used one of two weatherproof, day/night, 3.6-mm lens camera models at each nest (ZOSI CCTV ZG2116E, ZOSI Technology, Zhuhai, China or Rainbow NTSC BC70WIRC, Rainbow CCTV Integrated Products, Irvine, CA, USA). We used a 15-m cord to connect the camera to a digital video recorder and a 12-V battery that powered the system. The entire cord was covered in black, 2.5-cm Techflex (Techflex, Sparta, New Jersey, USA) to prevent damage from rodents. We disguised and partially covered the camera and cord using vegetation collected from the site (pine needles, dead leaves, sticks, etc.). For additional concealment, we covered the first 1 m of the cord closest to the nest in camouflage tape. The cameras used infrared light, which is discrete in the dark and likely not detectable by most predators (Sanders and Maloney 2002). We had a limited number of video-surveillance systems; if all surveillance systems were in use on other nests at the time a new nest was found, then it was not monitored with video surveillance.

We reviewed video using ALIBI (ALIBI Security, Austin, Texas, USA) and BORIS (Friard and Gamba 2016) software with the primary objective of identifying the predator species responsible for nest failure. If a partial depredation was evidenced from nest checks, then we also reviewed the video to identify the predator responsible for the partial depredation. For these nests, we targeted review to only a portion of the video until the predation event was seen. For each predation event, we recorded predator identity, date, and time of day. We reviewed video from a subset of nests (n = 22) from the first two seasons in full (not targeted for predation events only) using up to 16x viewing speed to detect attempted predation events where nest defense behavior was successful and therefore not detected using targeted reviewing. In our analysis, we include predators that were successful in nest depredation and predators that attempted nest depredation but were thwarted by a defensive parent.

From 2015 to 2018, we netted adult male Bachman’s Sparrows from late March to early June on the same 15-ha plots used for nest searching (Fig. 1), using recorded song playback to lure males into mist nets. We banded birds with a numbered aluminum United States Geological Survey band and a unique combination of three color bands and released them immediately. We performed surveys to re-sight marked birds from June to mid-August. Movements by males associated with prescribed fire (March and April) were likely done by the time we began surveys (Cox and Jones 2007). We walked through plots systematically along transects spaced every 60-m and used recorded song playback to increase resighting probability. We recorded any singing Bachman’s Sparrow that was using any part of the plot, and if banded, we recorded the band combination. We determined the presence of
bands and color combination using binoculars. We surveyed sparrows throughout the day, but mostly between 06:30 and 11:00. We did not survey in rain or excessive wind. We surveyed all 16 plots an equal number of times throughout a season and usually rotated through all plots within a 5-d period. Surveys were performed each year by the lead author of the study plus one additional, different observer each year. Within a year, plots were surveyed by both observers (i.e., plots were not assigned to a single observer), to minimize observer effects on re-sighting probability.

Data analysis
For analysis of nest survival, nest predator identity, and adult survival, we assessed the effect of the treatment using a BACI ratio, which provides an intuitive and straightforward interpretation of the results of a BACI study design and is directly applicable to management questions (Conner et al. 2016). We calculated the BACI ratio from Bayesian posterior distributions of estimates in treatment and control sites before and after the treatment was applied. These estimates were generated from a model including an interaction between a binary predictor for period (before or after treatment) and a binary predictor for treatment (treatment or control site). For each period (before and after), we divided the estimated posterior in the treatment sites by the estimated posterior in the control sites. We then had distributions of the ratio for before and after periods, and we divided the after-period ratio distribution by the before-period ratio distribution to get the BACI ratio (Conner et al. 2016). A BACI ratio <1 indicates a negative treatment effect, and a ratio of >1 indicates a positive treatment effect. We assessed the treatment effect using an 85% credible interval (CrI) of the distribution of the BACI ratio (Arnold 2010) and visual assessment of boxplots of the posterior distribution of demographic estimates in each site and period, with non-overlapping interquartile ranges indicative of group differences.

Additionally, we used deviance information criterion (DIC) model selection (Spiegelhalter et al. 2002) to infer treatment effects by comparing the following models: (1) an interaction between period (before or after) and treatment (treatment or control site), (2) annual changes, and (3) constant parameters through space and time. Models with only annual changes represented annual variation caused by factors other than hardwood reduction. We considered the model with the lowest DIC value and any model within two ΔDIC to be the best representation of the data.

We built and analyzed models using the program JAGS (Plummer 2013) implemented in R (3.3.3, R Development Core Team 2017) which deploys MCMC simulation to estimate parameters based on a posterior distribution. We used uninformative prior distributions for all parameters. We assessed convergence based on R-hat values and visual inspection of traceplots (Brooks and Roberts 1998).

Daily nest survival.—We used a Bayesian analysis of the logistic-exposure daily nest survival model (Royle and Dorazio 2008). Nest encounter histories consisted of observed nest states ($y_i,j$) for each nest ($i$) and daily interval of the nesting season ($j$), where $y_{i,j} = 1$ if a nest was active and $y_{i,j} = 0$ if it failed. The encounter histories informed survival, $\phi_i$, as

$$y_{i,j} \sim \text{Bernoulli}(\phi_i \times y_{i,j-1})$$

which we then modeled as a function of predictor variables using a logit link. For failed nests, this model treats intervals between the last check where the nest was known to be alive and the last check as missing data; thus, the probabilities for these intervals are regarded as parameters of the model and estimated from the posterior distribution by MCMC (Royle and Dorazio 2008). After the first two seasons of data collection, we used this model to test whether video surveillance affected daily nest survival by including surveillance as a binary predictor variable in our estimation of daily nest survival. With the first two seasons of data, there was no effect of surveillance; thus, we used surveillance on most nests found in the final two seasons (46 of 56 nests). We repeated this analysis with all four years of data and found that surveillance had a significant positive effect on daily nest survival ($\beta = 0.87, \text{CrI} = 0.18–1.53$), so we included this variable in all other models.

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2. Annual changes
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3. Constant parameters through space and time
1. constant survival through time and space: \( \phi_1 = \alpha \),
2. survival varied annually: \( \text{logit}(\phi_i) = \alpha + \beta_t \times \text{year}_i \),
3. survival varied as an interaction of treatment (treatment or control) and period (before or after): \( \text{logit}(\phi_i) = \alpha + \beta_1 \times \text{trt}_i + \beta_2 \times \text{period}_i + \beta_3 \times (\text{trt}_i \times \text{period}_i) \), where \( \text{trt}_i \) is a binary variable indicating a treatment site (before and after treatment = 1) or control site (0).

For analysis of each model, we initiated three MCMC simulation chains to estimate posterior distributions of model parameters based on 30,000 iterations and a burn-in of 15,000. We derived percent nest success by exponentiating the estimates of daily nest survival to the 22-d nest period (Haggerty 1988, Dunning et al. 2020).

Nest predator identity.—We used a multinomial generalized linear model (GLM) with a log link to analyze the impact of hardwood reduction on nest predator identity. For the response variable, we lumped predator species into four groups: (1) black racers (C. constrictor) and coachwhips (Masticophis flagellum), (2) species in the genus Pantherophis (including corn snakes and gray rat snakes), (3) mesomammals, and (4) other species (i.e., small mammals, avian, ants). We chose these groups based on the distribution of predator species we observed, the predator species’ ecology, and predicted response to the hardwood reduction treatment. We chose the other category as the reference category for the GLM analysis because we did not hypothesize the treatment to influence the frequency of observations in this category and the raw data indicated the number of observations was equivalent between treated and untreated sites.

Similar to the nest survival analysis, we compared the following models: (1) constant frequency for each predator category through space and time; (2) frequency for each predator category varied annually; and (3) frequency for each predator category varied by an interaction of treatment and period. We used three MCMC simulation chains to estimate posterior distributions based on 50,000 iterations and a burn-in period of 25,000.

RESULTS

Nest survival

We monitored 107 Bachman’s Sparrow nests (Table 1; \( n = 25, 26, 34, \) and 22 in each year of the study). Predation was the major cause of nest failure. Only one nest failed due to abandonment and we suspect it was due to disturbance by researchers. Despite equal nest searching effort across years and treatment and control sites, we only found two nests in the two seasons post-treatment in the treatment site at TT (Table 1).

The BACI ratio indicated there was no effect of the treatment on daily nest survival because CrIs overlapped 1 (mean = 0.96, CrI = 0.88–1.04).
Box plots of posterior distributions indicated daily nest survival was similar between before and after periods and in treatment and control sites (Fig. 2). The best model according to DIC included annual changes (Table 2); daily nest survival declined significantly with year ($\beta = -0.27, \text{CrI} = -0.52$ to $-0.02$; Table 3) starting at 0.94 ($\text{CrI} = 0.92$–0.96) in 2015 and declining to 0.88 ($\text{CrI} = 0.83$–0.92) in 2018. The probability of a nest with surveillance succeeding was 26%, 20%, 10%, and 6% in each consecutive year.

**NEST PREDATOR IDENTITY**

We monitored 83 nests with video surveillance and observed predators at 49 predation events. Snakes were the most common predators observed at nests (59%), followed by mesomammals (14%), small mammals (12%), Blue Jays (*Cyanocitta cristata*; 10%), and red-imported fire ants (*Solenopsis invicta*; 4%). Corn snakes and black racers were the most common snake predators, responsible for $31\%$ and $22\%$ of all observed predation events, respectively. Other snakes observed at nests include a coachwhip, a cottonmouth (*Agkistrodon piscivorus*), and two unidentified species. Mesomammals included coyotes (*Canis latrans*), bobcats (*L. rufus*), and one unidentified species. Small mammals included hispid cotton rats (*S. hispidus*), a cotton mouse (*Peromyscus gossypinus*), a Florida wood rat (*Neotoma floridana*), and one unidentified species. Most predators were effective in depredating nest contents, although on four of the 49 occasions, parents deterred the predator.

**Fig. 2.** Posterior distributions of estimates of daily nest survival rate (lower) and adult male annual survival (upper) of Bachman’s Sparrows at Dixie Plantation and Tall Timbers Research Station from 2015 to 2018 before and after treatment with mechanical hardwood reduction.

**Table 2.** Deviance information criterion (DIC) values for the three models that we compared to examine the influence of the hardwood reduction treatment on daily nest survival, nest predator identity, and adult survival of Bachman’s Sparrow at Tall Timbers Research Station and Dixie Plantation from 2015 to 2018.

| Model                  | Nest survival | Nest predator identity | Adult survival |
|------------------------|---------------|------------------------|----------------|
| Constant               | 388.5         | 137.6                  | 196.1          |
| Year                   | 383.5         | 140.6                  | 268.1          |
| Treatment $\times$ period interaction | 393.8 | 139.8 | 220.4 |

Note: Values in bold face indicate the lowest DIC.
The BACI ratios representing treatment effects on nest predator identity had poor precision did not indicate support for treatment effects on any predator type because CrIs overlapped 1 (racers, mean = 31.9, CrI = 0.12–91.1; corn snakes, mean = 0.40, CrI = 0.01–1.14; mesomammals, mean = 6.7, CrI = 0.17–17.5). Box plots of posterior distributions of frequency estimates indicated predator detections were approximately equal in control and treatment sites in the before period, but unequal in the after period (Fig. 3) and provide evidence for a treatment effect on nest predator identity. In the after period, the frequency of racer detections increased in treatment and control sites, but was higher in treatment sites (mean = 0.5, CrI = 0.28–0.72) than control sites (mean = 0.21, CrI = 0.11–0.33; Fig. 3). The frequency of corn snakes at nests in treatment sites decreased significantly from the before period to the after period and was lower in treatment sites (mean = 0.10, CrI = 0.01–0.25) than control sites (mean = 0.39, CrI = 0.26–0.52) in the after period (Fig. 3). Mesomammal detections in treatment sites did not change significantly between periods, although detections were more frequent in treatment sites (mean = 0.20, CrI = 0.05–0.39) than control sites (mean = 0.07, CrI = 0.02–0.15) in the after period (Fig. 3). The constant model was the best model indicated by DIC (Table 2).

ADULT SURVIVAL

We banded 113 adult male Bachman’s Sparrows during the four-year study and re-sighted 81 of them during at least one survey. We banded 57 adult males at Dixie (29 in the control, 28 in the treatment site) and 56 at TT (35 in the control, 19 in the treatment, two outside either site.

Table 3. Coefficients, standard errors (SE), and 85% credible intervals from the best model to explain variation in daily nest survival of Bachman’s Sparrow at Dixie Plantation and Tall Timbers Research Station from 2015 to 2018.

| Parameter | Mean coefficient estimate | SE  | 7.5% | 92.5% |
|-----------|---------------------------|-----|------|-------|
| Intercept | 1.80                      | 0.34| 1.17 | 2.52  |
| Surveillance | 1.02                     | 0.36| 0.31 | 1.70  |
| Year      | −0.27                     | 0.13| −0.52| −0.02 |

Fig. 3. Posterior distributions of estimates showing the frequency of each predator category observed at Bachman’s Sparrow nests at Dixie Plantation and Tall Timbers Research Station from 2015 to 2018, before and after treatment with mechanical hardwood reduction took place.
boundary). Of the 56 birds banded in the first year, 17, 10, and two were re-sighted in years two, three, and four, respectively. Of the 12 birds banded in the second year, four and two were re-sighted in years three and four, respectively. And of the 29 birds banded in the third year, 10 were re-sighted in year four. We did not find evidence that birds moved between treatment and control areas; re-sightings almost always occurred on the same plot that we banded the bird. On four occasions, we re-sighted a banded bird in a plot that was nearest the one we banded it in but within the same site.

The mean BACI ratio was 0.79 and CrIs overlapped 1 (CrI = 0.28–1.52), suggesting no effect of the treatment on adult survival. Box plots of posterior distributions indicated survival estimates were similar between control and treatment sites and changed little between periods (Fig. 2). The best model for detection probability included annual variability in detection, although CrIs overlapped among years. Mean annual estimates of detection probability ranged from 0.71 to 0.88. The best model for survival was the constant model and survival according to this model was 0.41 (CrI = 0.32–0.52; Table 2).

**DISCUSSION**

The effects on non-target species of habitat management practices directed at game species are not commonly monitored (Gallo and Pejchar 2016). To help address this dearth of information, we examined the impacts of hardwood reduction (a common technique for intensively managed bobwhite habitat) on vital rates and predator encounters at nests of Bachman's Sparrow. We predicted that mechanical reduction in mesophytic oak species might reduce hardwood-dependent predators and enhance terrestrial snakes benefiting from increased productivity in the understory layers released from shading (Perry et al. 2009). Given the complexity of the animal community that interacts with ground-nesting birds in this system (Ellis-Felege et al. 2012), we expected treatment effects on Bachman's Sparrow would depend on the dominance of predators at nests. We found evidence of a negative treatment effect on the most common nest-depreating snake species and no significant treatment effect on nest survival or adult survival in Bachman's Sparrow. Nest survival in the last years of our study and adult male survival were lower than in other studies conducted outside of the context of intensive bobwhite management (Cox and Jones 2007, 2010). Hardwood reduction, as implemented in this study, did not greatly enhance or decrease vital rates of Bachman's Sparrow. Our findings align with the few previous studies evaluating the effects of game management, in general, on non-game species; Gallo and Pejchar (2016) report 23% of studies (n = 26) found no effect on non-target species and an equal proportion found positive and negative effects. Our study represents a large-scale attempt at addressing these questions for pine savanna birds, with treatment plot sizes at least four times the recommended 100 hectares for avian population studies of relatively low-density tropical birds (Terborgh et al. 1990).

**Nest survival**

Bachman's Sparrow nest survival was not affected by hardwood reduction. While nest survival declined annually, this occurred in both control and treatment sites. However, we only found two nests in the treated area at TT, despite consistent search effort across years and sites and the occurrence of 13 nests in this area pre-treatment. This may be a result of early nest failures prior to discovery (Mayfield 1975), or because nesting efforts or breeding pair densities were affected by treatments. Either case implies a negative treatment effect that would not have been captured by our nest survival analysis. Nest survival is only one component of productivity and the components we did not measure may respond to hardwood reduction. For instance, if nesting density declined in treated areas, the overall effect of the treatment on productivity could be negative (Perot and Villard 2009).

Populations of some predator species may respond to structural changes following hardwood reduction at a time scale beyond the duration of our study. Morris and Conner (2016) found evidence that hardwood reduction decreased survival of artificial ground nests in fire-managed pine savanna, but not until 4–9 yr post-removal. However, the artificial nests in their study were intended to emulate bobwhite nests and were placed in the same location each year regardless of the microhabitat. Thus, their
predation rate was probably not representative of the cryptic ground nests in our study system. Other studies found time lags in avian nest response to cascading effects of changing density of predators or alternative prey (Ostfeld and Keesing 2000, Fiola et al. 2017). If some Bachman’s Sparrow predators respond numerically to structural changes following hardwood reduction, it may take longer than three years to see changes in nest survival.

Bachman’s Sparrow daily nest survival declined annually to a rate lower than reported in most previous studies. Annual variation in nest survival is typical for many species and could result from fluctuations in rainfall (Skagen and Adams 2012), predator abundance (Kurki et al. 1997), alternative prey abundance (Béty et al. 2002), insect availability (Zanette et al. 2003), or interactions of several factors (Morrison and Bolger 2002, Zanette et al. 2003). However, detecting causes of annual variation is beyond the scope of this study. We found most nests in the nestling stage, which is typical for this species and reflected in the nest survival estimates of previous studies. At two sites in the Red Hills (the closest geographic estimate), Jones et al. (2013) found daily nest survival was 0.96, considerably higher than our estimates for 2017 and 2018. These sites supported native ground cover burned every 1–2 yr and were not intensely managed for bobwhites like our study sites and most properties in the Red Hills region. On the northeastern periphery of the Bachman’s Sparrow range, on two sites managed for native pine savanna species, Winiarski et al. (2017) found daily nest survival rate of 0.94 and 0.95. Estimates from sites in central Florida dry prairie are similar to the last year of our study, at 0.89 (Perkins et al. 2003). Although these studies did not use surveillance cameras at nests, comparison to our study is valid because our analysis accounted for the effect of surveillance.

**Nest predator identity**

Hardwood reduction may have influenced the frequency at which different snake species visited Bachman’s Sparrow nests. While our sample sizes for each predator type were small and BACI ratio estimates were imprecise, we found opposing trends in frequencies of black racers and corn snakes at nests and evidence that the treatment had a negative effect on corn snakes and a positive effect on racers (Fig. 3). Perry et al. (2009) found that black racers in restored Arkansas pine savanna were associated with areas having less canopy cover and more ground level vegetation. Ellison et al. (2013) found that woodland-associated predators decreased in relative abundance while grassland predators increased following tree-row removal from grasslands. Fire can also influence predator-specific nest loss through structural changes in vegetation; Lyons et al. (2015) found that depredation of Grasshopper Sparrow (Ammodramus savannarum) nests by snakes (species unidentified), but not other predator types, was less likely in recently burned patches of grassland.

The frequency of mesomammals observed at Bachman’s Sparrow nests in treatment sites changed little following hardwood reduction (Fig. 3). We predicted depredations by raccoons would decrease (Kirby et al. 2016a, b), but we did not detect raccoons at Bachman’s Sparrow nests, despite their prevalence as a nest predator across studies, species, and locals (DeGregorio et al. 2014) and their presence and activity at our study sites (Malone 2019; Tall Timbers, unpublished data). The relationship between Bachman’s Sparrow nests and recent fires may explain this result, as they prefer nest sites burned within the last 12 months (Jones et al. 2013) and raccoons are less likely to forage in these areas (Jones et al. 2004). We did not have any strong expectations regarding the response of bobcats or coyotes to the hardwood reduction, yet these were the only mesomammalian species detected at nests. Mesomammal trapping is a ubiquitous management practice on large private properties that manage primarily for recreational bobwhite hunting across the Red Hills region. Outside of this regional management context, however, mesomammalian deprecation patterns at Bachman’s Sparrow nests may differ.

Nest depredations by red-imported fire ants did not increase following hardwood reduction and accounted for a very small proportion of nest depredations throughout the study. Red-imported fire ants associate with disturbed soil, such as that created by mechanical removal of hardwoods, and were the dominant predator of shrub nests in pine savanna in southern Georgia (Conner et al. 2010).
**Adult survival**

We did not find evidence that hardwood reduction affected annual survival of adult male Bachman’s Sparrows. This could be due to the duration of our study; annual fluctuations in adult survival are typical for many species and could mask any short-term impacts of the hardwood reduction. Long-term point count data at one of our study sites suggested the Bachman’s Sparrow population was stable (J. A. Cox, *personal communication*). Potential impacts of the treatment may take time to accumulate and could have greater implications in low density or isolated populations, which we were unable to explore in this study.

Our estimates of adult male survival are low compared with estimates by Cox and Jones (2007, 2010) from an old-growth tract of longleaf pine savanna in the Red Hills region. To our knowledge, no other studies using mark–resight data report annual survival estimates for comparison to our estimates. Cox and Jones (2010) recommended incorporating emigration into adult survival estimates for this species. Our sampling design allowed estimation of emigration from observations of banded males seen at a different site than their initial banding location (i.e., treatment vs. control at each property); however, we did not re-sight any banded birds indicative of movement between sites. Thus, we chose a survival estimator that did not incorporate emigration because it was not detected. However, movements could have gone undetected. If so, it would unlikely be enough to account for the difference in survival between this study (0.41) and that of Cox and Jones (2010; 0.68). Additionally, our estimate is low compared with another study, Cox and Jones (2007; 0.59), who used mark–resight data and the same model framework as this study (CJS model) to estimate adult male survival without incorporating emigration.

**Management implications**

Bachman’s Sparrow is an effective indicator species for management efforts aimed at restoring pine savanna vegetation structure to benefit a wide range of native species (McIntyre et al. 2019). This study suggests that mechanical hardwood reduction on sites with old-field ground cover that are managed intensively for bobwhite will not dramatically influence Bachman’s Sparrow populations via changes in vital rates. Combined with previous work on Bachman’s Sparrow fire-dependency (Tucker et al. 2004, Jones et al. 2013), our study suggests a moderate midstory canopy may not limit vital rates when management includes frequent prescribed fire. Although we were unable to explore it with this study, population density may be an important factor in cases where population restoration rather than maintenance is underway and small populations are a target of management. However, when considering restoration for Bachman’s Sparrow, managers should consider the financial cost of mechanical hardwood reduction (~$200 per ha) relative to prescribed fire (~$7.50 per ha). Long-term monitoring of Bachman’s Sparrow demographic rates on more properties would provide information on source-sink population dynamics in this region that is intensely managed for bobwhite. Low values of nest survival and adult survival in our study compared with previous studies on sites with native ground cover suggests possible differences in habitat quality for this species with strict requirements for ground cover characteristics (Dunning and Watts 1990).

Our results also suggest hardwood reduction may be an effective method to indirectly control some nest predators of ground-nesting birds when nest survival is limiting population growth. Habitat manipulation is often discussed as an alternative to lethal control of predators for endangered species or game species, although there are few published studies examining the efficacy of this strategy (Smith et al. 2010, Doherty and Ritchie 2017). This may be because data on cause-specific nest mortality is costly, but without it, it is difficult to distinguish the mechanism by which habitat improvements affect prey populations (Lyons et al. 2015). Inter-specific interactions among predators underscore the importance of monitoring nest predator identity, as these interactions are likely to be site- and community-specific and will influence the efficacy of efforts to reduce nest predation via habitat manipulation.

**Acknowledgments**

We thank the technicians who helped with field work and video review: Harrison Jones, Zachery...
Holmes, Camila Rodriguez, Lizabeth LaBriola, Karis Ritenour, Adriana Betancourt, Aaron Yappert, Lindsay Partymiller, Dylan Orlando, and Henry Brown. We thank Jim Cox for his guidance on Bachman’s Sparrow field techniques and for his feedback on an earlier draft of this manuscript. We also thank Bob Mc Cleery and Denis Valle for their feedback on an earlier draft. We thank the land management teams at Tall Timbers and Dixie Plantation for their logistical support in the field. Funding for this research was provided primarily by Tall Timbers and the University of Florida. This research would not be possible without funding provided through The Robert C. Balfour Game Bird Management Fellowship, Gerry Game Bird Endowment, and Pamela H. Firman Quail Management Research Initiative at Tall Timbers. The Florida Ornithological Society and American Ornithological Society also provided funding. Support also came from the USDA National Institute of Food and Agriculture, Hatch project #0215824, KES, PI. We carried out field activities for this study under the approval of institutional, state, and federal research permits. All authors conceived and designed the study. Theron M. Terhune and Kathryn E. Sieving provided funding. Kristen M. Malone collected and analyzed the data, with input from Theron M. Terhune. Kristen M. Malone wrote the first draft of the manuscript, and all authors contributed substantially to editing the manuscript.

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