




Fledgling Bachman's Sparrows in a longleaf pine ecosystem: survival, movements, and habitat selection

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Received 25 March 2020; accepted 3 August 2020

ABSTRACT. Fledgling ecology remains understudied for many passerine species, yet information about the fledgling life stage is critical for understanding full-annual life cycles and population recruitment. We examined the survival, habitat selection, and movements of fledgling Bachman's Sparrows (*Peucaea aestivalis*) in a longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) community managed with frequent prescribed fire. We captured and marked 36 fledglings on the day of fledging and used radio-telemetry to relocate them daily until independence during three breeding seasons (2014–2016). We visually confirmed the status of fledglings as live or dead during daily relocations and determined causes of mortality. We measured vegetation characteristics at fledgling locations and compared them to the characteristics of vegetation at the locations of adult males. We used a Known Fates analysis in Program MARK to estimate fledgling survival, and generalized linear mixed effect models to determine habitat selection. Estimated fledgling survival until independence was 0.31 (SE = 0.08), with most mortality during the first 4 d post-fledging. Fledglings with longer wing chords had higher rates of survival than those with shorter wing chords, possibly due to an increased ability to evade predators. Fledgling movements were restricted primarily to natal territories. Fledgling Bachman's Sparrows were located in areas with greater woody plant, forb, and grass cover and less bare ground than available in natal territories. Similar to fledglings of other songbirds, understory woody and herbaceous plants appear to provide critical cover for fledgling Bachman's Sparrows, and maintenance of such cover should receive consideration in management plans for longleaf pine communities.

RESUMEN. Volantones de Chingolo de Bachman en un ecosistema de pinos de hoja larga: supervivencia, movimientos y selección de hábitat

La ecología de los volantones permanece poco estudiada para muchas especies de paseriformes, sin embargo, la información sobre la etapa volantona de la vida es fundamental para comprender los ciclos de vida anuales completos y el reclutamiento de la población. Examinamos la supervivencia, la selección del hábitat y los movimientos del Chingolo de Bachman (*Peucaea aestivalis*) en una comunidad de pino hoja larga-pasto alambre (*Pinus palustris - Aristida stricta*) manejada con frecuentes incendios controlados. Capturamos y marcamos 36 volantones el día del abandono del nido y utilizamos radiotelemetría para reubicarlos diariamente hasta la independencia durante tres temporadas de cría (2014–2016). Confirmamos visualmente el estado de los volantones como vivos o muertos durante las reubicaciones diarias y determinamos las causas de mortalidad. Medimos las características de la vegetación en las ubicaciones de los volantones y las comparamos con las características de la vegetación en las ubicaciones de los machos adultos. Usamos un análisis de Destinos Conocidos en el Programa MARK para estimar la supervivencia de los volantones, y modelos lineales generalizados de efectos mixtos para determinar la selección del hábitat. La supervivencia estimada de los volantones hasta la independencia fue de 0.31 (EE = 0.08), con la mayor mortalidad durante los primeros cuatro días después del abandono del nido. Los polluelos con cuerdas alares más larga tenían tasas más altas de supervivencia que aquellos con cuerdas alares más cortas, posiblemente debido a una mayor capacidad para evadir a los depredadores. Los movimientos de volantones se restringieron principalmente a los territorios natales. Los volantones de Chingolo de Bachman se ubicaron en áreas con mayor cobertura de plantas leñosas, hierbas y pastos y menos terreno desnudo que el disponible en los territorios natales. Al igual que los polluelos de otras aves cantoras, las plantas leñosas y herbáceas del sotobosque parecen proporcionar una cobertura crítica para los volantones de Chingolo de Bachman, y el mantenimiento de dicha cobertura debería ser considerado en los planes de gestión para las comunidades de pinos de hoja larga.

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Key words: fledgling survival, habitat selection, movement, *Pinus palustris*, prescribed fire

After leaving nests, fledgling songbirds contend with simultaneous exposure to predators and weather events, causing mortality rates to be greatest during the first 4–5 d post-fledging (King et al. 2006, Yackel Adams et al. 2006, Rush and Stutchbury 2008, Ausprey and Rodewald 2011, Hovick et al. 2011). These high mortality rates are likely due to the limited flight and predator avoidance capabilities until 4–5 d after fledging (Young et al. 2019, Hovick et al. 2011). Flight capabilities increase with age and are associated with increased daily movements and decreased mortality rates (Kershner et al. 2004, Berkley et al. 2007, Davis and Fisher 2009, Verheijen 2017). To reduce predation risk, fledglings dependent on adult care typically move away from nest sites and may either remain in natal territories (Cohen and Lindell 2004, Vitz and Rodewald 2010) or disperse out of the territories (Yackel Adams et al. 2001, Vitz and Rodewald 2010). Fledglings typically move farther from nest sites as they age, often moving to areas that provide protection from predators (Kershner et al. 2004, Davis and Fisher 2009).

The characteristics of high-quality cover for fledglings vary among species and across land-cover types, but fledglings in many species select habitat patches that maximize predator avoidance (Champlin et al. 2009a,b, Vitz and Rodewald 2011, Streby and Andersen 2012) and food availability (Anders et al. 1998, Kershner et al. 2004, White et al. 2005, Dittmar et al. 2014, Streby et al. 2015, Martinez et al. 2019). For grassland-dependent species, high-quality cover for fledglings often consists of tall herbaceous vegetation, minimal amounts of litter, and moderate amounts of grass interspersed with bare ground (Jones and Bock 2005, Hovick et al. 2011, Giovanni et al. 2015, Small et al. 2015). Grassland in the absence of fire or other disturbance may become increasingly dense and restrict ground mobility (Taillie et al. 2015, Winiarski et al. 2017b). Although woody shrubs are not present in all grassland systems, when present, some bird species show avoidance (Young et al. 2019), whereas others show selection (Verheijen 2017). Woody shrubs in grasslands may either increase predator (e.g., snake) activity or provide thermal cover and suppress grass growth that enables ground movements (Young et al. 2019). Understanding how

fledgling songbirds select or avoid shrubs and other woody understory in herbaceous-dominated communities can ensure management actions that promote high-quality food and cover for all stages of reproduction.

Bachman's Sparrows (*Peucaea aestivalis*) are primarily associated with fire-maintained longleaf pine (*Pinus palustris*) communities with an understory dominated by wiregrass (*Aristida stricta*), but also occur in treeless, dry prairies in some parts of their range (Shriver et al. 1999). Bachman's Sparrows are sensitive to the amount of woody understory cover in breeding territories, typically abandoning areas with infrequent prescribed fire application and increasing cover and height of the woody understory (Engstrom et al. 1984, Tucker et al. 2004, Taillie et al. 2015). However, in frequently burned longleaf pine forests in southeastern North Carolina, territories of male Bachman's Sparrows typically included patches of woody cover within a matrix of grass-forb cover (Winiarski et al. 2017b). Winiarski et al. (2017b) suggested that some low woody cover provided singing perches for males (Dunning and Watts 1990, Haggerty 2000, Brooks and Stouffer 2010, Jones et al. 2013) and escape cover (Pulliam and Mills 1977, Dunning et al. 2020). Alternatively, woody cover is an important microhabitat feature for nest sites of Bachman's Sparrows and may provide a beneficial microclimate (Jones et al. 2013, Winiarski et al. 2017b). Although development of a dense woody understory can cause Bachman's Sparrows to abandon breeding sites, smaller numbers or isolated patches of woody plants may be used for nesting and predator avoidance.

Fledgling Bachman's Sparrows may select grass-dominated patches intermixed with bare ground as reported for grassland songbirds (Jones and Bock 2005, Hovick et al. 2011, Small et al. 2015) or they may select patches with woody cover like fledgling songbirds in forests (King et al. 2006, Ausprey and Rodewald 2011). Fledgling Bachman's Sparrows might be assumed to select conditions similar to those selected by breeding adults, but fledglings may select areas with greater woody understory cover or greater woody stem density to provide escape cover or thermal cover. If cover is not available near nests or in parental territories, fledglings may move large distances to reach cover, potentially increasing

exposure to predators. Hence, our objectives were to 1) quantify post-fledging survival and causes of mortality of fledgling Bachman's Sparrows, 2) evaluate movements of individual sparrows during the post-fledging period, and 3) characterize the vegetation where fledglings were located, including the amount of woody understory cover, during the post-fledging period.

METHODS

Study area. The Fort Bragg Military Installation (hereafter, Fort Bragg) is located in the Sandhills physiographic region of central North Carolina, USA. Fort Bragg contains ~62,100 ha of longleaf pine-wiregrass ecosystem (Sorrie et al. 2006). Longleaf pine uplands on Fort Bragg are typically burned every 3 yr, with emphasis on early, growing-season prescribed fire (Cantrell et al. 1993). However, some sections of Fort Bragg have been managed with dormant season prescribed fire or with variable fire-return intervals that included wildfires. This frequent fire regime has promoted an understory dominated by wiregrass and other herbaceous plants and reduced the prevalence of shrubs, small trees, and deep leaf litter (Lewis and Harshbarger 1976, Harper et al. 1997, Shriver and Vickery 2001, Lashley et al. 2014; Fig. 1). We selected six forested focal areas (mean = 754 ± 118 [SE] ha) managed with growing-season prescribed fire to monitor breeding Bachman's Sparrows and subsequently radio-track fledglings. The areas monitored shifted between years because post-fire vegetation succession caused Bachman's Sparrows to occupy different portions of the focal areas between years. Patches of dense, woody cover occurred in fire shadows along stream drainages, hillside seeps, and in canopy openings, including wildlife openings maintained with periodic disking or mowing. Smaller patches of tree sprouts and individual woody stems occurred throughout most uplands, with few areas completely devoid of woody stems. Many wildlife openings had previously been planted with species that provide forage for white-tailed deer (*Odocoileus virginianus*), but were often left fallow for several years before planting again. Fort Bragg contains drop zones ($N = 9$; mean = 250 ± 45 [SE] ha), artillery firing points ($N = 49$;

mean = 4.4 ± 0.4 [SE] ha), and wildlife openings ($N = 1283$; mean = 0.31 ± 0.02 [SE] ha), all of which lacked nesting Bachman's Sparrows (Fish et al. 2019).

Data collection. We located nests using a combination of monitoring radio-tagged females and opportunistic searches (Martin and Geupel 1993). Opportunistic searches were conducted when adults were observed building nests or feeding nestlings during weekly spot-mapping of adult territories throughout the breeding season (April–August; International Bird Census Committee 1970). We monitored nests every 2–4 d, but began daily monitoring near expected fledge dates, until nests either failed or fledged. On the day of fledging, we randomly selected 1–3 fledglings located near nest bowls and attached 0.5-g backpack-style radio-transmitters (Blackburn Transmitters, Nacogdoches, TX) using either the Rappole and Tipton (1991) or modified weak-link system (Kesler 2011) method. We only attached transmitters to fledglings from nests in monitored territories. Additionally, each fledgling was banded with a U.S. Geological Survey aluminum band and we recorded mass using a digital scale, wing chord length using a wing chord ruler, fat score, and ordinal fledge date (Pyle 1997). Transmitter batteries were programmed to last six weeks, and the weight of transmitters was ~3–4% of fledgling body mass.

We located fledglings once per day using the homing method (Small et al. 2015), visually confirming their status (e.g., alive or dead). If unable to locate a fledgling, we searched for a transmitter signal for three



Fig. 1. Typical longleaf pine forest occupied by breeding Bachman's Sparrows at Fort Bragg, North Carolina.

consecutive days, intensively searching an area within 500 m of the last location on foot, and scanning a radius of 1 km from the last location by vehicle. If the radio signal was not located for three consecutive days and the breeding pair, identified using color leg bands, was relocated without displaying brood protective behaviors (e.g., aggressive chipping and carrying food), we assumed the fledgling had been killed by a predator. Radio-transmitters had external wire leads that when damaged during a predation event can cause transmitter failure. When fledglings were predated and transmitters recovered, we identified the predator by searching the site for predator signs (e.g., chew marks on transmitters, plucked feathers, or flushing snakes from den sites; Suedkamp Wells et al. 2007, Hovick et al. 2011, Jones et al. 2017b). Additionally, when we located intact carcasses, we considered the cause to be either exposure or disease, depending on recent weather (Hovick et al. 2011, Lachish et al. 2012, Jones et al. 2017b) or the presence of epidermal sores on the feet and legs (Kirmse 1966, Alekseev 1998, Mete et al. 2014), respectively. We considered fledglings to have survived the post-fledgling life stage at 25 d post-fledgling, the age at which they have been reported to become independent (Haggerty 1988).

We recorded all fledgling locations using an eTrex handheld global positioning system (Garmin International, Inc., Olathe, KS). We used location averaging (>60 s with one location collected every second) at each fledgling location, increasing precision of the recorded location (Streby and Andersen 2013). We uploaded all fledgling locations into ArcMAP (Environmental Systems Research Institute, Inc., Redlands, CA) and used the measure tool to calculate the distance travelled between daily locations and distance from nests.

We measured vegetation cover at five randomly selected locations for each fledgling, but used fewer than five locations when predation events occurred during the first 5 d post-fledgling. We also measured vegetation cover at 10 randomly selected locations of adult males attending fledglings, considered representative of habitat availability. We identified male locations while spot-mapping breeding sparrows in a marked population from April to July 2014–2016 (Fish et al.

2019). Using a 2-m tall, 2.54-cm wide Wiens pole (Wiens 1974), we recorded vegetation contacts anywhere on the pole, along two perpendicular 10-m transects, centered over the locations of both fledglings and adult males (Brooks and Stouffer 2010, Fish et al. 2019). We classified vegetation contacts (hereafter, hits) as grass, forb, or woody (shrubs or regenerating trees). We recorded pole readings at the location and at 1-m intervals along each 10-m transect (Winiarski et al. 2017a). Additionally, we recorded the presence or absence of bare ground cover immediately beneath each Wiens pole reading. We calculated percent grass, forb, and woody cover at each location by calculating the proportion of the 21 Wiens pole readings with ≥ 1 hit of each vegetation type (Fish et al. 2018, 2019). We estimated percent bare ground cover by calculating the proportion of 21 Wiens poles readings classified as bare ground. We calculated woody plant height by recording the tallest woody stem hit to the nearest decimeter on each Wiens pole and averaged across each location plot. We calculated basal area using a 10-factor cruising prism from the center of the vegetation plot (Avery and Burkhart 2015).

Statistical analysis. We calculated cumulative fledgling survival and determined the proportion of fledglings surviving to independence, 25-d post-fledgling (Haggerty 1988). We evaluated the influence of several factors on fledgling survival using a Known Fates analysis in Program MARK (White and Burnham 1999). We constructed 10 *a priori* models to compare how ordinal fledge date, fledgling mass, wing chord, and fat score influenced survival. Ordinal date can be an important survival predictor because juveniles that fledge earlier in the breeding season may have a greater chance of survival (McKim-Louder et al. 2013). We examined how the condition of individuals at the time of fledgling influenced post-fledgling survival (Jones et al. 2017b). We did not include a year effect on survival because we monitored relatively few fledglings each year. Using Akaike information criterion corrected for small sample size (AIC_c) to rank model fit, we chose the model with the lowest AIC_c score as most parsimonious (Burnham and Anderson 2002). We considered models competitive if they differed by < 2 AIC_c units for every

additional one parameter of the top model, but ignored models with non-informative parameters (Arnold 2010). Non-informative parameters have beta coefficients with confidence intervals overlapping zero.

We characterized movements of fledglings throughout the post-fledging period in ArcMAP. We calculated the mean daily distance between relocations and mean daily distance from the nest site to determine initiation of natal dispersal (Vitz and Rodewald 2011). Boundaries of adult territories were delineated using minimum convex polygons generated with locations collected during spot-mapping. We also noted if a fledgling moved beyond territorial boundaries.

We compared vegetation conditions between fledgling locations and male locations using generalized linear mixed effect models. Models were constructed in a binomial framework, with fledgling locations being coded as a 1 and male locations as 0. Hence, fledgling selection for a vegetation covariate would result in either a positive or negative beta coefficient, depending on the directionality of selection. Beta values with confidence intervals overlapping zero would indicate a non-selected covariate. We included a random effect for individual males in the model to account for vegetation differences among territories. We ran 26 *a priori* models, including various combinations of percent grass, forb, and woody cover, bare ground cover, woody plant height, and basal area. We ranked models using AIC_c model selection identical to methods used in the Known Fates analysis. Values are provided as means \pm SE.

RESULTS

We located 110 nests, including 32 in 2014, 43 in 2015, and 35 in 2016. From these nests, we captured and marked 36 fledglings, including eight in 2014, 14 in 2015, and 14 in 2016. One fledgling in 2015 was censored from the survival analysis because the transmitter battery died prior to independence. We marked fledglings from 24 broods, averaging 1.5 fledglings per brood, and assumed survival for individuals from the same brood was independent. Mean fledgling mass was 14.2 ± 1.1 g, and radio-transmitters accounted for an average of $3.6 \pm 0.3\%$ of fledgling body mass; no transmitter exceeded 4.5% of fledgling body mass.

Of 35 fledglings, 11 survived until independent of adult care, resulting in a cumulative survival estimate of 0.31 ± 0.08 . Most fledgling mortality occurred during the first 4 d after fledging ($N = 12$), but continued throughout the post-fledging period ($N = 12$, Fig. 2). Three survival models were initially considered competitive, with two of these models including the addition of one non-significant covariate, for example, fledge date ($\beta = -0.01 \pm 0.01$ [SE]) or fledgling mass ($\beta = -0.01 \pm 0.01$ [SE]). Therefore, we accepted the top model identifying wing chord ($\beta = 0.17 \pm 0.05$ [SE]) as the best predictor of survival, receiving 0.42 of the overall model weight (Table 1); survival increased as wing chord length increased (Fig. 3). We documented 23 mortality events including predation by snakes ($N = 7$) and small mammals ($N = 3$), disease ($N = 3$), exposure ($N = 2$), and unknown causes because radio-transmitters were not relocated ($N = 8$). Snakes that predated fledglings included three corn snakes (*Pantherophis guttatus*), one black racer (*Coluber constrictor*), one eastern ratsnake (*Pantherophis alleghaniensis*), one copperhead (*Agkistrodon contortrix*), and one snake not identified to species. Most snake predation occurred during the first 4 d post-fledging ($N = 4$), but corn snakes ($N = 3$) continued to prey on fledglings up to 20 d post-fledging. Small mammals likely responsible for predation events were fox squirrels (*Sciurus niger*), gray squirrels (*Sciurus carolinensis*), or hispid cotton rats (*Sigmodon hispidus*), based on incisor indentations on transmitters. All predation by small mammals occurred during the first 2 d post-fledging.

Movements of 33 of 35 fledgling sparrows were restricted to natal territories. However, two fledglings temporarily left natal territories, when males and females in two family groups divided broods and provisioned independent of their mate. These fledglings left natal territories on days 5 and 7 post-fledging, respectively, and both remained with adult females for 10 d before both fledglings and females returned to their territories. Four fledglings began exploratory movements outside of territories at 24.8 ± 1.7 d post-fledging, moving an average distance of 122 ± 24.9 m from territory boundaries. This ranging phase included leaving the territory 1 d and returning the next, and preceded

dispersal. Natal dispersal was initiated an average of 30.4 ± 1.8 d post-fledging ($N = 9$ fledglings). The ranging phase was associated with greater variability in distances moved between daily relocations (Fig. 4). Fledglings moved increasingly farther from nest sites as they aged (Fig. 5). Two fledglings had not initiated dispersal by 30-d post-fledging and were not subsequently monitored to determine when they dispersed from natal territories.

We recorded between 0 and 45 locations per fledgling, with an average of 15.7 ± 2.5 locations per individual. Zero locations were collected when fledglings were predated immediately after marking and individuals were not relocated alive. We collected vegetation measurements at 118 fledgling locations and 210 male locations. Of the 26 *a priori* habitat-selection models, three models were initially considered competitive (Table 2). Of the competitive model set, two models differed from the top model by one parameter and two parameters, respectively. The full model was included in the competitive model set, indicating that all covariates had some influence on habitat selection. The top AIC_c supported model contained no non-significant parameters and was selected as the inference model. The model included a positive relationship with percent woody cover ($\beta = 0.54 \pm 0.13$ [SE]), percent forb cover

Table 1. Survival models for 35 fledgling Bachman's Sparrows, with number of parameters (K), Akaike information criterion corrected for small sample size (AIC_c), difference in AIC_c value (Δ AIC_c), and model weight (w_i), at Fort Bragg Military Installation, North Carolina, 2014–2016.

S()	K	AIC _c	Δ AIC _c	w_i
Wing	2	183.47	0.00	0.42
Wing + date	3	184.60	1.13	0.24
Wing + mass	3	184.74	1.27	0.22
Full	5	188.47	5.00	0.03
Date	2	188.54	5.07	0.03
Date + mass	3	190.00	6.53	0.02
Fat + date	3	190.38	6.91	0.01
Null	1	190.60	7.13	0.01
Date + mass + fat	4	191.94	8.47	0.01
Mass	2	192.04	8.57	0.01
Fat	2	192.31	8.84	0.00

($\beta = 0.45 \pm 0.13$ [SE]), and percent grass cover ($\beta = 0.27 \pm 0.13$ [SE]), and a negative relationship with percent bare ground ($\beta = -0.53 \pm 0.16$ [SE]). Fledglings selected sites with greater woody, forb, and grass cover and less bare ground cover than was available on average in male territories (Table 3).

DISCUSSION

Our survival estimate for fledgling Bachman's Sparrows (0.31) was similar to survival estimates reported for fledglings of grassland songbirds, ranging from 0.06–0.36 for Lark Buntings (*Calamospiza melanocorys*, Yackel Adams et al. 2006), Sprague's Pipits (*Anthus spragueii*, Fisher and Davis 2011), and Grasshopper Sparrows (*Ammodramus sava-narum*, Hovick et al. 2011). However, our survival estimate for fledgling Bachman's Sparrows was lower than that of fledglings of forest songbirds, ranging from 0.45 to 0.67 for White-throated Robins (*Irania gutturalis*, Cohen and Lindell 2004), Rose-breasted Grosbeaks (*Pheucticus ludovicianus*, Moore et al. 2010), and Ovenbirds (*Seiurus auro-capilla*, Haché et al. 2014). Fledgling songbirds in herbaceous-dominated vegetation must rely primarily on low-statured horizontal cover (e.g., grass and forbs), whereas fledglings in communities dominated by woody understory can use cover with more

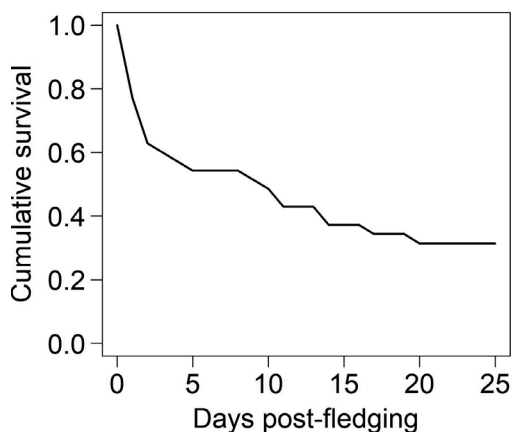


Fig. 2. Cumulative survival estimate for 35 fledgling Bachman's Sparrows on Fort Bragg Military Installation, North Carolina (2014–2016). Fledglings were considered independent at 25-d post-fledging.

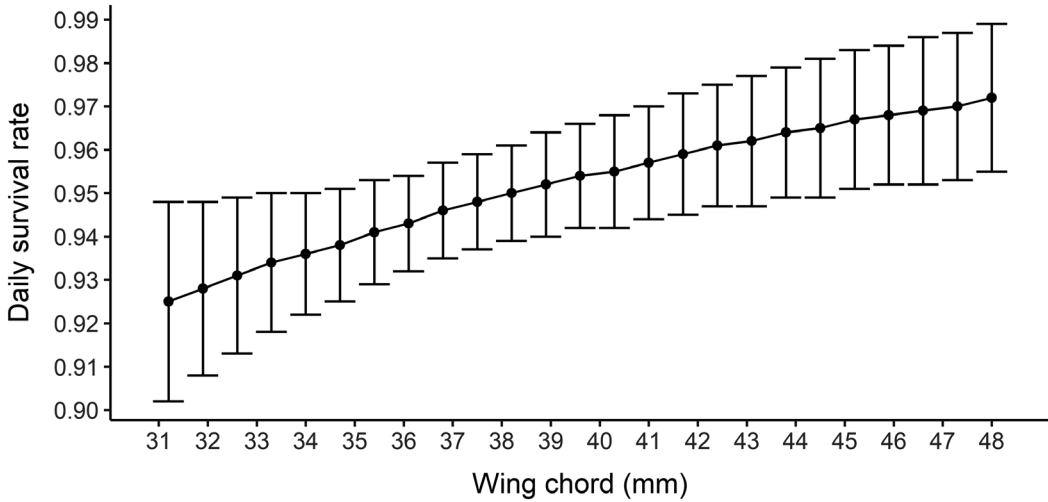


Fig. 3. Predicted daily survival rate (DSR) and 95% confidence intervals for 35 fledgling Bachman's Sparrows based on wing chord measurements on the day of fledging on Fort Bragg Military Installation, North Carolina (2014–2016).

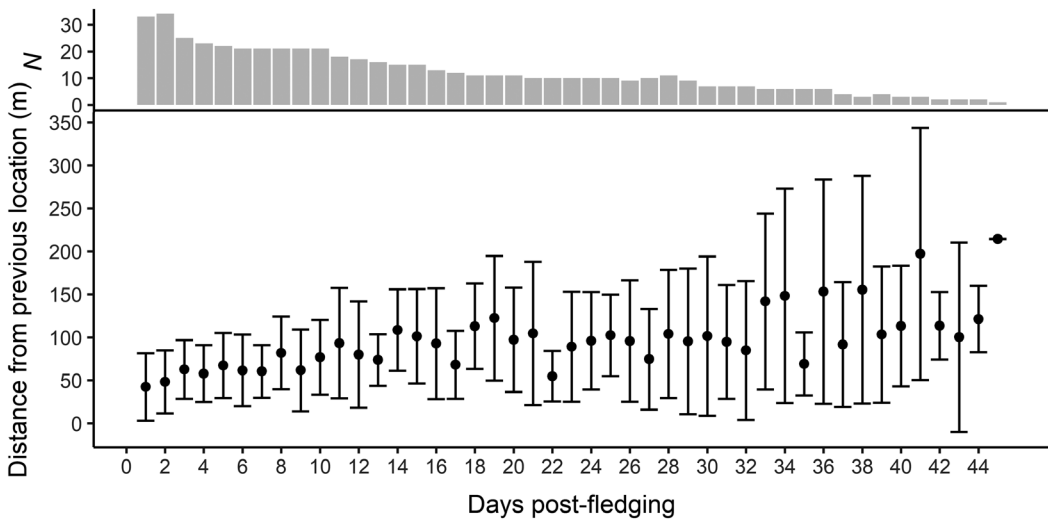


Fig. 4. Mean daily distance (\pm SD) travelled by fledgling Bachman's Sparrows between 1–45-d post-fledging on Fort Bragg Military Installation, North Carolina (2014–2016). Sample sizes (N) decreased as fledglings aged as a result of predation, dispersal, or transmitter failure.

prominent horizontal and vertical characteristics (e.g., shrubs, regenerating trees, and herbaceous plants). Fire-maintained longleaf pine communities are relatively unique forest types, often with dense understories dominated by herbaceous vegetation similar to grasslands, but also containing mature overstory and patchy woody cover in the midstory

and understory. We observed fledglings on the ground throughout our study and only observed fledglings perched in woody vegetation on three occasions, and always < 10 cm above ground. In forests, many fledgling songbirds select areas with greater vertical vegetation heterogeneity, including dense patches of woody cover (Anders et al. 1998, King

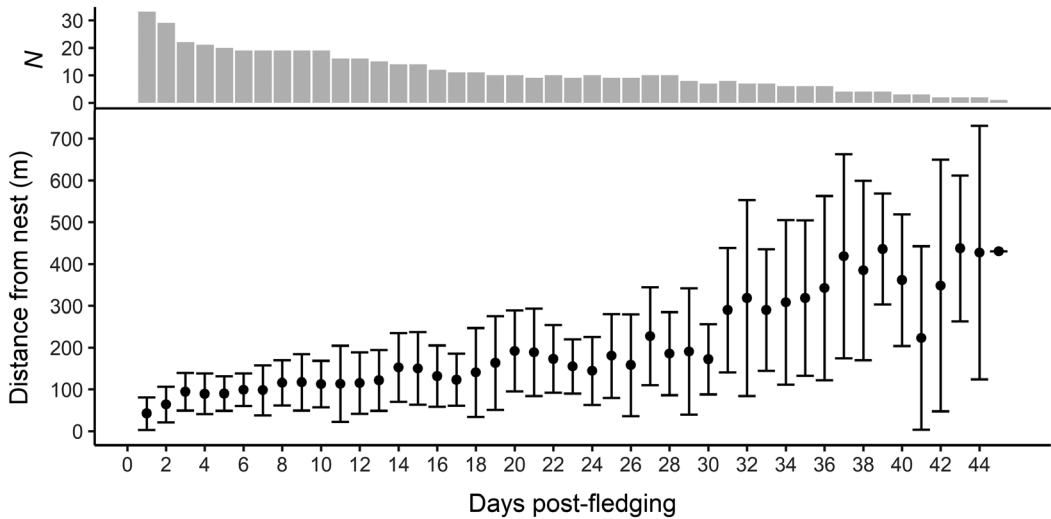


Fig. 5. Mean distance (\pm SD) of fledgling Bachman's Sparrows from nests during the post-fledging period on Fort Bragg Military Installation, North Carolina (2014–2016). Mean distance is bounded by black error bars representing one standard deviation. The sample size (N) decreased as fledglings aged due to predation, dispersal, or transmitter failure.

Table 2. The top 10 *a priori* habitat-selection models for fledgling Bachman's Sparrows at Fort Bragg Military Installation, North Carolina (2014–2016).

Model	K	AIC _c	Δ AIC _c	w_i
per.woody + per.forb + pg.bare + per.grs	6	427.6	0.00	0.45
per.woody + per.forb + pg.bare + ba.tot + per.grs	7	429.3	1.71	0.19
per.woody + per.forb + pg.bare	5	429.7	2.12	0.16
Full.mod	8	429.9	2.36	0.14
per.woody + per.forb + pg.bare + ba.tot	6	431.6	4.07	0.06
per.woody + per.forb	4	438.4	10.82	0.00
per.woody + per.forb + ba.tot	5	438.4	10.84	0.00
per.woody + pg.bare	4	440.3	12.78	0.00
per.frb + pg.bare	4	442.6	15.03	0.00
per.woody + max.wd	4	445.6	18.04	0.00

Number of parameters (K), Akaike information criterion corrected for small sample size (AIC_c), difference in AIC_c value (Δ AIC_c) and model weight (w_i).

et al. 2006, Bowen et al. 2007). Although the characteristics of vegetation where fledglings are located may influence their survival (King et al. 2006, Vitz and Rodewald 2011, Streby and Andersen 2013), we were unable to investigate this relationship because of our relatively small sample of surviving individuals.

As also reported in previous studies of fledgling songbirds (Vitz and Rodewald 2011, Haché et al. 2014, Streby et al. 2016, Goguen 2019), most predation of fledgling Bachman's Sparrows in our study occurred

during the first 4 d post-fledging. During this period, fledglings relied primarily on camouflage and exhibited limited mobility when we approached to document their locations. As fledglings aged, they became increasingly mobile and often ran or flushed as we approached. Limited flight ability and mobility during the first few days post-fledging likely contribute to the high predation rates. Predation of fledglings in our study continued until 20-d post-fledging, but at lower rates than earlier in the post-fledging period.

Table 3. The range of covariate values observed at locations of fledgling and male Bachman's Sparrows and Beta values from univariate generalized linear mixed effect models constructed in a binomial framework.

Covariate	Fledglings (used)			Males (available)		
	Min	Max	Mean	Min	Max	Mean
Bare ground ^a	0	1.00	0.10	0	0.81	0.17
Basal area ^b	0	2.87	1.20	0.11	2.64	1.15
Forb cover ^a	0	0.95	0.17	0	0.48	0.11
Grass cover ^a	0	1.00	0.68	0.05	1.00	0.69
Woody cover ^a	0	0.90	0.38	0	0.86	0.27
Woody height ^c	0	17.00	4.32	0	20.00	4.50

^aProportion of plot covered

^bm² per ha

^cDecimeters

Predation rates for most fledgling songbirds in grasslands typically plateau between 10 and 14 d post-fledging, with less predation after 14 d post-fledging (Yackel Adams et al. 2001, Berkley et al. 2007, Hovick et al. 2011, Verheijen 2017, Young et al. 2019).

Predation by snakes was the leading cause of mortality for fledgling Bachman's Sparrows in our study, when cause of mortality could be identified. Snakes can be the largest organismal clade preying on fledgling songbirds (Suedkamp Wells et al. 2007, Giovanni et al. 2015, Lehman 2017, Young et al. 2019) or just one of many clades contributing to predation events (Kershner et al. 2004, Jackson 2010, Cox et al. 2019). Although relatively few studies of survival of fledgling songbirds have been conducted in the southeastern United States, Lehman (2017) found that snakes accounted for over half of all known predation events on Golden-winged Warblers (*Vermivora chrysoptera*) in the Cumberland Mountains of Tennessee. Snake predation of fledgling songbirds is difficult to determine because investigators may not relocate individuals daily or make an effort to identify predators. However, in general, proportionately more snake-fledgling predation events have been documented in grasslands (Berkley et al. 2007, Hovick et al. 2011, Giovanni et al. 2015, Young et al. 2019) than in forests (Cohen and Lindell 2004, Streby et al. 2016), although there are exceptions (Lehman 2017). Most fledgling Bachman's Sparrows in our study were relocated on the ground,

perhaps increasing their exposure to snakes, especially during nocturnal periods when corn snakes typically forage (DeGregorio et al. 2016).

Our top survival model identified wing chord length as positively influencing fledgling survival, likely by increasing the ability of fledglings to escape from ground predators (Jones et al. 2017b). Wing chord in our analysis was synonymous with wing development, assuming that fledglings with longer wing chords have more developed flight feathers. Similarly, Jones et al. (2017b) reported that greater wing surface areas, a proxy for wing development, reduced fledgling predation risk for Dickcissels (*Spiza americana*). Jones et al. (2017b) also suggested that body size was not a significant factor in survival, but fledgling Dickcissels in better condition were less likely to die from exposure. Few other investigators have examined how individual condition influences fledgling survival. Even within nests, the condition or age of individual nestlings can vary due to asynchronous hatching or differential feeding rates (Evans et al. 2020). Conditions experienced in the nest likely have carryover effects during the post-fledging period.

We observed nestlings and fledglings with signs of disease (e.g., dermal sores and missing digits) throughout our study. We lacked the diagnostic capabilities to identify the disease(s) present in our population, but believe the birds were infested with mites of the genus *Knemidocoptes*. These infestations,

referred to as knemidocoptiasis, often result in swollen, scaly, or lost digits (Kirmse 1966, Alekseev 1998, Mete et al. 2014). Radio-telemetry studies have revealed that disease and starvation can be relatively common causes of mortality of fledgling songbirds (Kershner et al. 2004, Berkley et al. 2007, Jackson 2010), but identifying diseases is difficult because carcasses either decompose or are scavenged shortly after mortality.

Fledgling Bachman's Sparrows in our study were located in areas with less bare ground, and greater forb, grass, and woody understory cover. Similarly, Jones et al. (2017a) reported that newly fledged Dickcissels (*Spiza americana*) selected locations with denser herbaceous vegetation immediately after leaving nests before transitioning to areas with more open vegetation as they aged and were better able to evade predators. Fledglings in our study likely selected areas with greater grass and forb cover to aid in predator avoidance, especially early in the post-fledging period (Jones et al. 2017a, Young et al. 2019). Other investigators have also reported that fledgling Bachman's Sparrows likely selected areas with greater woody cover that provides protection from a range of predators and helps maximize survival and foraging efficiency in forested areas (Stoleson 2013, Burke et al. 2017).

Fledgling Bachman's Sparrows in our study initiated natal dispersal at an average age of 30.4-d post-fledging, with age of dispersal ranging from 23 to 40 d post-fledging. In addition, two 30-d old fledglings were still in natal territories when our study ended. Haggerty (1988) found that the average fledgling period (i.e., time from leaving nests to becoming independent of parents) for Bachman's Sparrows in Arkansas was 25 d, and ranged from 21 to 30 d. Dunning et al. (2020) suggested that the duration of fledgling periods of Bachman's Sparrows varied seasonally, with shorter fledgling periods earlier in the breeding season. One possible explanation for this is that Bachman's Sparrows are typically multibrooded and young that fledge earlier in the breeding season leave natal territories when parents begin to provision nestlings in second broods (Haggerty 1986). Other factors that can influence the timing of natal dispersal by young birds are sex (Alonso et al. 1998, Green and Cockburn 2001, Middleton and Green 2008),

dominance status (Nilsson and Smith 1985, 1988, Ellsworth and Belthoff 1999), and individual condition (Nilsson and Smith 1985). We did not investigate the specific mechanisms that might influence the timing of natal dispersal by young Bachman's Sparrows and, more generally, little is known about the duration of fledgling periods and timing of natal dispersal in other species in the genus *Peucaea*, so additional study is clearly needed.

Two fledglings temporarily left natal territories while being fed by their female parent, but both the fledglings and females returned to their territories between 15 and 17 d post-fledging, after which the males assumed food provisioning, and females re-nested. Such brood division may have been more common in our study, but was not detected because we only marked one or two fledglings in each family group. Factors that might contribute to brood division in Bachman's Sparrows are unclear, but one likely contributing factor is the number of fledglings that survive the first 4 d post-fledging.

Managing for the habitat requirements of fledglings is essential for addressing all aspects of the full-annual cycle of a species (Burke et al. 2017). Where Bachman's Sparrows are a focal species for managers, patches of low woody cover (i.e., re-sprouting trees and shrubs) should be available within or adjacent to male territories to provide escape, nesting, and fledgling cover (Winiarski et al. 2017a, b). Although we are not advocating the establishment of an extensive and tall woody understory, which would result in abandonment of territories by Bachman's Sparrows, we emphasize the importance of dispersed patches of low woody shrubs and tree sprouts in longleaf pine communities dominated by wiregrass and other herbaceous cover. Fledglings also selected for greater percent grass and forb cover, reinforcing the importance of extensive herbaceous cover for breeding Bachman's Sparrows.

ACKNOWLEDGMENTS

We thank J. Marcus, J. Winiarski, and staff in the Endangered Species Branch at Fort Bragg for thoughtful insight during the course of our study. M. Bennett, M. Boggess, E. Chen, D. Choi, H. Conley, S. Fenu, S. Rosche, M. Stevenson, and L. Williams assisted with

field work. Funding was provided by the Department of Defense and North Carolina State University. Funding agencies did not comment on the manuscript, beyond author contributions. This research was conducted under Institutional Animal Care and Use Committee permit number 14-011-O at North Carolina State University.

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