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Research Paper

Long-term monitoring identifies increase in Henslow's Sparrow (*Centronyx henslowii*) abundance following fire management in a North Carolina grassland

Emily A. Nastase[1], *Nathan J. Hostetter*[2], *John P. Carpenter*[3] *and Jaime A. Collazo*[1]
[1]North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA, [2]U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA, [3]North Carolina Wildlife Resources Commission, Raleigh, NC, USA

ABSTRACT. Understanding population responses to environmental change is critical for assessing vulnerability, resilience, and habitat management needs. We assessed Henslow's Sparrow (*Centronyx henslowii*) abundance and breeding productivity in an isolated North Carolina grassland (1149 ha) that transitioned from unmanaged to fire-managed during 2011–2024. Fire management was initiated in 2016, where approximately 1/3 of the grassland is burned annually in late summer on a rotating basis, resulting in a full burn cycle of roughly three years. We used hierarchical distance sampling models to estimate the change in Henslow's Sparrow abundance before and after fire management from point count data (45–50 locations surveyed annually). Estimated average abundances (i.e., expected number of singing male sparrows per site) significantly increased from 1.387 individuals per survey location pre-management (95% credible interval [CI]: 0.822–2.267) to 3.124 post-management (CI: 2.235–4.385), resulting in annual population sizes ranging from 56 singing male sparrows in 2012 (CI: 36–85), to 411 in 2022 (CI: 342–498). From 2022 to 2023, average brood size was 3.148 (95% confidence interval [CI]: 2.637–3.659) and survival probability for a 24-day nesting cycle was 0.693 (CI: 0.369–0.897). Apparent nesting success was 70–89%, much higher than reported in previous studies (19–62%). Increased abundance post-management indicates that Henslow's Sparrows are responding positively to the use of prescribed fire, while the estimated rates of breeding productivity indicate the species likely has the capacity to sustain the local population. This study provides baseline information for managers to monitor population status, while laying the foundation to identify regulatory mechanisms and gauge the effectiveness of the current fire management strategy in maintaining an isolated population of Henslow's Sparrows.

La surveillance à long terme met en évidence une augmentation de l'abondance du Bruant de Henslow (*Centronyx henslowii*) à la suite de mesures de gestion par le feu dans une prairie de Caroline du Nord

RÉSUMÉ. Il faut impérativement comprendre les réactions des populations aux changements environnementaux pour évaluer leur vulnérabilité, leur résilience et les besoins en matière de gestion des habitats. Nous avons évalué l'abondance et la productivité de reproduction du Bruant de Henslow (*Centronyx henslowii*) dans une prairie isolée de Caroline du Nord (1 149 ha) qui est passée d'un régime de gestion non interventionniste à un régime de gestion par le feu entre 2011 et 2024. La gestion par le feu a été mise en place en 2016 : environ un tiers des prairies est brûlé chaque année à la fin de l'été selon un système de rotation, ce qui donne un cycle complet de brûlage d'environ trois ans. Nous avons utilisé des modèles hiérarchiques d'échantillonnage par distance pour estimer l'évolution de l'abondance du Bruant de Henslow avant et après les interventions de gestion par le feu, à partir de données issues de comptages ponctuels (45 à 50 sites étudiés chaque année). Les abondances moyennes estimées (c.-à-d. le nombre prévu de bruants mâles chanteurs par site) ont augmenté de manière significative, passant de 1 387 individus par site d'étude avant la mise en œuvre des mesures de gestion (intervalle de crédibilité à 95 % [IC] : (0,822–2,267) à 3 124 après la gestion (IC : 2,235–4,385), ce qui correspond à des effectifs annuels allant de 56 bruants mâles chanteurs en 2012 (IC : 36–85), pour atteindre 411 en 2022 (IC : 342–498). De 2022 à 2023, la taille moyenne des couvées était de 3,148 (intervalle de confiance à 95 % [IC] : 2,637–3,659) et la probabilité de survie pour un cycle de nidification de 24 jours était de 0,693 (IC : 0,369–0,897). Le taux de réussite apparente de la nidification est situé de 70 à 89 %, un chiffre nettement supérieur à celui rapporté dans les études précédentes (de 19 à 62 %). L'augmentation de l'abondance observée après l'intervention indique que le Bruant de Henslow réagit favorablement aux brûlages dirigés. Par ailleurs, les taux estimés de productivité de reproduction suggèrent que l'espèce est probablement capable d'assurer la pérennité de la population locale. Cette étude fournit des données de référence aux responsables, leur permettant de suivre l'état de la population, tout en jetant les bases nécessaires pour définir des mécanismes réglementaires et évaluer l'efficacité de la stratégie actuelle de gestion par le feu dans la préservation d'une population isolée de bruants de Henslow.

Key Words: *breeding productivity; conservation; demography; habitat management; Henslow's Sparrow (Centronyx henslowii); nesting; prescribed burning; species recovery*

Corresponding author: Emily A Nastase, eanastas@ncsu.edu

INTRODUCTION

Understanding population responses to environmental change is critical for assessing vulnerability, resilience, and habitat management needs. For migratory songbirds, changes in vital rates at different stages of the annual cycle may influence population growth and abundance (Rushing et al. 2016, Stevens et al. 2024). Evaluating population-level responses to habitat management actions is essential for developing strategies to improve population status or mitigate stressors. Studies that connect habitat management to population changes are especially important for North American grassland songbirds, given their sweeping and persistent declines in recent decades (Rosenberg et al. 2019, Bernath-Plaisted et al. 2023). Habitat loss is consistently identified as the primary driver of these declines (Bernath-Plaisted et al. 2023). Management strategies that create or maintain grasslands offer a means to curtail declining trends for grassland songbird populations by providing new habitats or by making existing habitats consistently available.

Henslow's Sparrow (*Centronyx henslowii*) is among the grassland songbird species experiencing population declines due to breeding habitat loss (Cooper 2012, Rosenberg et al. 2016, Herkert et al. 2018, Sauer et al. 2019, Fink et al. 2023). The species predominantly nests in tallgrass prairies, hayfields or pastures, wet meadows, and reclaimed coal mines (Bajema et al. 2001, Monroe and Ritchison 2005, Herkert et al. 2018). Breeding habitats typically have a thick litter layer, hydric soils, and numerous forbs and standing dead woody stems that serve as perches for territorial male sparrows (Herkert et al. 2018). Grasslands with such specific vegetation and soil characteristics are continuously threatened by woody vegetation encroachment, and, if unmanaged, often transition into shrub-dominated systems (Briggs et al. 2005). State-shifts from grasslands to shrublands or woodlands, once they occur, may be difficult or costly to reverse (Ratajczak et al. 2014).

Prescribed fire is a common management strategy used to maintain grasslands, including those suitable for Henslow's Sparrow breeding sites (Mangun and Kolb 2000, Fuhlendorf et al. 2006, Keating et al. 2023). Prescribed fire increases the quality and availability of Henslow's Sparrow habitat by reducing woody encroachment and increasing vegetation diversity and productivity (Reinking et al. 2000, Burhans 2002, Tix et al. 2003, Hovick et al. 2015, Glass and Eichholtz 2023). For fire management to effectively suppress woody encroachment and reduce the likelihood of a state-shift into a shrub-dominated system, eastern grasslands are typically burned at frequent intervals (1–4 years; Ratajczak et al. 2014). Using prescribed fire to maintain vegetation structure in grassland systems has the added benefit of increasing avian community diversity and stability (Hovick et al. 2015).

In North Carolina, the southeasternmost extent of the Henslow's Sparrow breeding range, breeding populations have only been reliably detected at two sites since the 1990s (Mangun and Kolb 2000, Paxton and Watts 2002, Sullivan et al. 2009, NCWRC 2022, Nastase 2024). Of the two breeding sites, one is managed using prescribed fire and the other via semiannual mowing. Given the species' range-wide population declines, the prospect of continued declines (North American Bird Conservation Initiative 2022), and its limited distribution within the state, Henslow's Sparrow is considered endangered in North Carolina and is of high conservation priority (NCWRC 2020, 2022). Advancing conservation of Henslow's Sparrow in North Carolina requires a greater understanding of how populations are responding to different or changing management schemes.

In this study, we examined the effect of fire management on one of two isolated breeding populations of Henslow's Sparrow in North Carolina. We used hierarchical distance sampling models to estimate the change in Henslow's Sparrow average abundance before and after the transition to fire management in 2016 and derive annual population sizes of singing male sparrows from 2011 to 2024. We hypothesized that the Henslow's Sparrow population would exhibit a higher average abundance during the post-management period, based on the expectation that prescribed fire increases habitat quality and the availability of resources. Additionally, during 2022–2023, we assessed Henslow's Sparrow brood size and nest survival, two key drivers of per capita growth. We tested seven a priori hypotheses of Henslow's Sparrow nest survival in response to seasonal and habitat covariates. We hypothesized that breeding productivity would be high compared to other Henslow's Sparrow populations and would reflect the population's capacity to sustain itself through successful on-site reproduction.

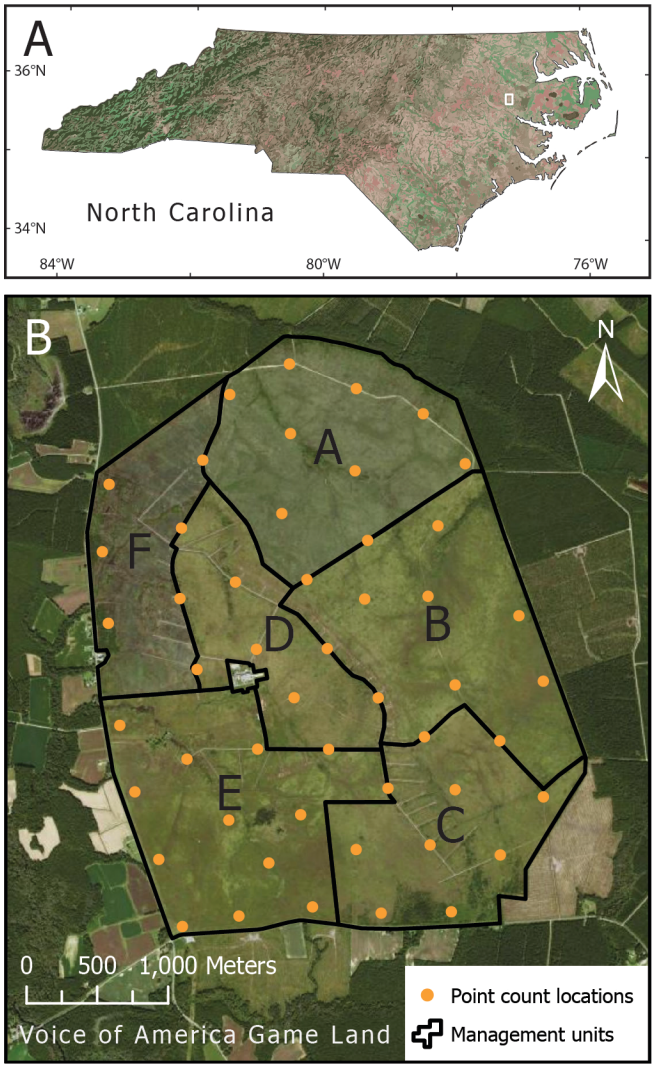
METHODS

Study area

We conducted our research at the Voice of America Game Land (VOAGL) in Beaufort County, North Carolina (35.7001°N, 77.1477°W; Fig. 1). The VOAGL is a 1149-hectare grassland that is divided into six management units (A–F), separated by a network of paved and grass roads. The dominant vegetation at the site consists of graminoids and forbs; however, there is woody encroachment along the site perimeter, and creeks, drainage ditches, and small wetlands throughout the property. The VOAGL is owned and managed by the North Carolina Wildlife Resources Commission. It is accessible to the public and is a popular destination for birders, hunters, and bikers.

Fire management at the VOAGL was initiated in 2016, with the goal of maintaining habitat for Henslow's Sparrow and other grassland species (NCWRC 2022). This entails management units being burned on a three-year rotation, where two management units (~1/3 of the site) are burned each year, resulting in a full burn cycle of roughly three years. Unlike other grassland systems in the Southeastern U.S. that are typically burned during the dormant season (December–April), the VOAGL is burned during the vegetation growing season (March–October). Growing season burns are more effective at preventing woody vegetation resprouting than dormant season burns (Robertson and Hmielowski 2014); they promote native grass species and old-growth grassland plant communities (Novak et al. 2021) and they enable litter accumulation prior to the next Henslow's Sparrow breeding season. However, burning in summer months coincides with the peak nesting period for Henslow's Sparrow (May–July; Herkert et al. 2018); thus, burns at the VOAGL are typically conducted in late July or early August to avoid nesting sparrows (NCWRC 2022).

Fig. 1. (A) The Voice of America Game Land (VOAGL; white rectangle) is one of two known breeding sites for Henslow's Sparrow (*Centronyx henslowii*) in North Carolina. Basemap modified from North Carolina satellite map (GISGeography 2023). (B) Inset map of the VOAGL with prescribed fire management units (A–F) outlined in black. Locations of 50 point count locations are marked with orange circles. Basemap: USDA FSA NAIP Imagery Hybrid (Esri 2023).



Estimating abundance

We conducted annual point count surveys of Henslow's Sparrow at the VOAGL from 2011 to 2024, following standard survey protocols (Buckland 2006). All surveys were conducted in late May or early June, when male sparrows are territorial and most detectable (Herkert et al. 2018). At each point, the observer recorded detections of Henslow's Sparrow within a fixed radius of 200 m for a period of six minutes. To prevent double counts, observers noted on data sheets the type of detection (i.e., singing, singing and visual, visual only), bearing to the bird, and the bird's distance (m) from the observer using a range finder. If distances could not be measured, observers estimated distances to the nearest five-meter interval. All observers were trained prior to conducting surveys to minimize violating model assumptions (Buckland et al. 2001, Buckland 2006). Point count surveys from 2011 to 2020 were conducted at 45 locations that were evenly spaced at 500-m intervals along the site's road network. Though non-random survey locations is not ideal for inference (Buckland et al. 2001), it likely had little effect in this case, as the VOAGL is vast and flat with nearly unimpeded views from survey locations. In 2021, we added five survey locations, which resulted in an array that systematically covered the full extent of the VOAGL. The 50 survey locations, with 200-m detection distance radii, covered ~55% (628 ha) of the property (Fig. 1).

To satisfy the assumptions of distance sampling models, we made a few revisions to the survey data. First, we reduced the dataset to only detections that included auditory cues. We discarded six visual only detections made over the 14-year time series because including them would have added undue complexity to models (i.e., separate detection process) with minimal inferential gains. Next, we determined bins for grouping data because earlier years (2011–020) had more heaped observations at approximated distances (e.g., 50 m, 100 m), while later years (2021–2024) had more exact distance measurements. We set cut points (30, 70, 120, 190 m) so bins were centered over distances with the greatest numbers of observations. We truncated observations at 190 m to account for the possibility that, in this open grassland system, some auditory detections made at distances exceeding our survey radius were inadvertently recorded as 200 m. Finally, though the use of prescribed fire at the VOAGL was initiated in 2016, we divided the time series into pre-management (2011–2018) and post-management (2019–2024) periods. The breakpoint at 2019 corresponds to the completion of the first full burn cycle at the VOAGL and an expected two- to three-year lag in population response to the changes in vegetation structure (Cully and Michaels 2000, Reinking et al. 2000, Keating et al. 2023).

We estimated Henslow's Sparrow expected annual abundances during the pre- and post-management periods at the VOAGL using a three-part conditional multinomial hierarchical distance sampling (HDS) model (Sillett et al. 2012, Kéry and Royle 2016). We modeled the observed distance bin (d = 1, 2, 3, 4 distance bins) for individual i in year t, $y_{i,t}$, as (Eq. 1):

$$y_{i,t} \sim \text{Categorical}(\pi_t^c) \quad (1)$$

Here, $\pi_t^c = \pi_t / \rho_t$, where π_t is the vector of bin-specific detection probabilities in year t and ρ_t is the probability of detection in year t. We modeled the decline in detectability from the observer with a half-normal detection function (Eq. 2):

$$\pi_{dt} = \exp\left(-\frac{x_d^2}{2\sigma_{k[t]}^2}\right) \quad (2)$$

where x_d is the midpoint of distance bin d (Kéry and Royle 2016). We modeled the detection scaling parameter ($\sigma_{k[t]}$, in m) separately for two time periods (k), where 2011–2020 was time period 1 and 2021–2024 was time period 2, to reflect the previously described

change in sampling protocols. The total detection probability in year t, ρ_t, was defined as the sum of bin-specific detection probabilities π_{dt} weighted by the proportion of the survey area covered by each bin (δ_d; Eq. 3):

$$p_t = \sum_{d \in D} \pi_{dt} \times \delta_d \quad (3)$$

The number of observed Henslow's Sparrows at survey location s in year t, $n_{s,t}$, was modeled as (Eq. 4):

$$n_{s,t} \sim \text{Binomial}(N_{s,t}, p_t) \quad (4)$$

where latent site-specific abundance, $N_{s,t}$, followed a Poisson distribution with an expected year-specific abundance, λ_t (Eq. 5):

$$N_{s,t} \sim \text{Poisson}(\lambda_t) \quad (5)$$

To evaluate mean abundance before and after implementation of fire management (2011–2018 vs. 2019–2024), we modeled the expected annual abundances, λ_t, as (Eq. 6):

$$\log(\lambda_t) \sim \text{Normal}(\mu_{g[t]}, \tau_{g[t]}) \quad (6)$$

Where μ_g is the mean log-abundance for management period g (pre-management [2011–2018]: μ_1; post-management [2019–2024]: μ_2), and standard deviation τ_g, representing annual variation within management periods. The difference in average abundances between the two management periods was quantified as $\exp(\mu_2) - \exp(\mu_1)$, with positive values indicating an increase in average abundance during the post-management period. Finally, annual site-wide population sizes of singing male Henslow's Sparrows (N_t^*) were derived by extrapolating the estimated annual densities of survey locations ($\Sigma_s N_{s,t} / \Sigma_s area_{s,t}$) across the total site area (1149 ha).

We fit the HDS model using JAGS (Plummer 2003) via the *jagsUI* package (Kellner 2024) in R 4.4.2 (R Core Team 2024). For priors, we specified: for the detection function scaling parameters σ_k; Normal(0, 0.01) for management period mean log-abundances (μ_g); and Uniform(0, 10) for the standard deviation of average abundances (τ_g). We ran three chains with 75,000 Markov chain Monte Carlo (MCMC) iterations each, discarding the first 5000 as burn-in, and thinned by an interval of two to reduce autocorrelation. The joint posterior had 105,000 samples. We verified convergence where all $\hat{R}$ values were < 1.1 and effective sample sizes were > 1000. We report results as posterior medians and 95% credible intervals. For pre- vs. post-management average abundances (μ_g), we report exponentiated posterior summaries representing the expected number of Henslow's Sparrows per survey location.

Nest survival and brood size

In the 2022 and 2023 breeding seasons, we found and monitored Henslow's Sparrow nests across four management units at the VOAGL (Fig. 2) using methods commonly employed in demographic studies of grassland birds (Winter 1999, Winter and Faaborg 1999, Davis 2005). We searched for nests during the species' peak breeding period, from early May to late July, between the hours of 0545 and 1100, when adult sparrows were actively incubating or feeding young at the nest. Nests were located in one of three ways: (1) by observers gently disturbing grasses with bamboo sticks while walking transects and flushing an incubating female off a nest; (2) by closely observing adult feeding behavior and following the parent to the nest site; or (3) by incidentally flushing a female sparrow off the nest while traversing the study area. When nests were found, we took GPS coordinates at the nest's location and marked nest sites with flagging tape on nearby vegetation. We took care to fluff up grass patches that had been matted down during our search and return the surrounding vegetation to an undisturbed state as much as possible. We revisited nests every 3–5 days until the offspring fledged or the nest failed (e.g., depredated). We considered nests successful if at least one nestling fledged from the nest and our estimates of brood size correspond to the number of fledglings produced. We acknowledge that our monitoring interval of 3–5 days resulted in uncertainty in approximated fledge dates; however, we opted to monitor cautiously to minimize disturbances at nests. We used the average 10-day Henslow's Sparrow brooding period (Herkert et al. 2018) as a frame of reference, in conjunction with nest-level observations (i.e., the presence of feces in the empty nest and/or a fully intact nest) and sparrow behavioral observations (i.e., adults making alarm calls nearby, fledgling peeps, or sighting a fledgling nearby the nest location), to determine if empty nests had fledged (Davis 2005). For nests that were found empty after surviving to a potential fledging age but lacked sufficient evidence to conclude nest fates (e.g., no signs of predation or fledglings nearby), observers used estimated nest ages and prior observations of nestling development to classify likely nest fate; however, we considered these nests to have "uncertain" fates and present a range of apparent nesting success estimates that includes and excludes these nests (Manolis et al. 2000).

Covariates of interest for our analysis of nest survival included year, day of the season nests were found, nesting stage (eggs vs. nestlings), nest age, vegetation height surrounding the nest, and nest entrance openness. For analysis of differences in survival of nest stages, we divided nest data into two groups corresponding to egg laying and incubation (group 1) and nestlings (group 2). Several nests were included in both groups because they were

Fig. 2. Left: Adult Henslow's Sparrow (*Centronyx henslowii*) carrying nesting material. Credit: Diane Nastase. Right: Henslow's Sparrow nestlings. Credit: Abigail Valine.

found during the egg stage and progressed through the nestling stage. For these nests, we partitioned data into groups by censoring the nest on the last day of the egg stage for inclusion in group 1 and initiating the nest on that day for group 2 (Dinsmore and Dinsmore 2007). Analyses including temporal trends required accurate nest initiation and fledge dates and precise estimates of nest ages corresponding to breeding season days. Nest age is a commonly evaluated predictor of nest survival and its incorporation as a covariate helps to correct for sampling bias of finding nests at ages greater than day zero (Weiser 2021). In 2022, we considered day 1 of the season to be the date that the first nest was located (May 12) and we aligned day 1 of the 2023 season accordingly. Nest initiation date was calculated by subtracting the average Henslow's Sparrow nesting cycle length (24 days) from the nest fledge date approximated from our monitoring data. We calculated nest ages for each day in the breeding season by creating a new variable (AgeDay1) that represented the difference between the estimated nest initiation date and day 1 of the season (Laake 2013).

For habitat covariates, we returned to nest sites within two weeks following estimated fledge dates to make measurements. We measured the average vegetation height surrounding the nest with a Robel pole (Robel et al. 1970) and estimated the degree of nest entrance openness using a partitioned paper disc placed within the nest cup (Davis and Sealy 1998; Appendix 1). The aim of the openness measurement was to characterize the degree to which nests were concealed, with a total possible score of 40. Higher scores correlated to a greater degree of nest entrance openness, while lower scores indicated more concealment. Although post-fledgling nest vegetation structure may not perfectly represent the conditions present when nests were initiated, we conducted measurements after nests had fledged or failed to reduce the risk of causing nest abandonment or predation. Given the species' relatively short nesting cycle length (~24 days), vegetation structure likely remained largely unchanged during this time frame.

Using the nest survival model in program MARK (White and Burnham 1999), accessed via the *RMark* package in R (Laake 2013), we tested seven a priori hypotheses about sources of variation affecting Henslow's Sparrow daily nest survival rates. We estimated survival rates using exposure periods first with a null model that assumed survival is unaffected by environmental, temporal, or other factors ("Constant"), and then with a series of six univariate models: year ("Year"), day of the season ("Time"), nesting stage ("Stage"), nest age ("NestAge"), nest site vegetation height ("Robel"), and nest entrance openness ("Open"). To avoid potential multicollinearity, we opted to test models with single predictors rather than models that evaluated multiple covariates simultaneously (Table 1). We used the change in Akaike's Information Criterion corrected for small sample size (ΔAICc) to compare candidate models (Dinsmore et al. 2002, Johnson and Omland 2004). When multiple models were competitive (ΔAICc < 2), we selected the most parsimonious model (i.e., the model with the fewest parameters; Arnold 2010). The NestAge model, however, produced implausibly low survival estimates (24-day survival < 0.04) because of limited observations of early-stage nests and thus large extrapolations back to nest age 1; therefore, we excluded the NestAge model from model comparison results. We calculated survival for a full nest cycle as the product of daily survival rates across a 24-day period and estimated associated standard errors using the delta method (Laake 2013).

Table 1. Seven a priori hypotheses of predictors affecting Henslow's Sparrow (*Centronyx henslowii*) daily nest survival at the Voice of America Game Land, North Carolina, USA.

Model	Hypothesis
S(~Constant)	Daily survival rates are constant through time
S(~Time)	Variations in environmental conditions decrease as the season progresses, thus daily survival rates increase over time
S(~Year)	Strong interannual population and/or environmental conditions result in variable daily survival rates between years
S(~Stage)	Parental care is expected to differ between nest stages (eggs vs. nestlings), thus daily survival rates differ between stages
S(~NestAge)	Nests are most vulnerable when first established, thus daily survival rates increase as the age of the nest increases
S(~Robel)	Daily survival rates change as a function of vegetation height surrounding the nest by reducing the risk of predation
S(~Open)	Daily survival rates change as a function of the level of nest concealment by reducing the risk of predation

Parameters estimated from frequentist models are presented with 95% confidence intervals and Bayesian parameter estimates are presented with 95% credible intervals. CI is used to denote both confidence and credible intervals.

RESULTS

Estimating abundance

We detected a total of 1097 singing male Henslow's Sparrows at the VOAGL from 2011 to 2024. Average abundance of sparrows at survey locations during the pre-management period (2011–2018) was 1.387 (CI: 0.822–2.267), while the post-management period (2019–2024) average abundance was more than two times greater, at 3.126 (CI: 2.235–4.385; Table 2; Fig. 3). There was a 0.99 probability that average Henslow's Sparrow abundance was greater during the post-management period (posterior probability $\mu_{post} > \mu_{pre} = 0.994$). Derived annual Henslow's Sparrow population sizes varied markedly over the 14-year time series, with the lowest estimate of singing males, 56 (CI: 36–85), in 2012, and the highest, 411 (CI: 342–498), in 2022 (Table 2).

Nest survival and brood size

During the 2022 and 2023 breeding seasons, we found and monitored 27 Henslow's Sparrow nests, of which 19 were confirmed to have fledged at least one young, five were believed to have fledged but had uncertain fates, and three nests failed. This yields an apparent nesting success ranging from 70% (19/27, confirmed successes only) to 89% (24/27, all likely successes). Combined, all likely successful nests produced 85 fledglings, with a range of 2–4 fledglings per nest. Average brood size was 3.148 ($n = 27$; SE: 0.249; CI: 2.637–3.659) fledglings per nesting attempt, and 3.542 ($n = 24$; SE: 0.134; CI: 3.264–3.820) per successful attempt. For confirmed successful nests, average brood size was 3.632 ($n = 19$; SE: 0.157; CI: 3.302–3.961). Of the three nests that were unsuccessful, two failures occurred during the egg stage and one during the nestling stage.

Table 2. Hierarchical distance sampling model parameter estimates and derived population sizes of singing male Henslow's Sparrows (*Centronyx henslowii*) at the Voice of America Game Land, North Carolina, USA from 2011 to 2024. We report: two values for the Half-normal distance function scaling parameter (σ) and probability of detection (ρ) based on year groups with differing data collection methods (2011–2020 and 2021–2024); the exponentiated average abundances at survey locations pre- and post-management (μ_{pre} and μ_{post}); the standard deviation in average abundances of management periods (τ_{pre} and τ_{post}); and the derived population sizes of singing male Henslow's Sparrows by year (N_t^*).

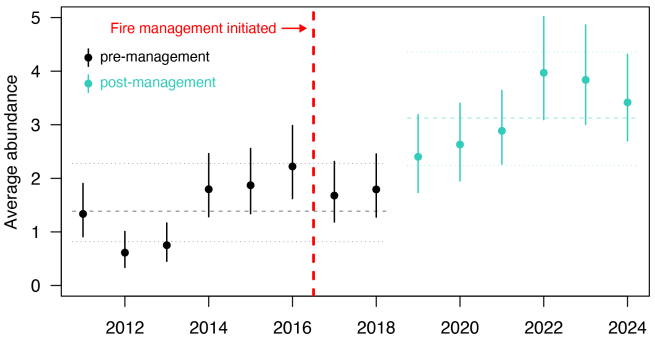
Parameter	Median	sd	2.50%	97.5%
$\sigma_{2011\text{-}2020}$	111.770	8.591	98.790	132.455
$\sigma_{2021\text{-}2024}$	147.654	20.311	122.621	199.793
$\rho_{2011\text{-}2020}$	0.529	0.043	0.456	0.625
$\rho_{2021\text{-}2024}$	0.680	0.057	0.582	0.805
μ_{pre}	1.387	0.388	0.822	2.267
μ_{post}	3.126	0.579	2.235	4.385
τ_{pre}	0.561	0.252	0.294	1.240
τ_{post}	0.277	0.201	0.090	0.818
N^*_{2011}	135.109	19.682	103.583	180.145
N^*_{2012}	56.295	12.520	36.029	85.569
N^*_{2013}	72.058	13.886	49.540	103.583
N^*_{2014}	184.649	24.085	144.116	238.692
N^*_{2015}	191.404	24.747	150.871	247.699
N^*_{2016}	229.685	28.016	182.397	290.484
N^*_{2017}	171.138	22.960	132.857	222.930
N^*_{2018}	184.649	24.042	144.116	238.692
N^*_{2019}	231.937	29.96	182.397	299.491
N^*_{2020}	258.959	31.041	204.915	326.513
N^*_{2021}	289.808	28.727	239.143	352.634
N^*_{2022}	411.406	39.508	342.501	498.551
N^*_{2023}	397.220	38.329	330.341	480.312
N^*_{2024}	357.763	34.982	297.791	434.278

The NestAge model was the top-ranked model based on AICc; however, the estimated 24-day nest survival probability (0.036; SE = 0.102; CI = 0.0001–0.925) was biologically implausible. Given the high apparent nesting success observed (≥ 70%), it is unlikely that only 4% of Henslow's Sparrow nests successfully fledged young at VOAGL. Extremely low daily survival in the NestAge model was likely driven by the small number of nests discovered during the egg stage (n = 6), two of which failed, leading to strong statistical support for the NestAge model but unreliable parameter estimates. Among the remaining models, Stage, Time, and Constant were highly competitive (ΔAICc ≤ 0.11, Table 3); however, effects of Stage and Time were not statistically significant, therefore we based inference on the Constant model (Arnold 2010). Under the Constant model, daily nest survival probability was 0.985 (SE = 0.009; CI = 0.954–0.995), corresponding to a 24-day nest survival probability of 0.693 (SE = 0.147; CI = 0.369–0.897).

DISCUSSION

We identified a significant increase in Henslow's Sparrow average abundance at the VOAGL after the implementation of fire management, lending support to the hypothesis that prescribed fire promotes larger Henslow's Sparrow populations at this site. Although we do not know the specific mechanisms driving increasing abundances over time, repeated treatments in

Fig. 3. Expected annual abundances (λ_t) of singing male Henslow's Sparrows (*Centronyx henslowii*) at survey locations in the Voice of America Game Land, North Carolina, USA from 2011 to 2024 (posterior medians and 95% credible intervals). Data are divided into pre-management (black) and post-management (teal) periods based on fire management starting in 2016 (vertical red dashed line) and an expected two-year lag in Henslow's Sparrow response. The average pre- and post-management period abundances (exp(μ_{pre}) and exp(μ_{post})) were 1.387 (0.822–2.267) and 3.126 (2.235–4.385) singing males per survey location, respectively (horizontal dashed lines), with a 0.99 probability that Henslow's Sparrow average abundance was greater post-management.



management units gradually increases habitat quality by reducing woody encroachment and enhancing primary productivity in habitat patches, thereby increasing or improving resources available to breeding Henslow's Sparrows throughout the VOAGL (Nastase 2024). Larger expected annual abundances post-management may be driven by how the entire site had been burned at least once starting in 2019. The positive relationship between fire management and Henslow's Sparrow abundance has been reported elsewhere in the breeding grounds (Fuhlendorf et al. 2006, Keating et al. 2023), as well as in the species' wintering grounds (Johnson 2006, Thatcher et al. 2006).

Our assessment of change in abundance in this population of Henslow's Sparrows is supported by the estimated levels of reproductive activity in 2022–2023. The estimate of daily nest survival probability (0.985) was greater than found in previous studies of the species (0.924–0.959; Winter and Faaborg 1999, Stauffer 2008, Crimmins et al. 2016), as was the estimate of apparent nesting success (70–89%), which has reportedly ranged anywhere from 19–62% (Monroe and Ritchison 2005, Stauffer 2008, Crimmins et al. 2016, Herkert et al. 2018). We note, however, our estimate of brood size for successful nests (3.54–3.63) was similar to other studies (3.30–4.21; Winter 1999, Reinking et al. 2000, Stauffer 2008). Relatively high reproductive rates in this Henslow's Sparrow population may be the product of multiple contributing factors, including the high-quality habitat and increased availability of resources from fire management, a smaller or maladapted predator community in the VOAGL, or as an artifact from our small sample size of nests. The estimated reproductive rates in 2022–2023, together with higher post-management population sizes, indicate the species likely has the capacity to sustain the local population.

Table 3. Model selection results for Henslow's Sparrow (*Centronyx henslowii*) nest survival at the Voice of America Game Land, North Carolina, USA for 2022–2023. We report differences in Akaike's Information Criterion corrected for small sample size (ΔAIC_c) between models and the best fitting model, model weight (w_i), number of parameters (k), and deviance.

Model	ΔAIC_c	w_i	k	Deviance
S(~Stage)	0.000[†]	0.250	2	19.364
S(~Time)	0.012	0.248	2	19.377
S(~Constant)	0.109	0.236	1	21.516
S(~Year)	2.002	0.092	2	21.366
S(~Robel)	2.067	0.089	2	21.432
S(~Open)	2.141	0.089	2	21.505

[†] AICc = 23.43.

Fluctuations in annual abundance appear to be a characteristic of this population. Historical data of Henslow's Sparrow at the VOAGL from 1994 to 2007, which consisted of raw counts of observed sparrows rather than abundance estimates, also varied annually (Appendix 2). Consistent with this pattern, our modeled estimates of abundance from 2011 to 2024 varied annually. Fluctuations in annual abundances may stem from unmodeled sampling heterogeneity (e.g., observation error, a misspecified model) or true stochasticity in the system (e.g., process variance). For example, inaccurate measurements of sparrow distances during point count surveys could bias density estimates in the HDS model and reduce model fit (Buckland et al. 2001). External regulatory factors, such as variable Henslow's Sparrow overwinter survival rates, may manifest as substantial interannual fluctuations in abundance on the breeding grounds (Sillett and Holmes 2002, Johnson 2006, Rushing 2019). Additionally, local factors, like habitat heterogeneity at the VOAGL and the timing of the annual prescribed burns, or regional factors, like the degree of connectivity (e.g., genetic, demographic) between the two North Carolina populations, could affect annual abundances (Rushing et al. 2016, Nastase 2024). The two Henslow's Sparrow breeding sites in North Carolina are separated by a distance of only ~26 km. Though there are no confirmed records of Henslow's Sparrows moving between these two grasslands, it is plausible that sparrows are opportunistically selecting breeding sites based on habitat conditions or breeding population densities, which would result in variable annual sparrow abundances at the VOAGL.

The shift in oscillations surrounding the lower pre-management average abundance to the higher post-management average abundance suggests a change in population size in response to management actions. The six-year period of sustained population growth from 2017 to 2022 hints that the implementation of fire management beginning in 2016 may be driving this response; however, additional years of data are needed to better detect population-level patterns in Henslow's Sparrow at the VOAGL. These possibilities highlight the importance of assessing Henslow's Sparrow populations throughout the species' annual cycle to characterize not just population change, but potential drivers and regulatory mechanisms affecting populations (Rushing et al. 2016, Stevens et al. 2024). Additionally, partitioning sources of error in abundance estimates is needed to fully understand if noise can be attributed to data collection methods, model specification and analysis, or to variation in the system itself (Caughley 1977, Humbert et al. 2009).

Our findings offer the foundation for reducing uncertainty in estimating Henslow's Sparrow abundance in the VOAGL and to begin identifying the underlying mechanisms driving change in this population. Continued implementation of fire management alongside the collection of additional years of monitoring data will likely improve our ability to detect population-level effects. Future efforts could include a well-designed mark-recapture study to estimate sex- and age-specific survival rates, temporary emigration, and recruitment at both North Carolina breeding sites to better characterize population dynamics in this portion of the Henslow's Sparrow range (DeSante et al. 1995, Kendall and Nichols 2002, Yirka et al. 2018). Additionally, though this population has exhibited increasing population sizes and high rates of reproduction in recent years, it may still be vulnerable to the effects of geographic isolation and lack of spatial redundancy in the region. Acquiring and managing additional grasslands in North Carolina could facilitate regional persistence of Henslow's Sparrow, especially given the species' ability to locate and colonize newly established grasslands (Herkert et al. 2018).

This study provides baseline data to gauge Henslow's Sparrow population status and response to management actions in a North Carolina grassland. Our analyses do not explicitly link change in abundance to the initiation of fire management at the VOAGL, though our findings are consistent with a positive response, and we expect this signal will strengthen in time with additional data. Increasing population sizes and relatively high reproductive output in this Henslow's Sparrow population diverge somewhat from the species' range-wide declining population trends but demonstrate the success of implementing fire management to benefit a vulnerable population at the trailing edge of the species' breeding range.

Author Contributions:

Conceived the idea, design, experiment: Collazo, J. C., Carpenter, J. P., Nastase, E. A.
Performed field data collection: Nastase, E. A., Carpenter, J. P., Collazo, J. C.
Wrote the paper: Nastase, E. A., Collazo, J. C., Hostetter, N. J., Carpenter, J. P.
Developed or designed methods: Collazo, J. C. , Hostetter, N. J., Nastase, E. A., Carpenter, J. P.
Analyzed data: Nastase, E. A., Collazo, J. C., Hostetter, N. J.
Contributed substantial materials, resources, or funding: Carpenter, J. P., Collazo, J. C.

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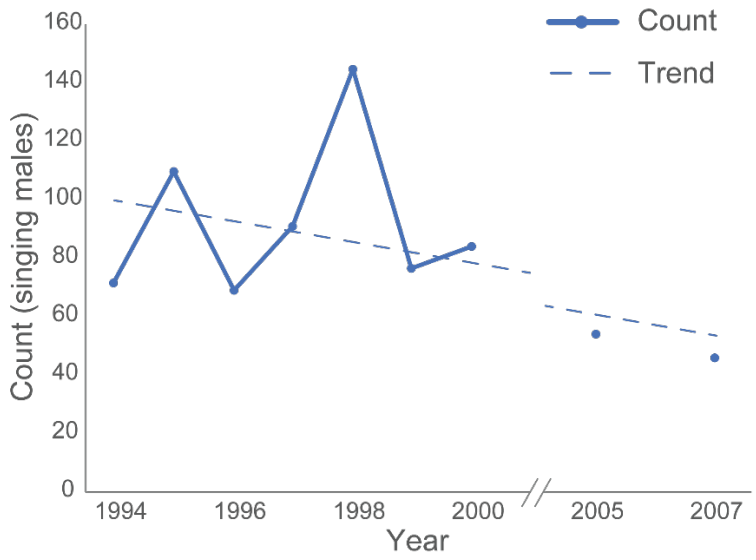
Appendix 1. Henslow's Sparrow nest habitat covariate data at the Voice of America Game Land, North Carolina, USA.

Please click here to download file 'appendix1.xlsx'.

Appendix 2. Counts of singing male Henslow's Sparrow at the Voice of America Game Land, North Carolina, USA from 1994–2007. Data are the total detections of sparrows, not model-derived abundance estimates. Counts were not conducted from 2001–2004 or in 2006. Data provided by John Wright.



Year	Count
1994	71
1995	109
1996	68
1997	90
1998	144
1999	76
2000	83
2005	53
2007	45