



Demography and site fidelity of a grassland bird, the Henslow's Sparrow, in powerline right-of-way habitat

Demografía y fidelidad al sitio de un ave de pastizal, el gorrión de Henslow, en el hábitat de derecho de paso de las líneas eléctricas

Elizabeth A. Hunter^{1,2} , Abigail Dwire³ and Todd M. Schneider⁴

ABSTRACT. Grassland birds are among the fastest declining avian species in North America, primarily due to habitat loss. In the southeastern United States, much grassland and open savanna habitat has been converted to timber production or agriculture, neither of which typically provides habitat for breeding or wintering grassland birds. Powerline right-of-ways could provide suitable habitat for many grassland species because these areas are maintained to be treeless. We studied the population dynamics of Henslow's Sparrows (*Centronyx henslowii*) wintering in powerline right-of-ways in southeastern Georgia through an 11-year mark-recapture study. We used a robust design Cormack-Jolly-Seber model to estimate probability of detection and apparent survival. Abundance varied substantially among years at each site, with density varying from 1.7 to 8.5 birds/ha. Within-year detection probability was moderately high at 28% (24-33%, 95% credible interval [CI]), but apparent survival was very low at 13% (9-17%, 95% CI). This low apparent survival was likely due to low return rates (and not necessarily low survival). However, birds that did return to the study sites had extremely high site fidelity, with 82% of across-year recaptures < 200 m apart. This apparent incongruity between low apparent survival rates (likely due to emigration from the study sites) and high site fidelity for returning individuals could be explained by the dependability of the right-of-way habitat, which differs from typically patchy and temporally variable grassland and savanna wintering habitats. Dependable habitat may allow for higher site fidelity than this species would otherwise have, potentially resulting in the high densities we observed. Thousands of miles of right-of-ways in Georgia, and other southeastern states, could be managed to maximize potential habitat for declining grassland bird species.

RESUMEN. Las aves de pastizal se encuentran entre las especies de aves que más rápidamente están disminuyendo en Norteamérica, debido principalmente a la pérdida de hábitat. En el sureste de Estados Unidos, una gran parte del hábitat de pastizal y de sabana abierta se ha convertido a la producción maderera o a la agricultura, que en ningún caso proporcionan hábitat apropiado para las aves de pastizal en época reproductiva o de invernada. Los derechos de paso de las líneas eléctricas podrían proporcionar un hábitat adecuado para muchas especies de pastizales, ya que estas zonas se mantienen sin árboles. Estudiamos la dinámica poblacional del gorrión de Henslow (*Centronyx henslowii*) en los derechos de paso de las líneas eléctricas en el sureste de Georgia durante la invernada, mediante un estudio de marcado y recaptura de 11 años. Se utilizó un modelo de diseño robusto Cormack-Jolly-Seber para estimar la probabilidad de detección y la supervivencia aparente. La abundancia varió sustancialmente entre años para cada sitio, con una densidad que osciló entre 1,7 y 8,5 aves/ha. La probabilidad de detección dentro del año fue moderadamente alta, de un 28% (24-33%, intervalo de credibilidad [IC] del 95%), pero la supervivencia aparente fue muy baja, un 13% (9-17%, IC del 95%). Esta baja supervivencia aparente se debió probablemente a las bajas tasas de retorno (y no necesariamente a la baja supervivencia). Sin embargo, aquellas aves que si regresaron a los lugares de estudio tuvieron una fidelidad al lugar extremadamente alta, con un 82% de recapturas interanuales a menos de 200 m de distancia. Esta aparente incongruencia entre las bajas tasas de supervivencia aparentes (probablemente debidas a la emigración de los lugares de estudio) y la alta fidelidad al lugar de los individuos que regresan podría explicarse por la fiabilidad del hábitat de derecho de paso, que difiere de los hábitats de invernada de pastizales y sabanas, que se presentan típicamente como parches y son variables temporalmente. La fiabilidad del hábitat llevaría a una mayor fidelidad al sitio que la que de otro modo tendría esta especie, lo que daría lugar a las altas densidades que observamos. Los miles de millas de los derechos de paso en Georgia, y en otros estados del sureste, podrían manejarse de manera tal de maximizar el hábitat potencial de las especies de aves de pastizal en declive.

Key Words: *Georgia; Henslow's sparrow; mark-recapture; site fidelity; survival*

INTRODUCTION

Grassland birds are some of the fastest declining bird species in North America (Vickery and Herkert 2001, Brennan and Kuvlesky 2005, Rosenberg et al. 2019), primarily due to widespread habitat conversion to agriculture (Herkert 1994, Vitousek et al. 1997). Remnant grasslands are not likely to support populations of even once common species over the long term

(With et al. 2008), and so improved management of “marginal” habitats, such as field margins and utility corridors, could be important for bolstering declining grassland species. Utility right-of-ways (RoWs) are by necessity managed to be treeless. Depending on the method of tree removal (i.e., mowing, herbiciding, or burning), species-rich grassland plant communities can flourish (Yahner and Hutnik 2005), potentially

¹U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, ²Department of Fish and Wildlife Conservation, Virginia Tech, ³Department of Biology, Georgia Southern University, ⁴Georgia Department of Natural Resources, Wildlife Resources Division, Wildlife Conservation Section

providing permanent habitat for grassland birds. Several studies have shown that grassland birds will use RoWs as both breeding and wintering habitat (Meehan and Haas 1997, Confer and Pascoe 2003, Bulluck and Buehler 2006), but whether RoWs can support grassland bird populations continuously over long time periods remains unknown.

One grassland bird species that could potentially benefit from RoW habitat is the Henslow's Sparrow (*Centronyx henslowii*), a migratory species that breeds in grasslands in the midwestern and northeastern United States and winters in southeastern coastal plain pine savannas (Herkert et al. 2020). Henslow's Sparrow populations declined steeply between 1966 and the late 1990s (Sauer et al. 2013, 2020), to the extent that species abundance declined by 95% over that time period (Herkert 2007). Grassland habitat restoration on the breeding grounds in the early 2000s reversed the declining trend in some populations (Herkert 2007), indicating that the species decline was likely due to habitat loss. Although the status of the species is likely driven primarily by conditions on the breeding grounds (McCauley et al. 2017), wintering habitat requirements also need to be met for long-term recovery. Southeastern coastal plain pine savannas have declined by over 90% (Landers et al. 1995) and were typically replaced with timber production or agriculture, neither of which provide much grassland bird habitat. Right-of-ways therefore could provide needed reliable wintering habitat for Henslow's Sparrows and other grassland birds because productive lands remain in high demand in the Southeast and are unlikely to be converted to conservation easements that could support early successional species (Burger 2000, Dale et al. 2017). Although RoWs may provide consistent early successional vegetation, their long-term utility to birds as habitat may be lessened due to their linear nature and high edge density (Chasko and Gates 1982); thus, it is important to assess bird use of these habitats over time.

To assess whether Henslow's Sparrows use RoW habitat consistently over long periods of time, we studied the demography and site fidelity of Henslow's Sparrow populations at three RoW sites in southeastern Georgia, USA. We conducted a mark-recapture study of wintering sparrows from 2011-2021. We sought to address the following questions: (1) what is the apparent survival probability and density of Henslow's Sparrows wintering in RoWs, and does it vary among years? and (2) what is the site fidelity for Henslow's Sparrows returning to RoW habitat? Addressing these questions will provide evidence as to whether Henslow's Sparrows have a consistent preference for RoW habitats and whether RoWs can provide reliable habitat for this at-risk species.

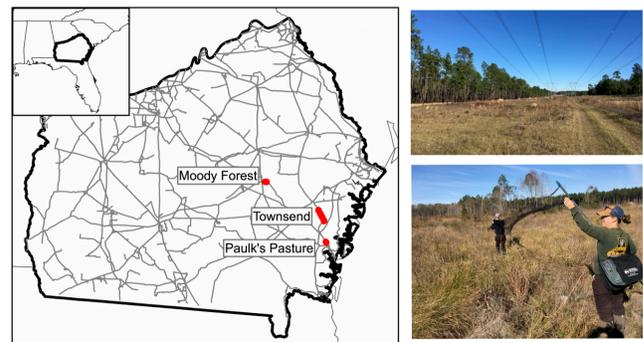
METHODS

Study sites

We sampled Henslow's Sparrow populations in powerline RoWs at three Wildlife Management Area (WMA) sites in southeastern Georgia: Paulks Pasture WMA, Townsend WMA, and Moody Forest WMA (Fig. 1). Sites and surveyed areas were chosen because of incidental observations of wintering Henslow's Sparrows or the presence of potentially suitable habitat. All sites are near the Altamaha River, but Paulks Pasture and Townsend are in the lower coastal plain with wetter soil conditions, and Moody Forest in the upper coastal plain is drier. Moody Forest also differs from the other two sites in that the RoW is surrounded

by active pine savanna restoration that is managed with thinning and burning; Paulks Pasture and Townsend are primarily surrounded by timber production. All RoWs were managed through mowing and selective herbiciding to remove woody vegetation that would interfere with powerlines. The herbaceous understory primarily consisted of *Aristida* spp., *Andropogon* spp., and *Dichantherium* spp. of grasses, although sites varied in composition and density of herbaceous species.

Fig. 1. Sites for study of Henslow's Sparrow (*Centronyx henslowii*) demography and site fidelity in the coastal plain (thick black line) of Georgia, USA from 2011-2021. Gray lines are powerline right-of-ways, and red areas are where the study was conducted. Photographs show example habitat at Moody Forest (top) and Townsend (bottom) Wildlife Management Areas (photo credit: Kevin Loope).



Survey methods

Each site was divided into survey transects and, typically, transects ran from one powerline pole to the next, with this distance varying among sites. We surveyed for Henslow's Sparrows by dragging a weighted rope with an effective width (accounting for slight bow in rope while dragging) of 20 m centered on the middle of the powerline. At Paulks Pasture, 20-m transects spanned 90% of the powerline width on average and were continuous across a total length of 2070 m. At Townsend, 20-m transects spanned 60% of the powerline width on average, and the 4185 m of transects were mostly discontinuous (i.e., most 200 m lengths of transect were separated from each other by unsampled areas, but some transects did abut each other in groups of two or three). At Moody Forest, 20-m wide transects spanned 35% of the powerline width on average and were continuous across a total length of 1880 m, except for a break due to a permanently flooded area. These discontinuities were not included in total area calculations for the sites (i.e., only sampled areas are included in site areas). Multiplying the effective transect width by the total transect length, the total surveyed area was 4.14 ha at Paulks Pasture, 8.37 ha at Townsend, and 3.76 ha at Moody Forest. Birds were only captured (with few exceptions) after being flushed by the dragged rope (instead of being flushed from adjacent areas that were not dragged), so these area calculations are representative of the site size for population density calculations.

We surveyed all transects three times in 2011-2018 and two times in 2019-2021 from early January to mid-March. By early January, most Henslow's Sparrows would have settled into their wintering

home ranges (Johnson et al. 2009). Each sampling round at a site was separated by approximately three weeks. On every survey occasion, we recorded the number of surveyors present, which typically consisted of a mix of experienced professionals and volunteers as well as novices. Having more people on a survey likely improved capture rates (more chances to spot a flushed bird and greater coverage for rushing birds into a mist net). We also recorded the flush location when it was known.

After flushing a bird, we set up a single mist net (12 m x 2.5 m x 30 mm mesh nylon) to capture it (Bechtold and Stouffer 2005). We outfitted each captured individual with a uniquely numbered USGS aluminum leg band and measured wing chord (mm) and mass (g). After processing each individual, we returned to the transect to continue from the flush point. Birds that were flushed but not captured were not included in subsequent analyses. Fieldwork methods were approved by the Institutional Animal Care and Use Committee of Georgia Southern University (#I19009) and the Georgia Department of Natural Resources (#1000838720).

Site fidelity

For all individuals that were captured at least twice (whether within year or across years) with a known flush location (~25% of captures had missing flush GPS coordinates), we calculated the maximum distance between flush locations. We also repeated this calculation using only across-year recaptures.

Population model

Annual apparent survival probability and within season capture probability were estimated from capture-recapture data using a Cormack-Jolly-Seber model (inclusion of individuals in the likelihood function was conditioned on initial capture; Royle and Dorazio 2008). We assumed population closure between mist-netting surveys within a year, or “secondary” capture occasions (standard “robust-design” assumption; Kendall et al. 1997), with populations open to mortality among years, or “primary” capture occasions (total of 11 years). We implemented this model in a Bayesian framework to obtain posterior distributions through Markov chain Monte Carlo (MCMC) simulations in the computer program Nimble (de Valpine et al. 2017) run through program R (R Core Team 2021).

We modeled expected probability of capture (p) as a logit-linear function of survey effort, which was the number of “person-days” spent surveying each site in a secondary survey period (e.g., it took 2 days to survey Townsend WMA in the first survey round in 2019, with 6 surveyors on the first day and 4 surveyors on the second day; thus, the effort for that survey round was 10 person-days). Because the sites varied in size (and thus required more or less effort to survey), we divided the number of person-days per secondary period by the site area in hectares (ha); thus, effort was measured in person-days/ha.

We modeled expected annual survival probability (ϕ) as a logit-linear function of individual mass in grams. If a bird was captured multiple times, we used the mean of mass measurements. The mass covariate was standardized across all sites. To account for missing mass information (8.3% of captures were missing mass data), we drew from a normal prior probability distribution.

We created four separate models for comparison: (1) a baseline model with only the above covariates (effort effect on capture

probability, mass effect on survival probability); (2) a $p(s,t)$ model in which capture probability varied by site (s) and year (t); (3) a $\phi(s,t)$ model in which survival probability varied by site and year; and (4) a $p(s,t)\phi(s,t)$ model in which both capture and survival probabilities varied by site and year. We compared the candidate models using the widely applicable information criterion (WAIC). The WAIC is analogous to the Akaike information criterion but is applicable to Bayesian models (Vehtari et al. 2017). We consider models within 2 WAIC units of the top model (lowest WAIC score) to deserve consideration, models within 3-7 WAIC units of the top model to have less support, and models with WAIC units > 7 from the top model to have no support (Spiegelhalter et al. 2002).

Prior to analysis, we standardized mass and effort covariates using z-score scaling to improve model convergence. We assigned vague prior probability distributions to all free parameters (Table 1). We ran 3 independent Markov chains, discarding the first 5000 samples as a burn-in and storing the remaining 5000 iterations for analysis. We tested for Markov chain convergence to a stationary posterior distribution with the Gelman-Rubin diagnostic, and we considered that convergence had occurred when the Gelman-Rubin statistic was < 1.1 for monitored parameters and derived quantities (Bolker 2008). We summarized posterior distributions for all parameters and derived quantities with the median of all MCMC samples as a point estimate and the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval (CI; Bolker 2008).

Table 1. Comparison of candidate models used to estimate detection probability (p) and apparent survival (ϕ) of wintering Henslow’s Sparrows (*Centronyx henslowii*) in the coastal plain of Georgia, USA, based on mark-recapture conducted from 2011-2021. Models allowed p and ϕ to vary across sites (s) or time (t) or were constant across sites and time (\cdot). The top model, $p(s,t)\phi(s,t)$, indicated that Henslow’s Sparrow apparent survival and detection probability varied across sites and over time, but other models indicating no variation across sites and time had similar levels of support. Data were analyzed in a Bayesian framework and models were compared using the widely applicable information criterion (WAIC). Models were ranked in order of descending WAIC values. The difference between a model’s WAIC value and the top model’s WAIC value (Δ WAIC) allows for model comparison.

Model Name	WAIC	Δ WAIC
$p(s,t)\phi(s,t)$	4327.8	0
$p(\cdot)\phi(s,t)$	4328.9	1.1
$p(s,t)\phi(\cdot)$	4332.7	4.9
$p(\cdot)\phi(\cdot)$	4333.2	5.4

For the final selected model, we calculated total abundance at each site using a Horvitz-Thompson estimator (McDonald and Amstrup 2001). To assess the goodness-of-fit of our final model, we measured the discrepancy between the actual dataset and data simulated under the estimated parameters to calculate a Bayesian p-value (values close to 0.5, and far from 0 or 1, indicate a well-fitting model). We simulated 1000 new datasets by drawing parameter values from posterior distributions (MCMC samples) with replacement and calculating apparent survival and capture

rates while conditioning on the exact same survey effort and numbers of new individuals at each site in each year as in the observed data. We then counted the number of individuals known to be alive at each site in each year (captured at least once) and the proportion of those individuals that were seen during any later year. We used the discrepancy in these proportions between actual and simulated datasets to calculate the Bayesian p-value (Ergon and Gardner 2014).

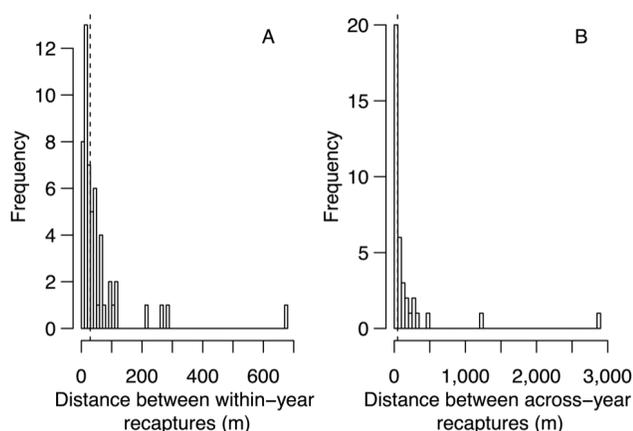
RESULTS

We captured 622 unique individuals across 798 total captures. Individuals were captured 1.28 ± 0.59 (mean \pm standard deviation) times on average (range 1-5), and 56 individuals were recaptured across years at least once (9% of individuals). Average effort per survey was 1.09 person-days/ha (range 0.24-3.86). Average wing chord length was 52.6 ± 1.7 mm, and average mass was 12.9 ± 0.9 g.

The maximum distance moved among captures was 27.7 km, i.e., a single individual that was captured and banded at Paulks Pasture WMA and recaptured at Townsend WMA 5 days later; however, this long-distance movement was an exception. Generally, recaptured birds did not travel far between captures (Fig. 2). Within-year recapture distance averaged 58.9 ± 103.3 m (median 29.3 m, range 3-672 m, excluding the 27.7 km movement described above) for $n = 54$ individuals, and across-year recapture distance averaged 192.1 ± 494.2 m (median 46.7 m, range 7-2875 m) for $n = 38$ individuals. Most (82%) across-year recapture distances were < 200 m apart (the typical transect length), indicating that returning birds generally had high site fidelity.

Capture probability increased with greater survey effort (0.44 [0.28-0.6, 95% CI] effect on logit scale, which translates to a 0.11

Fig. 2. Frequency of the maximum distance between within-year (A) and across-year (B) recaptures of Henslow's Sparrows (*Centronyx henslowii*) that were captured at least twice at three wildlife management areas in Georgia, USA from 2011-2021, showing generally small distances between recaptures. One within-year distance (27.7 km) was removed in A to improve visibility of the majority of the data. Dashed vertical lines indicate means.



increase in capture probability with an increase in effort from 1 person-day/ha to 2 person-days/ha). Apparent survival was not affected by mass. Based on WAIC, the best model was the $p(s,t)\phi(s,t)$ model in which both capture and survival probabilities varied by site and year (Table 1). We used this model to estimate capture probability and apparent annual survival for each site and year (Fig. 3). The Bayesian p-value of 0.46 indicated that the $p(s,t)\phi(s,t)$ model could have plausibly generated the observed data, and there was no observed lack of fit of the data to the model. However, the 95% credible intervals of the time and site varying effects on p and ϕ overlapped with zero, and all models were within 7 WAIC units of the top model, suggesting that there was no meaningful difference in capture probability or apparent survival among sites and years. Average within-year recapture probability was 0.28 (0.24-0.33, 95% CI). Average annual apparent survival probability was 0.13 (0.09-0.17, 95% CI). Abundance varied substantially among years at each site, with density varying from 1.7 to 8.5 birds/ha (Fig. 4). Average density across all years was 5.2 birds/ha at Paulks Pasture, 5.3 birds/ha at Townsend, and 3.8 birds/ha at Moody Forest. There was no apparent synchrony in abundance among sites, although the two sites in the lower coastal plain (Paulks Pasture and Townsend) experienced more similar increases and decreases in abundance compared to Moody Forest in the upper coastal plain (Fig. 4).

Fig. 3. Detection probability (black) and apparent survival (gray) of Henslow's Sparrow (*Centronyx henslowii*) populations at 3 sites (Paulks Pasture [A], Townsend [B], Moody Forest [C]) in Georgia, USA, showing similarity in estimates across sites and over time (2011-2021). Estimates are from a Cormack-Jolly-Seber mark-recapture model that allows detection probability and apparent survival to vary across sites and time (top model in Table 1). Points are medians and error bars represent 95% credible intervals.

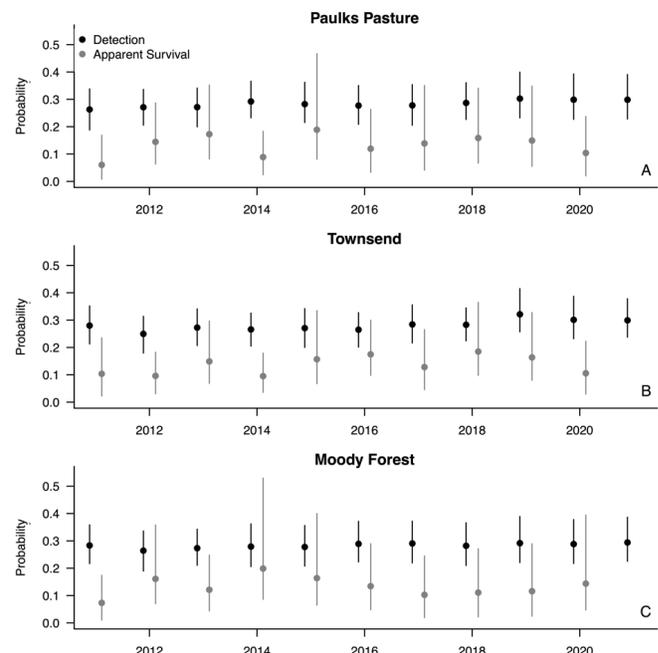
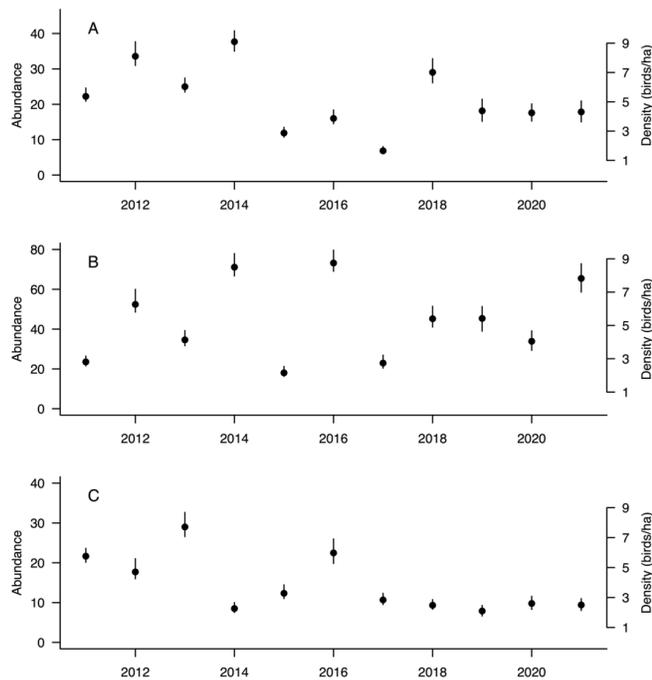


Fig. 4. Henslow's Sparrow (*Centronyx henslowii*) abundance (left axis) and density (right axis) derived from Cormack-Jolly-Seber mark-recapture model using mark-recapture data from 2011-2021 at three Wildlife Management Areas in Georgia, USA: Paulks Pasture (A), Townsend (B), and Moody Forest (C). Points are medians and error bars represent 95% credible intervals.



DISCUSSION

Our results demonstrate that utility right-of-ways (RoWs) can provide consistent habitat for wintering Henslow's Sparrows over a decadal time frame. Over the 11-year study period, all 3 WMAs were consistently occupied by high densities of Henslow's Sparrows, and individuals often returned to the same RoW segment. Densities at the three WMAs ranged between 3.8-5.3 birds/ha (averages across all years for a site), which is higher than most reported density estimates elsewhere in the species range. In Arkansas saline soil barrens, densities ranged 0.3-2.3 birds/ha (Holimon et al. 2008), and in longleaf pine savannas in Louisiana, densities ranged ~1-3 birds/ha (Palasz et al. 2010, Johnson et al. 2011). Some of the highest reported densities were in Mississippi, in bog habitat where densities reached 3.8 birds/ha and were higher than those in upland pine habitat managed for Red-cockaded Woodpeckers (*Leuconotopicus borealis*; Brooks and Stouffer 2011). This suggests that bog habitat can support more Henslow's Sparrows than upland savanna habitat (Plentovich et al. 1999), and our results reflect that pattern, too. Paulks Pasture and Townsend WMAs had wetter, boggy habitat and higher bird densities than the more upland Moody Forest WMA.

Many studies that report high densities of Henslow's Sparrows are conducted on lands that are managed with prescribed burning (e.g., Palasz et al. 2010, Brooks and Stouffer 2011, Johnson et al.

2011). Although burning occurred on RoWs at Moody Forest WMA occasionally, management of the RoWs was primarily through mowing and herbiciding, which are likely logistically easier for utility companies to implement (Arner 1977). It is possible that even greater numbers of Henslow's Sparrows could be supported if the habitat were managed through burning, but our results indicate that the current management regime is providing consistently suitable habitat. In fact, we report density estimates substantially higher than other studies (those cited in the previous paragraph). High density estimates could indicate one of two things. High density could indicate high habitat quality (e.g., high food availability), i.e., if birds are able to satisfy their needs in a small area, than more individuals can occupy a RoW. The selective herbiciding of woody vegetation in RoWs may maintain vegetation in a favorable state for longer periods of time compared to natural ecosystems where woody plants may become dominant more quickly. However, density is not always correlated with habitat quality (Van Horne 1983, Johnson et al. 2011), and density may even be inflated if there is not enough suitable habitat in the surrounding area to support the population of birds (Hobbs and Hanley 1990). If many of the birds use the RoW for some of their needs, but then use areas adjacent to the RoW as well, densities in the RoW may be artificially inflated. However, a telemetry study at these sites indicated that the vast majority of birds caught in the RoW (95%) only used habitat within the RoW and did not venture out to adjacent habitats (Dwire 2021). This suggests that our reported densities reflect truly high levels of RoW use. The management of these sites appears to be providing for a high density of Henslow's Sparrows, even though management is not focused specifically on this species nor is it coordinated among the three sites.

Although density estimates in RoWs were higher than those reported in more "natural" habitat, apparent survival rates (13% average annual apparent survival) appeared to be low. Johnson et al. (2011) estimated survival for the 5-month winter period to be 82%; extrapolating this estimate to an annual timeframe is challenging because survival is likely to be lower during migration, and there are no other studies that have attempted to estimate annual survival rates for Henslow's Sparrows. However, our estimate is much lower than annual survival estimates for other similar grassland bird species, such as Grasshopper Sparrows (*Ammodramus saviarum*) and Savannah Sparrows (*Passerculus sandwichensis*), which have annual survival estimates ranging from 30 to 80% (from multiple studies summarized in McCauley et al. 2017), and Henslow's Sparrows are unlikely to have such drastically lower survival rates. In addition, if annual survival were truly 13%, we would expect catastrophic population declines, which we did not observe at our sites, nor at the scale of the range (as evidenced by Breeding Bird Survey data, Sauer et al. 2020). A potential explanation is that birds could have moved slightly outside of the narrow 20-m rope drag transect and not been recaptured by our surveys. However, at Paulks Pasture, we covered 90% of the RoW width with a 20-m transect, and our detection and apparent survival rates were not higher at that site compared to the others in which a smaller proportion of the RoW width was surveyed (Fig. 3), indicating that our surveys were sufficient to accurately assess apparent survival.

Given these lines of reasoning, it is likely that our low apparent survival estimate is confounded by high rates of emigration from

the study sites and is not actually indicative of extremely high mortality rates. In other words, from one year to the next, many Henslow's Sparrows likely move to other areas that were not sampled. We found that this low apparent survival/high emigration rate was consistent across years and sites (Fig. 3), indicating that the volatility observed in abundance (Fig. 4) was likely driven by fluctuations in the number of new individuals arriving to the RoWs each year. This matches with a pattern of nesting success being driven by temperature and precipitation (McCauley et al. 2017) resulting in the number of successful fledglings (and therefore new individuals on the wintering grounds) varying from year to year, a pattern that has also been documented in other sparrow species (Rotenberry and Wiens 1991, Chase et al. 2005). Another potential explanation for fluctuations in the number of new individuals arriving to wintering RoWs each year could be changes in habitat conditions in nearby wintering sites. Right-of-ways remain in relatively stable condition, but nearby areas (e.g., old fields, clear cuts) could have greater variation in their quality and availability as habitat for Henslow's Sparrows from year to year. If there is low availability of alternative wintering sites, a RoW may "receive" more new individuals in a given year. Testing these alternative hypotheses would require knowledge of the connectivity between breeding and wintering populations and the state of alternative wintering sites near RoWs each year.

Despite the high evident emigration inferred from low "apparent survival" rates, those individuals that were recaptured across years generally returned to nearly the same location where they were previously captured. We found that more than three-fourths of across-year returning individuals returned to within 200 m of the original site of capture. Other studies have reported high within-year site fidelity (Plentovich et al. 1998, Johnson et al. 2009), but this is the first study to report on across-year site fidelity in Henslow's Sparrows. What could explain the apparent contradiction of high emigration rates (inferred from low apparent survival) coupled with high across-year site fidelity for some individuals? It is likely that "natural" Henslow's Sparrow habitat would have been spatially and temporally variable; this is evidenced by the strong habitat selection for sites that have been recently burned (Bechtoldt and Stouffer 2005, Thatcher et al. 2006). The location of recently burned areas changes from year to year, so Henslow's Sparrows may have adapted habits of not returning to the same area from one winter to the next (or returning to the previous site first to assess habitat condition and then moving on to a new site). After Henslow's Sparrows arrive on the wintering grounds in October and November, there is still substantial movement of birds among sites (Johnson et al. 2009), suggesting that individuals seek out and assess ideal wintering habitat after migrating. Because we always began surveys after this fall "settling in" period (starting in January), we do not know whether this movement also occurs in the RoW habitat. It is possible that because the RoW habitat is generally surrounded by unsuitable areas (e.g., pine plantations), some individuals forego this seeking behavior and return directly to the RoW. Therefore, the high site fidelity that we observed may be a more recent phenomenon made possible by RoWs that are managed to be in a consistent favorable state through herbicide and mowing.

Our results may indicate that RoWs are providing a different type of habitat than typical grassland or savanna ecosystems; however,

this is not necessarily a detriment. Right-of-ways clearly can provide consistent habitat over long periods of time (our study spanned several generations of Henslow's Sparrows) indicating that this relatively small feature on the landscape can be discovered by migrating individuals and may act as a refuge when other habitats are not available or not in good condition. The high densities that can be supported within RoWs could also act as propagule sites to seed new populations as "natural" savanna habitat is restored nearby. This process may already be happening at Moody Forest WMA, which has well-managed pine savanna habitat adjacent to the RoW. Given that RoWs are long, linear features, they could also act to maintain connectivity of populations (Komonen et al. 2013). The sheer quantity of potential habitat in RoWs in the state of Georgia alone represents a huge opportunity to create suitable habitat for wintering (and potentially breeding; Meehan and Haas 1997) grassland birds. Georgia Power is the primary utility company with powerlines in Georgia and manages 140,000 kilometers of powerlines (Fig. 1). Not all RoWs have the same vegetative characteristics as those we studied but directed management could potentially create thousands of hectares of habitat, providing a needed refuge for declining grassland birds.

Responses to this article can be read online at:

<https://journal.afonet.org/issues/responses.php/77>

Acknowledgments:

The authors thank Allison Colter, Chris Coppola, Chris Depkin, Clyde Dixon, Dana Dixon, Tony Dodd, Ann Gilmore, Ashley Harrington, Eddie Hatchet, Ethan Hatchet, Rob Hicks, Robert Horan, Alex Isenberg, John Jensen, Gene Keferl, Tim Keyes, Jason Lee, Kevin Loope, Chuck Martin, Charlie Muise, Kara Nitschke, Jim Ozier, Sean Peacock, Perri Rothemich, Bob Sattelmeyer, Evan Schneider, Christian Scott, Fletcher Smith, Matthew Stoddard, Amanda Tveite, Miranda Wilkinson, and many other volunteers for their help in the field. We thank the Georgia Power Company for granting access to powerline right-of-ways and Tony Dodd and Jim Ozier of Georgia Power as well as Chuck Martin of The Nature Conservancy who assisted with access and logistics. We thank Phil Stouffer and two anonymous reviewers for reviews of this manuscript. This research was funded by the Georgia Department of Natural Resources Wildlife Resources Division through a U.S. Fish and Wildlife Service State Wildlife Grant and Georgia Southern University. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

Data Availability:

The datalcode that support the findings of this study are openly available in GitHub at https://github.com/lelizabetahunter/Henslows_Sparrows. Ethical approval for this research study was granted by the Institutional Animal Care and Use Committee of Georgia Southern University (#I19009).

LITERATURE CITED:

- Arner, D. H. 1977. Transmission line rights-of-way management. Series Number 76/20.2 Department of the Interior, Fish and Wildlife Service, Office of Biological Services, Washington, D.C., USA.
- Bechtoldt, C. L., and P. C. Stouffer. 2005. Home-range size, response to fire, and habitat preferences of wintering Henslow's Sparrows. *Wilson Bulletin* 117:211-225. <https://doi.org/10.1676/04-110.1>
- Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, New Jersey, USA.
- Brennan, L. A., and W. P. Kuvlesky, Jr. 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69:1-13. [https://doi.org/10.2193/0022-541x\(2005\)069<0001:nagbau>2.0.co;2](https://doi.org/10.2193/0022-541x(2005)069<0001:nagbau>2.0.co;2)
- Brooks, M. E., and P. C. Stouffer. 2011. Interspecific variation in habitat preferences of grassland birds wintering in southern pine savannas. *Wilson Journal of Ornithology* 123:65-75. <https://doi.org/10.1676/10-039.1>
- Bulluck, L. P., and D. A. Buehler. 2006. Avian use of early successional habitats: are regenerating forests, utility right-of-ways and reclaimed surface mines the same? *Forest Ecology and Management* 236:76-84. <https://doi.org/10.1016/j.foreco.2006.08.337>
- Burger, W. 2000. Wildlife responses to the Conservation Reserve Program in the Southeast. Pages 55-74 in W. L. Hohman and D. J. Halloum, editors. A comprehensive review of farm bill contributions to wildlife conservation, 1985-2000. U.S. Department of Agriculture, Natural Resources Conservation Service, Wildlife Habitat Management Institute, Technical Report, USDA/NRCS/WHMI-2000.
- Chase, M. K., N. Nur, and G. R. Geupel. 2005. Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: a long-term study. *Auk* 122:571-592. <https://doi.org/10.1093/auk/122.2.571>
- Chasko, G. G., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* 82:3-41.
- Confer, J. L., and S. M. Pascoe. 2003. Avian communities on utility rights-of-ways and other managed shrublands in the northeastern United States. *Forest Ecology and Management* 185:193-205. [https://doi.org/10.1016/S0378-1127\(03\)00255-X](https://doi.org/10.1016/S0378-1127(03)00255-X)
- Dale, V. H., E. S. Parish, K. L. Kline, and E. Tobin. 2017. How is wood-based pellet production affecting forest conditions in the southeastern United States? *Forest Ecology and Management* 396:143-149. <https://doi.org/10.1016/j.foreco.2017.03.022>
- de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. T. Lang, and R. Bodik. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics* 26:403-413. <https://doi.org/10.1080/10618600.2016.1172487>
- Dwire, A. W. 2021. Habitat use of wintering Henslow's Sparrows (*Centronyx henslowii*) in power line right-of-ways. Thesis. Georgia Southern University, Statesboro, Georgia, USA. [online] URL: <https://digitalcommons.georgiasouthern.edu/cgi/viewcontent.cgi?article=3526&context=etd>
- Ergon, T., and B. Gardner. 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture-recapture data. *Methods in Ecology and Evolution* 5:1327-1336. <https://doi.org/10.1111/2041-210X.12133>
- Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecological Applications* 4:461-471. <https://doi.org/10.2307/1941950>
- Herkert, J. R. 2007. Evidence for a recent Henslow's Sparrow population increase in Illinois. *Journal of Wildlife Management* 71:1229-1233. <https://doi.org/10.2193/2006-029>
- Herkert, J. R., P. D. Vickery, and D. E. Kroodsma. 2020. Henslow's Sparrow (*Centronyx henslowii*), version 1.0. In P. G. Rodewald, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.henspa.01>
- Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54:515-522. <https://doi.org/10.2307/3809344>
- Holimon, W. C., C. T. Witsell, W. H. Baltosser, and C. W. Rideout. 2008. Density and habitat associations of Henslow's Sparrows wintering in saline soil barrens in southern Arkansas. *Journal of Field Ornithology* 79:364-370. <https://doi.org/10.1111/j.1557-9263.2008.00194.x>
- Johnson, E. I., J. K. DiMiceli, and P. C. Stouffer. 2009. Timing of migration and patterns of winter settlement by Henslow's Sparrows. *Condor* 111:730-739. <https://doi.org/10.1525/cond.2009.080025>
- Johnson, E. I., J. K. DiMiceli, P. C. Stouffer, and M. E. Brooks. 2011. Habitat use does not reflect habitat quality for Henslow's Sparrows (*Ammodramus henslowii*) wintering in fire-managed Longleaf pine savannas. *Auk* 128:564-576. <https://doi.org/10.1525/auk.2011.10287>
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563-578. [https://doi.org/10.1890/0012-9658\(1997\)078\[0563:eteucr\]2.0.co;2](https://doi.org/10.1890/0012-9658(1997)078[0563:eteucr]2.0.co;2)
- Komonen, A., T. Lensu, and J. S. Kotiaho. 2013. Optimal timing of power line rights-of-ways management for the conservation of butterflies. *Insect Conservation and Diversity* 6:522-529. <https://doi.org/10.1111/icad.12009>
- Landers, J. L., D. H. van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance? *Journal of Forestry* 93:39-44. [online] URL: https://www.srs.fs.usda.gov/pubs/ja/ja_landers001.pdf
- McCauley, L. A., C. A. Ribic, L. Y. Pomara, and B. Zuckerberg. 2017. The future demographic niche of a declining grassland bird fails to shift poleward in response to climate change. *Landscape Ecology* 32:807-821. <https://doi.org/10.1007/s10980-017-0487-x>
- McDonald, T. L., and S. C. Amstrup. 2001. Estimation of population size using open capture-recapture models. *Journal of Agricultural, Biological, and Environmental Statistics* 6:206-220. <https://doi.org/10.1198/108571101750524553>

- Meehan, A. L., and C. A. Haas. 1997. Use of a powerline corridor by breeding and wintering birds in Giles County, Virginia. *Virginia Journal of Science* 48:259-264.
- Palasz, L. M., M. E. Brooks, and P. C. Stouffer. 2010. Regional variation in abundance and response to fire by Henslow's Sparrows in Louisiana. *Journal of Field Ornithology* 81:139-150. <https://doi.org/10.1111/j.1557-9263.2010.00271.x>
- Plentovich, S., N. R. Holler, and G. E. Hill. 1999. Habitat requirements of Henslow's Sparrows wintering in silvicultural lands of the Gulf Coastal Plain. *Auk* 116:109-115. <https://doi.org/10.2307/4089458>
- Plentovich, S. M., N. R. Holler, and G. E. Hill. 1998. Site fidelity of wintering Henslow's Sparrows. *Journal of Field Ornithology* 69:486-490.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: <https://www.R-project.org/>
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. *Science* 366:120-124. <https://doi.org/10.1126/science.aaw1313>
- Rotenberry, J. T., and J. A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology* 72:1325-1335. <https://doi.org/10.2307/1941105>
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego, California, USA. <https://doi.org/10.1016/B978-0-12-374097-7.50001-5>
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski, Jr. 2013. The North American breeding bird survey 1966--2011: summary analysis and species accounts. *North American Fauna* 79:1-32. <https://doi.org/10.3996/nafa.79.0001>
- Sauer, J. R., W. A. Link, and J. E. Hines. 2020. The North American breeding bird survey, analysis results 1966-2019. U.S. Geological Survey data release, U.S. Geological Survey, Washington, D.C., USA. <https://doi.org/10.5066/P96A7675>
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society, Series B* 64:583-639. <https://doi.org/10.1111/1467-9868.00353>
- Thatcher, B. S., D. G. Krementz, and M. S. Woodrey. 2006. Henslow's Sparrow winter-survival estimates and response to prescribed burning. *Journal of Wildlife Management* 70:198-206. [https://doi.org/10.2193/0022-541x\(2006\)70\[198:hswear\]2.0.co;2](https://doi.org/10.2193/0022-541x(2006)70[198:hswear]2.0.co;2)
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901. <https://doi.org/10.2307/3808148>
- Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27:1413-1432. <https://doi.org/10.1007/s11222-016-9696-4>
- Vickery, P. D., and J. R. Herkert. 2001. Recent advances in grassland bird research: where do we go from here? *Auk* 118:11-15. <https://doi.org/10.1093/auk/118.1.11>
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494-499. <https://doi.org/10.1126/science.277.5325.494>
- With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141:3152-3167. <https://doi.org/10.1016/j.biocon.2008.09.025>
- Yahner, R. H., and R. J. Hutnik. 2005. Plant species richness on an electric transmission right-of-way using integrated vegetation management. *Journal of Arboriculture* 31: 124-130. <https://doi.org/10.48044/jauf.2005.015>