Occupancy Patterns of Regionally Declining Grassland Sparrow Populations in a Forested Pennsylvania Landscape

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Abstract: Organisms can be affected by processes in the surrounding landscape outside the boundary of habitat areas and by local vegetation characteristics. There is substantial interest in understanding how these processes affect populations of grassland birds, which have experienced substantial population declines. Much of our knowledge regarding patterns of occupancy and density stem from prairie systems, whereas relatively little is known regarding how occurrence and abundance of grassland birds vary in reclaimed mine grasslands. Using distance sampling and single-season occupancy models, we investigated how the occupancy probability of Grasshopper (Ammodramus savannarum) and Henslow’s Sparrows (A. henslowii) on 61 surface mine grasslands (1591 ha) in Pennsylvania changed from 2002 through 2011 in response to landscape, grassland, and local vegetation characteristics. A subset (n = 23; 784 ha) of these grasslands were surveyed in 2002, and we estimated changes in sparrow density and vegetation across 10 years. Grasshopper and Henslow’s Sparrow populations declined 72% and 49%, respectively, from 2002 to 2011, whereas overall woody vegetation density increased 2.6 fold. Henslow’s Sparrows avoided grasslands with perimeter–area ratios ≥ 0.141 km/ha and woody shrub densities ≥ 0.04 shrubs/m². Both species occupied grasslands ≤ 13 ha, but occupancy probability declined with increasing grassland perimeter–area ratio and woody shrub density. Grassland size, proximity to nearest neighboring grassland (x̄ = 0.2 km), and surrounding landscape composition at 0.5, 1.5, and 3.0 km were not parsimonious predictors of occupancy probability for either species. Our results suggest that reclaimed surface mine grasslands, without management intervention, are ephemeral habitats for Grasshopper and Henslow’s Sparrows. Given the forecasted decline in surface coal production for Pennsylvania, it is likely that both species will continue to decline in our study region for the foreseeable future.

Keywords: Ammodramus sparrows, area sensitivity, fragmentation effects, perimeter–area ratio, population declines, reclaimed surface mine grasslands

Patrones de Ocupación de Poblaciones Regionalmente Declinantes de Gorriones de Pastizales en un Paisaje Boscoso de Pennsylvania

Resumen: Los organismos pueden ser afectados por procesos en el paisaje que los rodea por fuera de los límites de las áreas de hábitat y por las características de la vegetación local. Hay un interés sustancial en entender cómo estos procesos afectan a las poblaciones de aves de pastizales, las cuales han experimentado declinaciones sustanciales en la población. Mucho de nuestro conocimiento con respecto a los patrones de ocupación y a la densidad parten de sistemas de praderas, mientras que relativamente se sabe poco con respecto a cómo la ocurrencia y la abundancia de las aves de pastizales varía en pastizales de minas de superficiales reclamadas. Usando muestreo a distancia y modelos de ocupación de una sola temporada, investigamos cómo la probabilidad de ocupación de los gorriones Ammodramus savannarum y A. henslowii en 61 pastizales de minas superficiales (1591 ha) en Pennsylvania, que han cambiado desde 2002 y basta el
2011 n respuesta a las características de paisaje, pastizales y de la vegetación local. Un subconjunto (n = 23; 784 ha) de estos pastizales fue muestreado en 2002 y estimamos cambios en la densidad de gorriones y en la vegetación a lo largo de 10 años. Las poblaciones de A. savannarum y A. henslowii declinaron 72% y 49% respectivamente de 2002 a 2011, mientras que la densidad de la vegetación leñosa en general incrementó al 2.6. Los gorriones A. henslowii evitaron los pastizales con radios de área-perímetro ≥0.141 km/ha y con densidades de arbustos leñosos ≥0.04 arbustos/m². Ambas especies ocuparon pastizales ≤13 ba, pero la probabilidad de ocupación declinó con el incremento en el radio área-perímetro de los pastizales y la densidad de arbustos leñosos. El tamaño del pastizal, la proximidad al pastizal vecino más cercano (= 0.2 km) y la composición de los paisajes circundantes en 0.5 km, 1.5 km y 3.0 km no fueron indicadores parsimoniosos de la probabilidad de ocupación para ambas especies. Nuestros resultados sugieren que los pastizales de minas superficiales reclamadas, sin intervención del manejo, son hábitats efímeros para gorriones A. savannarum y A. henslowii. Dada la declinación predictiva en la producción de carbón superficial para Pennsylvania, es probable que ambas especies continúen declinando en nuestra región de estudio en el futuro.

Palabras Clave: Declinación de poblaciones, efectos de la fragmentación, gorriones Ammodramus, pastizales de minas superficiales reclamadas, radio perímetro-área, sensibilidad de área

Introduction

Human activity has greatly altered the natural landscape (Vitousek et al. 1997; Millennium Ecosystem Assessment 2005), which has resulted in grasslands being among the most critically endangered ecosystems in the United States (Noss et al. 1995). With the extensive loss of grasslands, grassland birds as a group have declined by 37% across North America from 1968 to 2008 (Sauer & Link 2011). This decline has received much attention, and the consensus is that population declines of grassland bird species are caused by a combination of several factors such as habitat loss, changes in farming practices, and woody vegetation encroachment (Samson & Knopf 1994; Askins et al. 2007). Habitat loss and the fragmentation of remaining habitat results in lower species richness (Herkt 1994; Bollinger 1995) and negative effects from edges, such as higher nest predation rates adjacent to grassland edges (Herkt et al. 2003) and lower breeding density along grassland boundaries (Helzer 1996). Woody vegetation encroachment, likewise, has been linked to lower reproductive success (Graves et al. 2010) and lower breeding density (Coppedge et al. 2001; Scheiman et al. 2003; Grant et al. 2004) of grassland birds.

Determining the ultimate cause of these observed effects remains challenging because several factors may be operating simultaneously and the presence and density of organisms are affected by processes at multiple spatial and temporal scales (Andrén 1994). For example, in many obligate grassland bird species, such as Grasshopper (Ammodramus savannarum) and Henslow’s Sparrows (Ammodramus henslowii), breeding density may decline with grassland size (Bakker et al. 2002; Davis 2004). The shape of the grassland, also is important, and the perimeter-area ratio (a measure of size and shape complexity) of the grassland can be a better predictor of abundance and occurrence than grassland size alone (Helzer & Jelinski 1999; Davis 2004). Less isolated Great Plains grasslands in the United States are more likely to be occupied by grassland passerines (Johnson & Igl 2001), but isolation effects may be reduced if the surrounding landscape contains a critical threshold amount of grassland habitat (sensu Andrén 1994). Alternatively, although internal vegetation characteristics may largely determine the density of some grassland bird species (Winter et al. 2005), other species may be largely influenced by the surrounding landscape composition (Coppedge et al. 2001; Winter et al. 2006). When detection probability is not explicitly incorporated into statistical analysis, however, misleading associations between species and their use of habitats can be generated, especially when habitat variables affect both the probability of detection and occupancy (MacKenzie et al. 2006).

With these ideas in mind, we used transect sampling methods (Buckland et al. 2001) and single-season occupancy models (MacKenzie et al. 2002), which explicitly model detection probability and incorporate unobserved individuals into the analysis. We surveyed 61 surface mine grasslands (1591 ha) in Pennsylvania to examine how landscape and internal grassland vegetation characteristics influence occupancy probability and density of Grasshopper and Henslow’s Sparrows: the 2 most abundant passerines on our study sites. These obligate grassland species are predominantly found within reclaimed surface mine grasslands within our study area (Mattice et al. 2005), and the distribution of Henslow’s Sparrows in Pennsylvania closely follows the distribution of surface mine grasslands (Brauning 1992). Reclaimed surface mine grasslands are dominated by non-native grasses, are created in the reclamation process that follows surface mining, and provide important habitat for several species of grassland birds (Bajema & Lima 2001; Scott et al. 2002). A subset (n = 23; 784 ha) of these grasslands were initially surveyed for grassland sparrows during 2002 (D.R.D., unpublished data), and we used this subset to examine changes in grassland vegetation and grassland sparrow changes in density across this region of Pennsylvania. We partitioned the 61 grasslands surveyed in 2011.
into 4 groups based on their woody vegetation densities and perimeter-area ratios and examined corresponding changes in sparrow density.

We hypothesized that the occupancy probability of both species would be positively related to grassland size and inversely related to the perimeter-area ratio (Helzer & Jelinski 1999; Winter & Faaborg 1999; Davis 2004). We expected that relatively isolated grasslands would have a lower occupancy probability (Johnson & Igl 2001), and that occupancy probability would increase as the percentage of grassland increased in the surrounding landscape. We hypothesized that the density of both species would be negatively associated with the perimeter-area ratio and woody vegetation density and that their change in density from 2002 to 2011 would reflect the population declines observed within the Appalachian Mountains (Sauer et al. 2012).

Methods

Study Area and Site Selection 2002 and 2011

We delineated a 77,334 ha study area that included portions of Clearfield, Centre, and Cambria Counties, Pennsylvania (Fig. 1). We chose this area for its representativeness of this region in 2002 (see Results). This 9 county region (18,405 km²) was largely forested (76%) in 2002. Agricultural (13%), developed (7%), open water (1%), and grassland (3%) areas (Homer et al. 2004) were interspersed with reclaimed surface mine grasslands. It is unknown if grassland birds inhabited this region of Pennsylvania prior to European colonization. This region of Pennsylvania was likely not glaciated during the last glacial period and has likely been dominated by forests since at least 4000 years before present. Burning and clearing by Native Americans was sporadic (Brose et al. 2001). This fire regime would have created and maintained herbaceous forest clearings and meadows (Denevan 2005) that grassland birds may have occupied.

We delineated surface mine grasslands with ERDAS Imagine software in 2002 (Leica Geosystems Geospatial Imaging, Norcross, Georgia) by digitizing reclaimed sites as identified from LANDSDET 7 imagery from 1999. We used U.S. Geological Survey (USGS) topographic land cover maps and extensive ground truthing to identify 129 surface mine grasslands (4212 ha) with little or no woody vegetation. We randomly selected 23 (784 ha; \( \bar{x} = 34.1 \text{ ha} \) [26.7], min–max 4.6–109.7 ha) of the 129 grasslands surveyed in 2002 to revisit in 2011. In 2011, we used aerial photography (National Agriculture Imagery Program 2010) to identify an additional 201 surface mine grasslands with more extensive woody vegetation that we would not have considered grassland bird habitat in 2002 or that were created since 2002 so that our results would be applicable to the full range of reclaimed surface mine grasslands that existed in 2011. We randomly selected an additional 38 of these grasslands to survey in 2011 for a total of 61 grasslands (1591 ha; \( \bar{x} = 26.1 \text{ ha} \) [21.9], min–max 2.2–109.7 ha).

Grassland Sparrow Surveys

We used line transect distance sampling methods (Buckland et al. 2001) to monitor grasslands for the presence and density of Grasshopper and Henslow’s Sparrows. Observers in both years used the same survey protocols to monitor grassland bird populations, except that observers in 2002 only recorded singing individuals, whereas observers in 2011 recorded all sparrows. To facilitate statistical comparisons between years, nonsinging birds were excluded for within-year analyses for 2011.

In both years, single observers surveyed grasslands between 0530 and 1000, except during heavy rain or excessive wind. Using aerial photos and global positioning system (GPS) units for orienting, an observer slowly walked (approximately 2 kph) along parallel transects (\( n = 2–8 \)) every 200–250 m apart after initially choosing a random starting point. Transects were generally placed perpendicular to the long axis of a grassland and at least 100 m from the edge of the grassland. When an observer visually encountered a sparrow from a transect, the observer recorded her location on the transect with the GPS unit, noted the singing behavior of the bird (in 2011), and determined the distance and direction to the bird with a laser range finder and compass.

We used ArcMap (Environmental Systems Research Institute, Redlands, California) to measure the length of each transect, calculate grassland area, perimeter, perimeter-area ratio, and the distance to the nearest neighboring grassland. In ArcMap we determined the bird’s geographic coordinates and the perpendicular distance between the bird and the transect. Using information from the start of a survey, we created variables related to the detection process (hereafter, detection covariates) that represented observer identity, wind speed, temperature and temperature squared (temp\(^2\)), minutes past sunrise, hour, and days since 1 May. We obtained wind speed and temperature data from the Clearfield-Lawrence Airport Weather Station, Clearfield, Pennsylvania (26 km from the study area center). In 2002, one of 2 observers surveyed each of the 23 grasslands once between 22 May and 1 July. During 2011, one of 2 observers surveyed each of the 61 grasslands twice, 12–16 d apart. The first survey occurred between 17 May and 24 June, and the second survey occurred between 3 June and 8 July.

Vegetation Monitoring and Land Cover Classification

We used the same protocols for measuring vegetation in both years, and sampled vegetation between 23 May
Figure 1. The 77,334 ha study area (circle) that included portions of Clearfield, Centre, and Cambria Counties, Pennsylvania, where Grasshopper and Henslow’s Sparrow populations were monitored in 2002 and 2011. The area of detail (square) shows all 329 potential reclaimed surface mine grasslands we identified (gray polygons) and the 61 grasslands we surveyed in 2011 (black polygons).

and 18 July 2002 and between 7 July and 27 July 2011. We measured vegetation characteristics at a systematic random sample of locations on transects every 200 m (n = 2–16 sampling locations per grassland; all grasslands in 2011 had ≥3 sampling locations). We slightly adjusted (<20 m) the location of some sampling points near grassland boundaries to avoid sampling forest vegetation. If grasslands were too small to include 3 sampling locations spaced 200 m apart, alternatively, we placed sampling sites equidistant from each other.

At each location, we measured the density of woody vegetation (shrubs/m²) by counting woody shrubs within a 0.04 ha circle of the sampling point in 3 height categories: small (0.5–2.5 m), medium (>2.5–5 m), and large (>5 m). For statistical analysis we combined all 3 shrub height categories. We used a 1 m² quadrat to estimate grass, forb, and bare ground percent cover at the center of the sampling point. At each corner of a quadrat, we measured thatch depth and maximum grass height. For each variable, we averaged these measurements for each sampling location.

In ArcMap, we delineated areas 0.5, 1.5, and 3.0 km outward from the border (hereafter buffers) of each grassland and quantified the land cover type at those 3 spatial scales with the USGS 2001 National Landcover Database (Homer et al. 2004) and the 2011 Pennsylvania Cropland raster data (United States Department of Agriculture 2012). At each spatial scale we reclassed data layers within the raster data set into 5 categories: grassland (grasslands and barren land cover types), forest, agriculture, developed, and water.

Occupancy Models 2011

We used a hierarchical modeling approach and fitted single-season occupancy models with a logit link (MacKenzie et al. 2002) with our data from 2011 to examine the influence of within-patch and surrounding landscape characteristics on the occupancy probability (ψ) after adjusting for detection probability (P). First, we considered models with species-specific and species-combined detection and occupancy functions to identify the most parsimonious base model. Second, to this base model we singly added detection covariates to the detection function. Our sampling effort (i.e., length of all transects surveyed within a grassland) was a function of the grassland’s shape and size and varied considerably between grasslands. Ignoring this discrepancy likely would have favored detection in large grasslands and made investigations into area effects challenging (Johnson et al. 2001). To account for the unequal sampling efforts, we also compared models with
of any model within \( \Delta \text{AIC}_c \) of the most parsimonious model.

We created 4 groups (i.e., strata) based on the median value of the perimeter–area ratio (0.141 km/ha) and woody vegetation density (0.04 shrubs/m\(^2\)), and assigned each of the 61 grasslands to a single group based on their covariate values. We partitioned the 61 grasslands into large (\( \geq 0.141 \) km/ha) or small (\(<0.141 \) km/ha) perimeter–area ratio grasslands and grasslands with high (\( \geq 0.04 \) shrubs/m\(^2\)) or low (\(<0.04 \) shrubs/m\(^2\)) amounts of woody vegetation. We used program Distance (Thomas et al. 2009) to estimate the density of Grasshopper and Henslow’s Sparrows within these 4 groups of grasslands. We used the same model selection process as in the multiyear distance sampling comparison, except that we also used singing behavior as a covariate. We calculated density variance and 84% confidence intervals and compared models as described previously.

**Results**

In 2002 and 2011, the study area consisted of 74% and 76% forest, 3% and 8% grassland, 8% and 8% developed, 15% and 7% cropland, and 1% and <1% water, respectively. Woody vegetation increased from 2002 to 2011 at the average vegetation sampling point by 2.6-fold overall and increased within all 3 size classes of shrubs (Table 1). Grass height and percent cover decreased over these 10 years (Table 1).

**Distance Sampling**

HN and HZ models with the observer covariate were included in our 90% confidence set (Supporting Information). The model-averaged detection rate of singing males within 123 m of the transect was 0.43 (95% CI: 0.39–0.48). Model-averaged estimates suggested that Grasshopper and Henslow’s Sparrow populations declined between 2002–2011 by 72% and 49%, respectively. We estimated the Grasshopper Sparrow density in 2002 as \( \hat{D} = 0.45 \) (SE = 0.05) (84% CI: 0.38–0.53) and in 2011

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**Table 1. Mean values of vegetation characteristics from sampling locations in 2002 (\( n = 94 \)) and 2011 (\( n = 119 \)) across 23 reclaimed surface mine grasslands in Pennsylvania.**

<table>
<thead>
<tr>
<th>Covariate</th>
<th>2002 (SD)</th>
<th>2011 (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare cover (%)</td>
<td>16.2 (20.3)</td>
<td>15.1 (23.9)</td>
</tr>
<tr>
<td>Forb cover (%)</td>
<td>21.4 (13.6)</td>
<td>24.2 (22.6)</td>
</tr>
<tr>
<td>Grass cover (%)</td>
<td>62.0 (22.7)</td>
<td>60.7 (33.2)</td>
</tr>
<tr>
<td>Thatch depth (cm)</td>
<td>4.2 (2.7)</td>
<td>3.7 (2.9)</td>
</tr>
<tr>
<td>Maximum grass height (cm)</td>
<td>69.7 (19.6)</td>
<td>58.1 (26.9)</td>
</tr>
<tr>
<td>No. shrubs 0.5 to &lt;2.5 m</td>
<td>7.4 (11.1)</td>
<td>13.6 (26.7)</td>
</tr>
<tr>
<td>No. shrubs 2.5 to &lt;5.0 m</td>
<td>0.5 (2.1)</td>
<td>5.9 (11.1)</td>
</tr>
<tr>
<td>No. shrubs &gt;5.0 m</td>
<td>0.2 (1.4)</td>
<td>1.5 (3.6)</td>
</tr>
</tbody>
</table>

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**Distance Sampling**

We used program Distance (Thomas et al. 2009) to estimate the density (\( \hat{D} \)) of Grasshopper and Henslow’s Sparrows in 2002 and 2011 on the 23 grasslands surveyed in both years. We stratified our observations by year and species and used a global detection function based on sightings of both species during both years. Goodness-of-fit tests within program Distance (Thomas et al. 2009) indicated our nontruncated models adequately fit the data (\( p > 0.05 \)). To model the shape of the detection function, we examined models with uniform (UF), half-normal (HN), and hazard-rate (HZ) key functions with cosine series expansions (Buckland et al. 2001). To each of the HN and HZ models, we added a covariate representing observer identity to account for variation among observers. We only examined models with global detections functions created from all observations of both species in a given year because sample sizes were too low in some groups to allow for strata-specific detection functions. We calculated density variance and 84% confidence intervals by resampling (\( n = 999 \)) with replacement from our transect data through a nonparametric bootstrapping procedure (Buckland et al. 2001). We calculated 84% confidence intervals of density, as opposed to 95%, which enabled us to compare confidence intervals akin to a hypothesis test while maintaining a type I error rate of approximately 5% (Payton et al. 2005). We used AICc to compare models (Burnham & Anderson 2002) and calculated model-averaged parameters (unconditional SE)

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**Detection covariates for transect length and transect length quadratic term.**

Third, after identifying the most parsimonious detection covariates, we systematically introduced covariates in an additive procedure to the occupancy parameters representing vegetation, landscape, and grassland characteristics to potentially further improve the model. We started with covariates from the largest landscape scale down to within-grassland characteristics. We created a confidence set consisting of models within \( \Delta \text{AIC}_c \) bias-corrected Akaike’s information criterion) of the most parsimonious model and model-averaged parameters across these models. All occupancy model results presented are model-average estimates (unconditional SE) with 95% confidence intervals. We did not include efforts from 2002 in our occupancy analysis because those grasslands were only surveyed once, and we could not independently estimate a detection function for those data. Fourth, we assessed model goodness of fit and overdispersion (\( \hat{c} \)) with the parametric bootstrap procedure in program Mark (White & Burnham 1999) following White et al. (2001). Our global model adequately fit the model assumptions and there was no indication of overdispersion (\( p = 0.88, \hat{c} < 1 \)).

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**Distance Sampling**

We used program Distance (Thomas et al. 2009) to estimate the density (\( \hat{D} \)) of Grasshopper and Henslow’s Sparrows in 2002 and 2011 on the 23 grasslands surveyed in both years. We stratified our observations by year and species and used a global detection function based on sightings of both species during both years. Goodness-of-fit tests within program Distance (Thomas et al. 2009) indicated our nontruncated models adequately fit the data (\( p > 0.05 \)). To model the shape of the detection function, we examined models with uniform (UF), half-normal (HN), and hazard-rate (HZ) key functions with cosine series expansions (Buckland et al. 2001). To each of the HN and HZ models, we added a covariate representing observer identity to account for variation among observers. We only examined models with global detections functions created from all observations of both species in a given year because sample sizes were too low in some groups to allow for strata-specific detection functions. We calculated density variance and 84% confidence intervals by resampling (\( n = 999 \)) with replacement from our transect data through a nonparametric bootstrapping procedure (Buckland et al. 2001). We calculated 84% confidence intervals of density, as opposed to 95%, which enabled us to compare confidence intervals akin to a hypothesis test while maintaining a type I error rate of approximately 5% (Payton et al. 2005). We used AICc to compare models (Burnham & Anderson 2002) and calculated model-averaged parameters (unconditional SE)
Table 2. Grasshopper and Henslow’s Sparrow density ($\hat{D}$) estimates derived from distance sampling models from 61 reclaimed surface mine grasslands with large (\geq 0.141 km/ha) or small (<0.141 km/ha) perimeter–area (P:A) ratio grasslands and high (\geq 0.04 shrubs/m$^2$) or low (<0.04 shrubs/m$^2$) amounts of woody vegetation in Pennsylvania, 2011.

<table>
<thead>
<tr>
<th>Species</th>
<th>P:A</th>
<th>Woody shrubs</th>
<th>n</th>
<th>No. grasslands</th>
<th>$\hat{D}$/ha</th>
<th>SE</th>
<th>84% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Henslow’s Sparrow</td>
<td>large</td>
<td>high</td>
<td>0</td>
<td>15</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00–0.00</td>
</tr>
<tr>
<td></td>
<td>large</td>
<td>low</td>
<td>30</td>
<td>16</td>
<td>0.10</td>
<td>0.02</td>
<td>0.07–0.13</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>high</td>
<td>2</td>
<td>15</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01–0.06</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>low</td>
<td>57</td>
<td>15</td>
<td>0.21</td>
<td>0.04</td>
<td>0.16–0.27</td>
</tr>
<tr>
<td>Grasshopper Sparrow</td>
<td>large</td>
<td>high</td>
<td>15</td>
<td>15</td>
<td>0.08</td>
<td>0.03</td>
<td>0.05–0.13</td>
</tr>
<tr>
<td></td>
<td>large</td>
<td>low</td>
<td>119</td>
<td>16</td>
<td>0.23</td>
<td>0.03</td>
<td>0.19–0.28</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>high</td>
<td>23</td>
<td>15</td>
<td>0.23</td>
<td>0.05</td>
<td>0.17–0.30</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>low</td>
<td>50</td>
<td>15</td>
<td>0.19</td>
<td>0.02</td>
<td>0.15–0.22</td>
</tr>
</tbody>
</table>

as $\hat{D} = 0.12$ (0.02) (84% CI: 0.10–0.16). Similarly, we estimated the Henslow’s Sparrow density in 2002 as $\hat{D} = 0.13$ (0.03) (84% CI: 0.10–0.18) and in 2011 as $\hat{D} = 0.07$ (0.02) (84% CI: 0.05–0.09).

Density Analysis Results 2011

Overall detection probability for individuals of either species ranged from 0.37 to 0.45 within 98 m of the transect (Supporting Information). The HN model that accounted for observer and singing behavior in the detection function was selected as the most parsimonious model (Supporting Information), indicating that observers ability to detect these species declined as a function of distance from the transect. No Henslow’s Sparrows were detected in grasslands with both a large perimeter–area ratio (\geq 0.141 km/ha) and high areal coverage of woody vegetation (\geq 0.04 shrubs/m$^2$). Henslow’s Sparrow density was greatest on grasslands with small perimeter–area ratios (<0.141 km/ha) and low areal coverage of woody vegetation (<0.04 shrubs/m$^2$; Table 2). Grasshopper Sparrows were least dense on grasslands with large perimeter–area ratios and high amounts of woody vegetation, but density was similar among the 3 remaining categories of grasslands.

2011 Occupancy Estimation

We detected Grasshopper Sparrows in 37 (61%) grasslands and Henslow’s Sparrows in 20 (33%) grasslands. We detected Grasshopper Sparrows in grasslands as small as 4.6 ha and Henslow’s Sparrows in grasslands as small as 12.9 ha. The maximum perimeter–area ratio for a grassland where Henslow’s Sparrows were detected was 0.16 km/ha, and Grasshopper Sparrows were detected in grasslands with perimeter–area ratios as high as 0.25 km/ha. A model with a constant detection function pooled across both species was parsimonious (Table 3), and adding detection covariates to the detection parameter did not improve any of the models. As expected, transect length was positively associated with sparrow detections ($\beta_{\text{slope}}$ [SE]: 0.96 [1.04], 95% CI: −1.08–2.99) and modified by a quadratic term for transect length ($\beta_{\text{slope}}$: −0.13 [0.36], 95% CI: −0.83–0.57; Fig. 2). We estimated the combined detection function of both

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Table 3. Single-season occupancy models of Grasshopper and Henslow’s Sparrows on 61 reclaimed surface mine grasslands in Pennsylvania, 2011 with >1% of model weights ($w_i$).

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
<th>$K^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>${P(\cdot) + TL + TL^2}$ $\psi$ (species + P:A + DENWOOD)$^a$</td>
<td>0.00</td>
<td>0.47</td>
<td>7</td>
</tr>
<tr>
<td>${P(\cdot) + TL + TL^2}$ $\psi$ (species + P:A + PFORB)$^a$</td>
<td>0.36</td>
<td>0.36</td>
<td>7</td>
</tr>
<tr>
<td>${P(\cdot) + TL + TL^2}$ $\psi$ (species + P:A + PGRASS)$^a$</td>
<td>3.75</td>
<td>0.07</td>
<td>7</td>
</tr>
<tr>
<td>${P(\cdot) + TL + TL^2}$ $\psi$ (species + P:A)</td>
<td>4.15</td>
<td>0.06</td>
<td>6</td>
</tr>
</tbody>
</table>

$^a$Abbreviations: P (.), detection probability for both species; TL, transection length; TL$^2$, TL quadratic term; $\psi$, occupancy probability; P:A, perimeter–area ratio (km/ha); DENWOOD, woody shrub density (shrubs/m$^2$); PFORB, percent cover of forbs; PGRASS, cover of grass; $^c$, model included in the confidence set ($\Delta AIC_c < 4.0$).

$^b$Bias-corrected Akaike’s information criterion

$^c$Number of parameters
sparrow species over both surveys as \( P = 0.79 \) (0.06) (95% CI: 0.63–0.89).

Grasshopper Sparrows were more likely to occupy grasslands within our study area than Henslow’s Sparrows (\( \hat{\psi} \) [SE] = 0.67 [0.09], 95% CI: 0.47–0.82, and \( \hat{\psi} = 0.24 \) [0.07], 95% CI: 0.13–0.40, respectively). The distance to the nearest neighboring grassland (\( x \) [SD] = 0.2 km [0.3], range 0.018–1.310 km) and the surrounding land cover were not related to occupancy probability. The landscape surrounding the 61 grasslands at 0.5, 1.5, and 3.0 km averaged 8–9% grassland (Supporting Information). Grasshopper (\( \beta_{\text{intercept}} \) [SE]: 4.87 [1.38], 95% CI: 2.17–7.58) and Henslow’s (\( \beta_{\text{intercept}} \) [SE]: 3.00 [1.12], 95% CI: 0.80–5.20) Sparrows were more likely to occupy grasslands with small perimeter–area ratios (\( \beta_{\text{slope}} \) : –22.18 [5.98], 95% CI: –33.90–10.45; Fig. 3a), low woody shrub density (–12.91 [5.92], 95% CI: –24.51–1.31; Fig. 3b), and a small forb (–4.63 [2.03], 95% CI: –8.61–0.66) and large grass component (1.88 [1.22], 95% CI: –0.51–4.28) to the ground cover.

Discussion

We documented how vegetation and grassland characteristics are related to the density and occupancy probability for Grasshopper and Henslow’s Sparrows on reclaimed surface mine grasslands over 10 years and at multiple spatial scales. Previous studies of grassland sparrows have generally relied on simple counts of singing males (e.g., Bajema & Lima 2001; Davis 2004), but we explicitly accounted for detection probability in our association of habitat features with density estimates and occupancy probabilities for these species. Our transect survey methods detected approximately 44% of the available sparrows, suggesting that simple counts could have underestimated the density by as much as 56%. If density of these species declines with patch size (Bollinger 1995; Winter & Faaborg 1999), then small grasslands might have been disproportionately misclassified as unoccupied in previous studies (cf., Johnson 2001).

Previous research suggests that Grasshopper and Henslow’s Sparrows are area sensitive species (Winter & Faaborg 1999; Davis 2004), but that area effects may vary regionally for Grasshopper Sparrows (Johnson & Igl 2001). Our findings indicate grassland size is only a component of the density and occupancy patterns of these species, at least on reclaimed surface mine grasslands in the Appalachian Mountains. Our findings indicate that both species are less likely to occupy small grasslands—especially when those grasslands have complex shapes. Similar to the findings of Helzer and Jelinski (1999), we found that grassland area itself was insufficient to explain occupancy patterns in these grassland sparrows and that shape complexity additionally needed to be considered. Grasslands with irregular shapes (e.g., stellate) have a greater proportion of their area adjacent to the edge of the grassland than do grasslands of the same size with simpler shapes (e.g., circular). Irregular-shaped grasslands subject a greater proportion of their internal area to edge effects, and Grasshopper and Henslow’s Sparrows are edge sensitive species (Johnson 2001; Patten et al. 2011). Simple avoidance of edges could explain why we observed lower densities of Henslow’s Sparrows in small grasslands with large perimeter–area ratios. Grasshopper Sparrow density, however, was not consistently related to the perimeter–area ratio (Table 2), which suggests that habitat selection by Grasshopper Sparrows is less influenced by edge effects than Henslow’s Sparrows.

Across a wide range of taxa habitat patch area generally has a larger effect on species occupancy than the isolation of a patch (Watling & Donnelly 2006). The landscape surrounding a patch, however, can affect avian populations in a multitude of ways, including nest success in grassland-nesting waterfowl (Horn et al. 2005). These landscape effects should be more pronounced as the habitat (i.e., grassland) becomes increasingly rare in the landscape (Andrén 1994). Landscape characteristics, however, did not influence the occupancy probability for Henslow’s and Grasshopper Sparrows in our largely forested study region in 2011, where grasslands composed approximately 8% of the landscape. Our findings are similar to the landscape insensitivity that has been reported for these sparrow species in prairies (Bakker et al. 2002) and surface mine grasslands elsewhere (Bajema & Lima 2001). These cumulative results suggest that Grasshopper and Henslow’s Sparrow occupancy patterns are largely driven by internal vegetation characteristics such as grass and forb cover (Scott et al. 2002; this study). Our study results suggest that area effects (including habitat patch shape complexity) have a larger role in the composition of grassland bird communities on surface mine grasslands than do isolation effects. The timeframe of our study, however, precludes us from assessing temporal variation in landscape effects within this system.

Landscape effects may vary regionally or with organism abundance (Flather & Sauer 1996), and Henslow’s Sparrows are generally less abundant and have a more restricted geographic range than Grasshopper Sparrows (Sauer et al. 2012). Grasshopper Sparrow abundance is positively associated with neighboring grassland cover within southeastern Pennsylvania (Wentworth et al. 2010). Grassland passerines, however, are patchily distributed in this agricultural region of Pennsylvania (Brauning 1992), and this sporadic distribution may hinder the colonization of new habitats by Grasshopper Sparrows (Wilson & Brittingham 2012). In contrast, our grasslands were relatively close to neighboring grasslands (\( x = 165 \) m), and most grasslands were occupied by Grasshopper Sparrows. When our results are considered in this context, they suggest forested landscapes, at the scale of

**References**

Bajema & Lima 2001

Bakker et al. 2002

Bollinger 1995

Brauning 1992

Flather & Sauer 1996

Horn et al. 2005

Johnson 2001

Johnson & Igl 2001

Scott et al. 2002

Sauer et al. 2012

Winter & Faaborg 1999

Wilson & Brittingham 2012
our study area, are not effective barriers to dispersal and colonization for Grasshopper and Henslow’s Sparrows, even when >80% of the landscape is unsuitable (Supporting Information). These results may not be surprising considering that the modern Pennsylvania forest with grassy clearings created by coal mining may superficially resemble the precolonial forests with grassy clearings created by fire and Native Americans (Denevan 2005).

Several studies have documented the negative effects of increased levels of woody vegetation on the occurrence of obligate grassland bird species (Coppedge et al. 2001; Scheiman et al. 2003; Grant et al. 2004). We observed overall subtle herbaceous vegetation changes from 2002 to 2011, but the amount of woody vegetation increased on all 23 grasslands whereas Grasshopper and Henslow’s Sparrow populations declined. Assuming a linear rate of decrease our data suggest average annual reductions of approximately 13% for Grasshopper Sparrows and 7% for Henslow’s Sparrows, which exceeds the estimated annual rate of decline for Grasshopper (5%) and Henslow’s (3%) sparrows in the Appalachian Mountains from 2000 to 2011 (Sauer et al. 2012).

Surface mine grasslands typically contain scattered amounts of woody vegetation, and yet they provide extensive areas of habitat for Grasshopper and Henslow’s Sparrows in Appalachia (McWilliams & Brauning 2000). Black locust (*Robinia pseudoacacia*), the most common shrub on reclaimed surface mine grasslands in central Pennsylvania (J.M.H. personal observation), readily survives fire and mowing and responds by spreading via rhizomatic growth (Anderson & Brown 1980). Bituminous surface-mined coal production and the number of new surface coal mines permitted each year has decreased in Pennsylvania since the 1980s and is projected to decline for the foreseeable future (Pennsylvania Department of Environmental Protection 2010). The projected decline in surface mine permits and tonnage suggests that many fewer reclaimed surface mine grasslands will be created in Pennsylvania then are currently. Mining companies frequently plant woody shrubs in dense configurations during the reclamation process (Ashby et al. 1985), and woody vegetation density on existing surface mine grasslands will likely increase through natural recruitment (this study). Thus, populations of both Grasshopper and Henslow’s Sparrows are likely to decline for the foreseeable future in our study region, and the large extent of private grassland ownership in this region (98%, this study) may complicate coordination of management efforts.

Our results suggest that without management intervention reclaimed surface mine grasslands are ephemeral habitats for Grasshopper and Henslow’s Sparrows but both grassland sparrow species will use openings in small and irregularly shaped grasslands with moderate amounts of woody vegetation. Population estimates for Grasshopper and Henslow’s Sparrows that do not account for their presence on small and woody grasslands (e.g., Mattice et al. 2005) are likely underestimates of true population size. Future studies could improve on ours by documenting interannual occupancy and movement patterns across forested landscapes (e.g., using mark-resight models), which would lead to an improved understanding of population connectedness and metapopulation dynamics for Grasshopper and Henslow’s Sparrows in Appalachia.
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Supporting Information

The 90% confidence sets of distance sampling models (Appendix S1) and landscape composition surrounding grasslands in 2011 (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited


