EXPERIMENTAL REMOVAL OF WOODY VEGETATION DOES NOT INCREASE NESTING SUCCESS OR FLEDGLING PRODUCTION IN TWO GRASSLAND SPARROWS (AMMODRAMUS) IN PENNSYLVANIA

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Abstract.—The influence of vegetation structure on the probability of daily nest survival (DNS) for grassland passerines has received considerable attention. Some correlative studies suggest that the presence of woody vegetation lowers DNS. Over 3 years (2009–2011), we monitored 215 nests of the Grasshopper Sparrow (*Ammodramus savannarum*) and Henslow's Sparrow (*A. henslowii*) on 162 ha of reclaimed surface-mine grasslands in Pennsylvania. We removed shrubs from treatment plots with \leq 36% areal coverage of woody vegetation in a before-after-control-impact-pairs (BACIP) design framework. Daily nest survival (95% CI: 0.94–0.96) was as high as previous studies have reported but was not associated with woody vegetative cover, proximity to woody vegetation, or woody stem density. Variation in DNS was best explained by increasing nonwoody-vegetation height. Grasshopper Sparrow fledgling production on treatment plots in 2010 (95% CI: 3.3–4.7) and 2011 (95% CI: 3.8–5.0) was similar to baseline conditions of treatment plots (95% CI: 3.4–4.9) and control plots (95% CI: 3.2–4.5) in 2009. Fledgling production was associated with thatch depth ($\hat{\beta} \pm SE = 0.13 \pm 0.09$) and bare ground ($\hat{\beta} \pm SE = -2.62 \pm 1.29$) adjacent to the nest and plot woody vegetative cover ($\hat{\beta} \pm SE = -3.09 \pm 1.02$). Our experimental research suggests that overall reproductive success of Grasshopper and Henslow's sparrows on reclaimed surface-mine grasslands is driven by a suite of largely nonwoody-vegetation components, and both species can successfully nest and produce young in habitats with greater amounts of scattered woody vegetation than has generally been considered. *Received 18 December 2012, accepted 7 June 2013*.

Key words: A mmodramus, before-after-control-impact design, grassland birds, habitat alteration, nest survival, vegetation structure, woody vegetation.

La Remoción Experimental de la Vegetación Leñosa No Incrementa el Éxito de Anidación ni la Producción de Volantones en dos Especies de *Ammodramus* en Pensilvania

Resumen.—La influencia de la estructura de la vegetación en la probabilidad de supervivencia diaria de los nidos en paserinos de pastizales ha recibido considerable atención. Algunos estudios correlativos sugieren que la presencia de vegetación leñosa disminuye la supervivencia diaria de los nidos. Por tres años (2009–2011) monitoreamos 215 nidos de *Ammodramus savanarum* y de *A. henslowii* en 162 ha de pastizales recuperados de minas superficiales en Pensilvania. Removimos los arbustos de las parcelas del tratamiento con \leq 36% de su área cubierta con vegetación leñosa en un diseño por pares antes-después de impacto controlado. La supervivencia diaria de los nidos (95% IC: 0.94–0.96) fue tan alta como la reportado en estudios previos pero no estuvo asociada con la cobertura de vegetación leñosa, la proximidad o la densidad de tallos. La variación en la supervivencia diaria de los nidos fue mejor explicada por el incremento en la altura de la vegetación no leñosa. La producción de volantones de *A. savanarum* en las parcelas tratamiento en 2010 (95% IC: 3.3–4.7) y 2011 (95% IC: 3.8–5.0) fue similar a las condiciones iniciales en las parcelas tratamiento (95% IC: 3.4–4.9) y a las parcelas control (95% IC: 3.2–4.5) en 2009. La producción de volantones estuvo asociada con la profundidad de la paja ($\hat{\beta} \pm SE = 0.13 \pm 0.09$) y el terreno desnudo ($\hat{\beta} \pm SE = -2.62 \pm 1.29$) adyacente al nido, y la cobertura de vegetación leñosa en la parcela ($\hat{\beta} \pm SE = -3.09 \pm 1.02$). Nuestra investigación experimental sugiere que, en general, el éxito reproductivo de *A. savanarum* y *A. henslowii* en pastizales recuperados de minas superficiales se debe a un conjunto de vegetación compuesta principalmente por elementos no leñosos, y que ambas especies pueden anidar y producir descendencia exitosamente en hábitats con mayores cantidades de vegetación leñosa esparcida de lo que ha sido considerado.

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Measures of vegetation structure are common components of models predicting avian habitat use (Hildén 1965, Rotenberry and Wiens 1980). Such models are best viewed as a hierarchical decision-making process whereby birds are simultaneously selecting features of their environment at multiple scales (Cody 1981). Presumably, hierarchical models should provide greater insight into habitat use than models that take a single-scaled approach (Kristan 2006). Models that correlate organism abundance to habitat attributes are useful, but measurements of individual fitness components offer a more complete costbenefit analysis of surviving in that environment (Pulliam 1988). Without assessment of reproductive success (e.g., nest survival or fledgling production), habitat selection models based on abundance alone can lead to erroneous conclusions regarding the quality of a habitat (Vickery et al. 1992), potentially with unintended results (Best 1986).

Grassland bird species have experienced substantial population declines, and their populations continue to decline throughout North America at a rate faster than other habitat guilds (North American Bird Conservation Initiative 2011, Sauer and Link 2011). Population declines of grassland birds have occurred alongside increasing encroachment by woody vegetation from forest succession and fire suppression (Briggs et al. 2005) and widespread losses in acreage of most North American grassland types, including tallgrass prairies (≥90% loss) and native California grasslands (99% loss; Noss et al. 1995). Grasslands on surface-mine sites in forested landscapes, by contrast, continue to be produced by reclamation activities following the cessation of mining. There are >800,000 ha of reclaimed surface-mine grasslands in Pennsylvania alone (Yahner and Rohrbaugh 1996). These savanna-like grasslands are globally important habitats for grassland-obligate bird species (Brothers 1990, Bajema et al. 2001, Stauffer et al. 2011), but they can have considerable amounts (>1 shrub per 1.5 m²) of woody vegetation (Ashby et al. 1985, J. M. Hill unpubl. data).

The decline of most North American grassland bird populations (Sauer and Link 2011) has created interest in the effect of woody vegetation on grassland passerines' abundance and demographic parameters in all grasslands (Askins et al. 2007), and specifically in reclaimed surface-mine grasslands (Graves et al. 2010). Many grassland bird species are negatively affected by proximity to woody ecotones where they experience increased rates of brood parasitism (Patten et al. 2006) and nest predation (Johnson and Temple 1990; but see Conover et al. 2011). Woody-vegetation effects have been documented for many grassland bird species (reviewed in Bakker 2003), but few studies have found negative effects of woody vegetation within grasslands on components of fitness (With 1994, Graves et al. 2010, Klug et al. 2010), and some have not found any (Sutter and Ritchison 2005, Conover et al. 2011). The best measure of reproductive success is juvenile recruitment into the population, but given the exceeding difficulty of acquiring those data (Newton 1989), most authors assess nesting or fledging success as an index of recruitment (see Weatherhead and Dufour 2000).

Grasshopper Sparrows (*Ammodramus savannarum*) and Henslow's Sparrows (*A. henslowii*) are common residents of reclaimed surface-mine grasslands in the eastern United States (Scott and Lima 2004). Populations of both species have declined substantially in the Appalachian Mountains (Sauer et al. 2012),

perhaps in part because of an increase in woody vegetation within grasslands (Scheiman et al. 2003, Graves et al. 2010), but we know of no studies that have related fledgling production in either species to vegetation characteristics. We designed a multiyear manipulative removal experiment to examine the response of nesting success and fledgling production in Grasshopper and Henslow's sparrows to woody vegetation. We conducted our research on reclaimed surface-mine grasslands in Pennsylvania from 2009 to 2011 in a before-after-control-impact-pairs (BACIP) design framework (Stewart-Oaten et al. 1986). We identified four pairs of study plots and removed woody vegetation from each randomly assigned treatment plot. Our goal was to test the hypothesis that daily nest survival (DNS) and fledgling production would decline in the presence of woody vegetation and that the removal of woody vegetation from treatment plots would improve DNS and fledgling production for both sparrow species.

METHODS

Study area and experimental design.—Our study sites consisted of eight equally sized 20.2-ha plots of reclaimed surface-mine grasslands located on large grassland complexes on public lands within Cambria (40°38'21"N, 78°30'15"W) and Clarion counties (41°08'33"N, 79°29'20"W), Pennsylvania. The landscape (200 km²) around the Cambria and Clarion county plots, respectively, consisted of agricultural lands (2% and 18%), developed areas (3% and 8%), forestlands (88% and 59%), grasslands (7% and 13%), and other land-cover types (<1% and 2%) (U.S. Department of Agriculture, National Agricultural Statistics Service, 2010 Pennsylvania Cropland Data Layer; see Acknowledgments). Both landscapes contained a mosaic of large reclaimed grasslands and active surface mines. The plots located in Clarion County were reclaimed during the 1970s and were within a Globally Important Bird Area, as designated by the National Audubon Society, for their large populations of grassland birds. The plots within Cambria County were reclaimed at various times before the 1990s. Vegetative cover on all plots consisted of predominantly non-native cool-season grasses (e.g., fescue [Festuca spp.] and Timothy [Phleum pretense]), forbs (e.g., goldenrods [Solidago spp.] and Queen Anne's Lace [Daucus carota]), and woody shrubs (predominantly Black Locust [Robinia pseudoacacia], which is planted by mining companies during the reclamation process for its nitrogen-fixing abilities).

We selected plots as part of a BACIP design, with paired plots located 0.3–1.2 km apart. Plots were located within a 200-ha area and a 2,900-ha area in Clarion and Cambria counties, respectively. For each pair of plots, we randomly selected one plot as a treatment plot, and the other plot was designated the control. We paired plots on the basis of similarities in vegetation, past management practices, landscape context, and time since reclamation. We avoided areas of extremely dense woody vegetation and/or areas where woody vegetation exceeded 3.0 m in height. We delineated plot boundaries to include areas with scattered shrubs that a grassland bird could identify as potential breeding habitat. Areal coverage of shrubs ranged from 5% to 36%, as estimated by our first-year plot-wide vegetation sampling.

No treatments were applied in the first year of the study (2009). During winter 2010, when the ground was frozen, we pulverized all standing woody vegetation to ≤ 0.3 m on the four

treatment plots using track loaders (Caterpillar, Peoria, Illinois) equipped with masticating heads and a Hydro-Ax (Blount, Portland, Oregon). On steep slopes, we felled and removed shrubs by hand in early April, before grassland sparrows had returned to the plots. Some deciduous shrubs (e.g., Black Locust and European Black Alder [Alnus glutinosa]) resprouted from stumps in spring 2010. These stump sprouts were above the grass layer by mid-May. In September 2010, we air-blasted herbicide onto treatment plots with a combination of Garlon 3A (triclopyr) and Escort (metsulfuron methyl) at a rate of 1 quart of Garlon 3A and 1 ounce of Escort per gallon of water to kill woody vegetation with minimal harm to grasses and forbs. During winter 2011, we again pulverized any standing woody vegetation. No other management actions or domestic grazing occurred on our research plots from 2009 to 2011. We estimated a cost of \$100 ha-1 for a one-time herbicide application and up to \$100 ha-1 for the removal of the physical woody structure.

Nest monitoring.—We first observed grassland sparrows on study plots in late April. Once a week, we systematically searched plots for nests from May through mid-July. To discover nests, we systematically walked parallel transects across plots starting at sunrise and found nests by flushing incubating females or by observing adults carrying food. We marked nests with a flag placed 5 m from the nest and monitored nests every 3-4 days until fledging or failure occurred. At each nest visit, we observed the nest contents and checked for the presence of Brown-headed Cowbird (Molothrus ater) eggs and nestlings. We aged nestlings using a photographic reference card made with photographs from nestlings of known age and through the descriptions of Stauffer et al. (2011). When nestlings were ~6 days old they were fitted with a U.S. Geological Survey aluminum leg band and a single color band as approved by the Institutional Animal Care and Use Committee at Penn State University (IACUC no. 33097). We classified a nest as successful if it fledged ≥1 young. We confirmed fledging by observing nest areas for parental feeding activity of fledged young on the expected fledging date and the subsequent 2 days if necessary. We used the "Last Active-B" method of Manolis et al. (2000) to adjust the number of exposure days for 7 nests with ambiguous fate.

Vegetation sampling.—From 22 July to 5 August of each year, we measured vegetation characteristics at nests and across each plot because predator abundance at grassland bird nests is best reflected by multiscale models (Klug et al. 2009). We chose to measure vegetation during this 2-week period each year after the peak of vegetation growth to reduce temporal variation in the nest vegetation data and to facilitate the comparison of vegetation data collected at the nest and plot levels (Grant et al. 2006). We quantified vegetation at three distinct scales: ≤1 m from the nest ("immediate nest vegetation"), 5–25 m from the nest ("adjacent nest vegetation"), and at the plot level.

We sampled vegetation using a combination of point-transect sampling and 1-m^2 quadrats. We considered a "shrub" any woody plant with ≥ 1 stem originating from a basal clump that exceeded 0.5 m in height. To measure immediate nest vegetation, we placed one quadrat centered over the nest and in each corner measured litter depth (cm) and maximum grass and maximum forb heights (cm). We estimated the cover of bare ground, grasses, and forbs within each quadrat in five categories: <5%, >5% to 25%, >25% to 75%, >75% to 95%, and >95%. To measure adjacent nest

vegetation, we averaged these same measurements (using the midpoint of the category) collected at four additional quadrats placed 5.5 m from the nest, starting at 45° (NE) and at every subsequent increment of 90°. We counted all shrubs within 6 m of the nest (hereafter "woody stem count"), and we measured the distance from the nest to the nearest shrub (m). We estimated percent woody vegetative cover using line-intercept sampling with distances recorded at 25-cm intervals. To improve normality of model residuals when woody-vegetation covariates were included, we square-root transformed woody vegetative cover and transformed woody stem count and the distance to the nearest shrub by taking the natural log of each value + 1. For plot vegetation sampling, we located 50 equally spaced points on each plot using ARCGIS (ESRI, Redlands, California). We sampled all 50 points for each plot in 2009 and 12-16 randomly selected points on each plot in subsequent years.

Nest survival analysis.-We used Program MARK (White and Burnham 1999) to identify temporal and vegetative features related to daily nest survival of Grasshopper and Henslow's sparrows. These two species have similar vegetation preferences for nesting locations on eastern reclaimed surface-mine grasslands (Graves et al. 2010, Stauffer et al. 2011), so we jointly analyzed their DNS rates (Galligan et al. 2006) and grouped the data by year and plot status (control vs. treatment). We followed the systematic and hierarchical approaches of Dinsmore et al. (2002) and Hovick et al. (2012) to select and compare models with Akaike's information criterion adjusted for small sample size (AIC, Burnham and Anderson 2002) using five model-selection steps. We retained the most parsimonious model (i.e., the model with the lowest AIC, value) from each step for use in the subsequent step, which included the most parsimonious model from the previous step if adding an additional covariate did not improve the parsimony of the model.

First, we compared 13 *a priori* models with immediate and delayed treatment effects and models without treatment effects (Table 1); these models contained constant (.), linear (T), and quadratic (TT) time trends. Second, we included a dummy variable to represent a species effect. Third, we singly added plot-wide vegetation covariates. Fourth, we singly added the adjacent vegetation covariates. Lastly, we singly introduced the immediate nest vegetation covariates. We modeled vegetation covariates using both linear and quadratic terms in the final three model-selection steps.

We removed nested models with one additional parameter (K+1) that fell within $\Delta {\rm AIC}_{\rm c} < 2$ of the simpler model with K parameters (Burnham and Anderson 2002, Arnold 2010). We then created a confidence set of models, which included the models with an accumulated 90% of ${\rm AIC}_{\rm c}$ weights, and then model averaged the coefficients in the 90% confidence set (Burnham and Anderson 2002). We calculated overall nesting success, using the delta method (Powell 2009), as the product of model-averaged DNS estimates based on mean covariate values in the 90% confidence set. We assumed a 23-day and 24-day nesting period for Henslow's and Grasshopper sparrows, respectively (Stauffer et al. 2011). We used a 23.5-day nesting period (the midpoint between Henslow's and Grasshopper sparrows' nesting periods) to estimate the combined nesting success of both species.

Fledgling production.—We estimated fledgling production only for Grasshopper Sparrows because we monitored

TABLE 1. The 12 *a priori* models with *K* parameters that we used to compare temporal variation in daily nest survival of Grasshopper and Henslow's sparrows on reclaimed surface-mine grasslands in Pennsylvania, 2009–2011. Models included constant (.), linear (T), and quadratic time trends (TT) to model variation in daily nest survival on control and treatment plots. We removed woody vegetation from treatment plots initially in winter 2010 and again in winter 2011. We hypothesized that the probability of daily nest survival might vary between treatment and control plots immediately following removal of woody vegetation in winter 2010 (immediate treatment effect), following the second removal of woody vegetation in winter 2011 (delayed treatment effect), or not at all (no treatment effect).

Model	Hypothesized treatment effect	К
Constant survival across all years	None	1
Constant survival by plot	None	8
T across years	None	2
Constant by year	None	3
TT across years	None	3
T by year	None	6
TT by year	None	9
2009 & 2010–2011 control plots(.) + 2010– 2011 treatment plots(.)	Immediate	2
2009 & 2010–2011 control plots(.) + 2010– 2011 treatment plots(T)	Immediate	3
2009 & 2010–2011 control plots(.) + 2010– 2011 treatment plots(TT)	Immediate	4
2009(.) + 2010 by treatment(.) + 2011 by treatment(.)	Immediate	5
2009(T) + 2010–2011 control plots(T) + 2010–2011 treatment plots(T)	Immediate	6
2009(.) + 2010(.) + 2011 by treatment(.)	Delayed	4

few Henslow's Sparrow nests that survived to fledging (n = 11)successful nests of 20 discovered nests). Using the lme4 package in Program R (Bates et al. 2011, R Development Core Team 2012), we estimated the mean number of fledgling Grasshopper Sparrows (Y_{iikl}) produced per *i*th successful nest with *j*th treatment and kth year from the means parameterization of a two-way random-effects analysis of variance (ANOVA), $Y_{iikl} = (\alpha_{ik} + \mu_{ol})^*$ $B_{0i} * B_{1i} + \varepsilon_i$, where α_{ik} is the expected number of fledged young in each jth treatment and kth year, $\mu_{ol} \sim N(0, \tau^2)$ is the random deviation of the *l*th plot, B_{0i} is the treatment effect, and B_{1i} represents the year effect with residuals $\varepsilon_i \sim N(0, \sigma^2)$ (Kéry 2010). This method estimates the expected number of fledglings produced from a successful Grasshopper Sparrow nest in each combination of treatment and year after taking the random effect (i.e., plot) into consideration. We calculated 95% highest-probability density intervals (HPDI) for the parameter estimates using 100,000 Markov chain Monte Carlo (MCMC) iterations implemented in the lme4 package (Bates et al. 2011).

On the basis of the results of the two-way random-effects ANOVA, we then used mixed-effects random-intercept models with an identity link to examine the relationship between Grasshopper Sparrow fledgling production and vegetation characteristics. We began our hierarchical model selection by first fitting a simple, random-effects ANOVA, $y_i = \alpha_j + \varepsilon_i$, where y_i is the observed number of young successfully fledged from a

Grasshopper Sparrow nest, and $\alpha_j \sim N(\mu, \tau^2)$ is the expected number of fledged young from a nest on the jth plot with residuals $\varepsilon_i \sim N(0, \sigma^2)$. We then followed model selection steps 3–5, described previously, to compare AIC_c values of models. Using maximum likelihood estimation (MLE) to fit models, we retained the most parsimonious model from each step and created a 90% confidence set of models. We created a composite model, fitted with restricted maximum likelihood estimation (REML), with the vegetation covariates included in the 90% confidence set of models (Zuur et al. 2009). We created 95% HPDI for parameter estimates as previously described.

RESULTS

We found 71% (n=153) of the 195 Grasshopper Sparrow nests and 20 Henslow's Sparrow nests prior to hatching. Fifty-seven percent (n=112) of Grasshopper Sparrow nests and 55% (n=11) of Henslow's Sparrow nests were successful. We did not detect any Brown-headed Cowbird parasitism over the 3 years of the study, nor did we observe cowbirds on our study plots. Our earliest nest initiation dates for Grasshopper and Henslow's sparrows were 12 May and 15 May, respectively, and our last fledging dates were 25 July and 12 July, respectively. Henslow's Sparrows preferred taller vegetation and were less tolerant of woody vegetation than Grasshopper Sparrows (Fig. 1). Our treatment actions reduced woody vegetative cover on treatment plots, and most nonwoody-vegetation covariates were similar between control and treatment plots (Fig. 2).

A constant survivorship \times plot model across years most parsimoniously explained variation in DNS for both species (Table 2). We found no support for DNS models with immediate or delayed treatment effects, and we found no differences between Grasshopper and Henslow's sparrow DNS rates. Nests of both species (combined) were equally likely to succeed on all plots in 2009 + 2010–2011 control plots (0.30 \pm 0.04; 95% confidence interval [CI]: 0.22–0.40) as they were on treatment plots from 2010–2011 (0.32 \pm 0.07; 95% CI: 0.21–0.48). The DNS

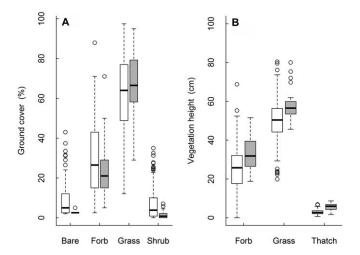


Fig. 1. (A) Ground cover and (B) vegetation height at Grasshopper (white) and Henslow's (gray) sparrow nests (2009–2011, combined) on reclaimed surface-mine grasslands in Pennsylvania.

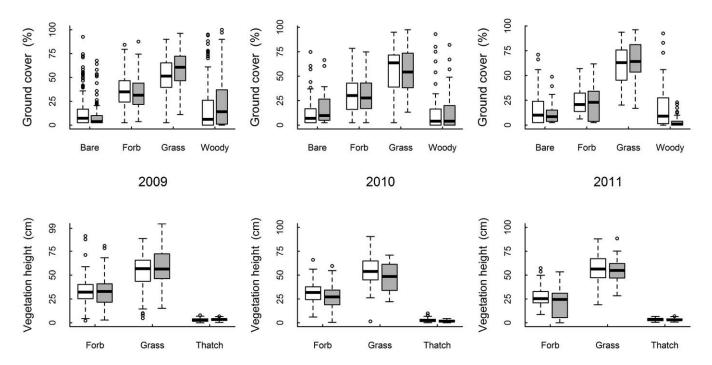


Fig. 2. Vegetation characteristics of 20.2-ha control plots (white, n = 4) and treatment plots (gray, n = 4; where woody vegetation was removed during winter 2010) on reclaimed surface-mine grasslands in Pennsylvania, 2009–2011.

model was not improved with the addition of plot-level vegetation covariates such as the woody stem count ($\hat{\beta} \pm SE = -0.03 \pm 0.08$; 95% CI: -0.19 to 0.13), distance to nearest shrub ($\hat{\beta} \pm SE = 0.03 \pm 0.14$; 95% CI: -0.24 to 0.31), or woody vegetative cover ($\hat{\beta} \pm SE = 0.03 \pm 0.74$; 95% CI: -1.42 to 1.47) (Fig. 3). Our hierarchical model-selection procedure favored models that included adjacent and immediate grass height and immediate forb height (Fig. 4); quadratic terms for these covariates were not supported (Table 2). The composite model from our 90% confidence set explained DNS as a function of constant survivorship across both species and all years (model-averaged $\hat{\beta} \pm SE = 1.19 \pm 0.67$; 95% CI: -0.11 to 2.51) on each plot ranging from 0 (randomly chosen reference plot) to 1.66 \pm 0.64 (95% CI: 0.40–2.92) + immediate grass height

TABLE 2. Models explaining variation in daily nest survival (DNS) of n=215 Grasshopper and Henslow's sparrows on reclaimed surface-mine grasslands in Pennsylvania, 2009–2011. Models were compared using the Akaike's information criterion corrected for small sample size (AIC_c) and are listed with their Akaike weight (w_i) and number of parameters (K). Survivorship (S) was best explained by constant (.) survivorship across all years and species, an individual plot effect, and nest-specific covariates measured at ≤ 1 (immediate) and S=25 (adjacent) m from the nest.

Model	$\Delta {\rm AIC_c}$	W_{i}	K
S(Plot(.)) + adjacent grass height + immediate grass height ^a	0.00	0.58	10
S(Plot(.)) + adjacent grass height + immediate forb height ^a	2.42	0.17	10
S(Plot(.)) + adjacent grass height ^a S(Plot(.))	2.51 4.10	0.17 0.08	9 8

^a Model included in the 90% confidence set.

($\hat{\beta}$ ± SE = 0.02 ± 0.01; 95% CI: 0.001–0.033) + adjacent grass height ($\hat{\beta}$ ± SE = 0.01 ± 0.01; 95% CI: -0.01 to 0.04) + immediate forb height ($\hat{\beta}$ ± SE = 0.01 ± 0.01; 95% CI: -0.004 to 0.027). Three models explaining variation in nest survivorship were included in our

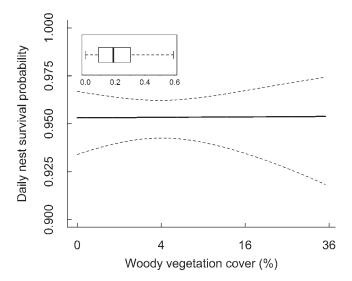


Fig. 3. Probability of daily nest survival (DNS) of Grasshopper and Henslow's sparrow nests (combined) on reclaimed surface-mine grassland plots in Pennsylvania, 2009–2011, as a function of woody vegetative cover (%) within 25 m of the nest, with 95% confidence intervals (dotted lines). Woody vegetative cover was square-root transformed (inset) but was not selected as part of our hierarchical model-selection procedure. Main panel shows woody vegetative cover back-transformed to avoid confusion in interpretation.

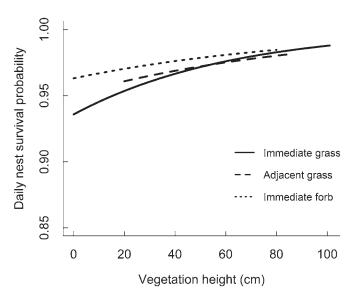


Fig. 4. Vegetation covariates included in the 90% confidence set of models explaining variation in daily nest survival for Grasshopper and Henslow's sparrows, 2009–2011, on reclaimed surface-mine grasslands in Pennsylvania. Immediate grass and forb heights were measured within 1 m of the nest, and adjacent grass height was measured at multiple locations ~6 m from the nest. Fitted lines are plotted from the minimum to maximum values recorded for a given covariate, and each line shows the estimated probability of daily nest survival for that covariate, whereas the other two vegetation covariates are held at their mean value.

90% confidence set (Table 2). Overall DNS probability for both species combined was estimated as 0.95 \pm 0.01 (95% CI: 0.94–0.96). We estimated overall nesting success as 0.34 \pm 0.04 (95% CI: 0.26–0.42) for Henslow's Sparrows and 0.32 \pm 0.04 (95% CI: 0.25–0.41) for Grasshopper Sparrows.

Considering only nests that fledged ≥1 young, Henslow's Sparrows produced a similar number of fledglings per nest as Grasshopper Sparrows ($\bar{x} \pm SD = 3.7 \pm 1.1 [n = 11]$ and 4.0 ± 1.1 [n = 112], respectively). The two-way random-effects ANOVA suggested that Grasshopper Sparrow fledgling production did not differ substantially among years or between treatments (Fig. 5). The subsequent random-effects composite model constructed from the 90% confidence set of models (Table 3) explained fledgling production as a function of a global intercept ($\beta \pm SE = 4.20 \pm$ 0.41; 95% HPDI: 3.35-5.05), decreasing plot-level woody vegetative cover ($\beta \pm SE = -3.09 \pm 1.02$; 95% HPDI: -5.12 to -0.72), decreasing bare ground within 6 m of the nest ($\beta \pm SE = -2.62 \pm 1.29$; 95% HPDI: -5.22 to -0.10), and increasing thatch depth within 6 m of the nest ($\beta \pm SE = 0.13 \pm 0.09$; 95% HPDI: -0.06 to 0.32). On the basis of this composite model and mean covariate values, we would expect a successful Grasshopper Sparrow nest to produce 4.4 fledglings on a plot without woody vegetative cover and only 3.3 fledglings on a plot with 35% woody vegetative cover.

DISCUSSION

Our research suggests that overall reproductive success of Grass-hopper and Henslow's sparrows on reclaimed surface-mine grasslands is driven by a suite of largely nonwoody vegetation

TABLE 3. Mixed-effects models explaining Grasshopper Sparrow fledgling production on reclaimed surface-mine grasslands in Pennsylvania, 2009–2011. Vegetation was measured across each 20.2-ha plot, at 5–25 m (adjacent) and ≤ 1 m (immediate) from the nest cup. Models with K fixed-effect parameters were compared using Akaike's information criterion corrected for small sample size (AIC $_c$) and are listed with their Akaike weight (w_i).

Model	$\Delta {\rm AIC_c}$	W _i	К
Plot woody vegetative cover – adjacent bare ground cover ^a	0.00	0.74	3
Plot woody vegetative cover + adjacent thatch height ^a	2.28	0.24	3
Plot woody vegetative cover – adjacent woody vegetative cover	6.57	0.03	3
Random effects ANOVA without vegetation covariates	11.70	<0.01	1

^a Model included in the 90% confidence set.

components. These findings are consistent with other research in these species in suggesting that a suite of vegetation covariates are better than a single variable in predicting habitat occupancy and territory placement (Wiens 1969), adult density (Winter 1999), and nest success (Stauffer et al. 2011). The abundance and nest success of bird species are likely affected by processes at multiple spatial scales (Andrén 1994, Stephens et al. 2003). Both fledgling production and DNS in our study, likewise, were more

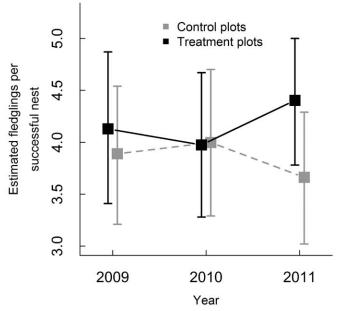


Fig. 5. Estimated number of fledgling Grasshopper Sparrows produced from a successful nest on control (gray) and treatment (black) plots on reclaimed surface-mine grasslands in Pennsylvania, 2009–2011. We used the means parameterization of a two-way random-effects ANOVA (with plot treated as a random effect) to estimate the mean number of fledglings (squares) produced from an average nest. The overlapping 95% highest-probability density intervals suggest that fledgling production on treatment plots did not change at a rate greater than expected by chance alone following the removal of woody vegetation.

parsimoniously explained by vegetation characteristics measured at multiple spatial scales than by models with only a single spatial scale represented.

Our DNS (95% CI: 0.94-0.96) and nesting success (NS) estimates for Grasshopper Sparrows (NS 95% CI: 0.25-0.41) and Henslow's Sparrows (NS 95% CI: 0.26-0.42) suggest that our study plots provided a relatively high-quality nesting habitat for grassland sparrows. Other published Grasshopper Sparrow estimates are, on average, lower for prairies (DNS = approximately 0.87-0.92, NS = approximately 6.5-17.0% [Rohrbaugh et al. 1999]; DNS = 0.93, NS = 22.0% [Winter and Faaborg 1999]), Conservation Reserve Program lands (DNS = 0.936-0.956, NS = 0.30 [Patterson and Best 1996]; DNS = 0.914-0.950, NS = 10.6-28.5% [Koford 1999]), and pastures (DNS = 0.90-0.94, NS = unknown [Renfrew et al. 2005]). Our DNS and NS estimates were generally as high as those reported in other studies of Henslow's Sparrows in prairies (DNS = 0.95, NS = 39.5% [Winter and Faaborg 1999]; DNS = ~0.956, NS = unknown [Winter et al. 2000]) and in a remnant native grassland type in Indiana (DNS = 0.947, NS = 28.7% [Robb et al. 1998]). We found few Henslow's Sparrow nests, but our sample size (n = 20) was similar to those in other studies that have produced DNS estimates for Henslow's Sparrows from reclaimed surface-mine grasslands (n = 21, Galligan et al. 2006; n = 18, Graves et al. 2010; n = 33, Stauffer et al. 2011). Although DNS estimates for these two species on reclaimed surface-mine grasslands are at least as high as those for other types of grasslands, breeding-adult density estimates of these species tend to be lower on reclaimed surface-mine grasslands than on other grasslands (Herkert 2003).

Our composite nest survival model contained relatively small positive effect sizes (<0.03 per unit change on the logit scale) for individual vegetation covariates: immediate grass height, adjacent grass height, and immediate forb height (Fig. 2). These small effect sizes may be a reflection of the relatively high DNS rates reported in our study, or further indication that no structural component of the vegetation singly drives patterns in nest survivorship on our study plots. Our results are similar to those of Galligan et al. (2006), who found a positive relationship between Grasshopper Sparrow DNS on reclaimed surface-mine grasslands and vegetation height within 1 m of the nest, which has also been supported for other grassland bird species (e.g., Winter 1999). Ammer (2003), however, found no relationship between DNS and grass height at Grasshopper Sparrow nests on reclaimed surface-mine grasslands. Presumably, greater density of vegetation around a nest prohibits visual, olfactory, and auditory discovery by predators (Martin and Roper 1988, Stauffer et al. 2011), but this relationship may depend on the composition of the predator assemblage (Wray et al. 1982, Sutter and Ritchison 2005).

Removing a single structural component of the grassland vegetation (e.g., woody vegetation) is unlikely to affect all these predator populations equally and is unlikely to produce the same effect from one grassland type to another, given the large amount of variation in predator biomass and diversity across different types of grasslands (Grant and Birney 1979). The small-mammal community also can substantially fluctuate among years within one grassland type (Grant and Birney 1979). If woody vegetation in grasslands is associated with increased nest predation (Klug

et al. 2010), then the removal of woody vegetation could reduce predation pressure on other grassland nest predators, which might negate any positive effect of predator abundance reduction. Over time, birds should evolve nesting strategies to reduce predation risk to specific predator assemblages (Weatherhead and Blouin-Demers 2004), and indeed, some grassland passerines seem able to detect and respond to the density of mammalian predators and adjust their territories by shifting to habitats with less predation risk (Thieme 2011).

We did not find support for negative effects of woody vegetation on the daily survival rate of Grasshopper and Henslow's sparrow nests. Graves et al. (2010) found support for the hypothesis that the presence or proximity of woody vegetation is associated with decreased nesting success for Grasshopper and Henslow's sparrows on reclaimed surface-mine grasslands. Graves et al. (2010) combined several metrics of woody vegetation (distance to woodland edge, and the number of woody patches and percent cover of woody vegetation within 100 m of the nest) into a single variable for their DNS models. Both species of sparrow are known to be edge sensitive to a variety of ecotones with and without woody vegetation (reviewed in Johnson 2001, Renfrew et al. 2005). Several studies have reported decreased nesting density or nesting success near woodland edges (Johnson and Temple 1990, Winter et al. 2000) and linear rows of woody vegetation along roads and fence lines (O'Leary and Nyberg 2000, Patten et al. 2006). The findings of Graves et al. (2010) may reflect this negative edge relationship; the differences between our results and those of Graves et al. (2010) may suggest that grassland sparrows perceive scattered woody vegetation within grasslands differently from woody ecotones.

Predator movements in grasslands also may be influenced by the presence of woody vegetation. Klug et al. (2010) studied the Eastern Yellowbelly Racer (*Coluber constrictor flaviventris*) and the Great Plains Rat Snake (*Pantherophis emoryi*) in Kansas prairies and documented that *C. c. flaviventris*, but not *P. emoryi*, disproportionately used areas of greater shrub cover and that the combined DNS of all grassland bird species on their plots was negatively associated with increasing shrub cover. We may not have found similar effects on DNS (Klug et al. 2010) in our study because *C. c. flaviventris* does not occur in Pennsylvania (although *C. c. constrictor* occurs there), and because 70% (n = 156) of the nests in their analysis were Dickcissel (*Spiza americana*) nests. Dickcissels frequently nest in shrubs and forbs and only rarely nest directly on the ground (reviewed in Temple 2002), and *C. c. flaviventris* may be cueing in on shrubs in search of Dickcissel nests.

Our research further confirmed that incidences of Brownheaded Cowbird parasitism are uncommon for grassland birds on reclaimed surface-mine grasslands in this region (Wray et al. 1982, Ammer 2003). By contrast, parasitism rates are higher for Wood Thrushes (*Hylocichla mustelina*) in Pennsylvania (21%; Hoover and Brittingham 1993) and for forest-nesting birds (32%) and field-or-edge-nesting species (7%) in New York (Hahn and Hatfield 1995). Cowbird parasitism of grassland birds has been associated with increasing amounts of woody vegetation in prairies (Patten et al. 2006). Despite the large amounts of woody vegetation on some of our plots, we detected no cowbird parasitism. Given the lack of cowbirds on our study area, the generalization of our results may be limited to other reclaimed surface-mine grasslands with low cowbird parasitism risk.

Offspring production in birds is most strongly influenced by nest predation rates, but food limitation is likely important as well (Martin 1992). Partial predation events are not uncommon for grassland bird species (e.g., Pietz and Granfors 2000), so our estimates of fledgling production are not direct measurements of parental quality or food availability at a nest site. Nevertheless, our estimates of fledgling production for the average successful nest were generally higher than other estimates for Grasshopper Sparrows (3.71 [McCoy et al. 1999]; 3.5–4.1 [Wray et al. 1982]; 3.7 [Rohrbaugh et al. 1999]; 4.05 [Stauffer et al. 2011]) and Henslow's Sparrows (4.0 [Robb et al. 1998]; 2.64 [Monroe and Ritchison 2005]; 3.95 [Stauffer et al. 2011]).

Removing shrubs from >80 ha did not increase Grasshopper Sparrow fledgling production on treatment plots (Fig. 5), but woody vegetative cover was associated with the production of fewer fledglings among successful Grasshopper Sparrow nests. Our findings suggest a fitness cost for Grasshopper Sparrows nesting in areas with elevated woody vegetative cover that is not immediately relieved following removal of woody vegetation. These results may indicate that our treatment actions (e.g., herbicide application) had unintended effects that largely negated the positive benefits of removing the woody vegetation. For example, the herbicide application may have reduced insect populations on our treatment plots (Taylor et al. 2006), or surface disturbance from our heavy machinery use may have unintentionally altered the plant community (Zarnetske et al. 2010). Woody vegetation levels, additionally, may not directly influence fledgling production in Grasshopper Sparrows; increasing levels of woody vegetation may be initially correlated with decreasing food availability or lower social status (sensu Ekman and Askenmo 1984).

Some researchers (e.g., Graves et al. 2010, Klug et al. 2010) have identified the removal of woody vegetation from grasslands as a management action to benefit grassland birds. Our results, however, suggest that removal of woody vegetation may not result in short-term nesting benefits, if any, to Grasshopper and Henslow's sparrows. Lesser Prairie-Chickens (Tympanuchus pallidicinctus), similarly, do not experience increases in nest survival in the 4 years following herbicide application to kill shrubs (Patten and Kelly 2010). Eventually, successional processes will increase woody vegetative cover to levels that prohibit use by grassland sparrows (Hill 2012). Reducing the amount of woody vegetation within these grasslands would reduce recruitment of woody vegetation (Scott and Lima 2004) by reducing the source of propagules (e.g., seeds and shoots), which would likely increase the duration that these grasslands remain suitable for grassland birds.

Our research supports the findings of other researchers that reclaimed surface-mine grasslands are valuable and productive habitats for some grassland sparrow species, but our experimental manipulation did not result in increased DNS rates or Grasshopper Sparrow fledgling production. Our overall DNS estimate was at least as high as other studies have reported from grasslands with few woody plants. Given that both sparrow species are more likely to occupy grasslands with few woody plants (Coppedge et al. 2001), there may be long-term benefits to removing woody vegetation. The cost of such actions, however, may be prohibitive. Acquiring and maintaining grasslands with little woody vegetative cover may be a more cost-effective strategy than

removing existing woody vegetation from reclaimed surface-mine grasslands.

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