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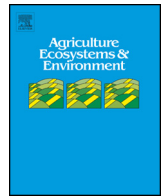
Original research paper

Effects of crop type and harvest on nest survival and productivity of dickcissels in semi-natural grasslands

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A B S T R A C T

Recent focus on climate change and global energy production has increased interest in developing biofuels including perennial native grasses (e.g. switchgrass [Panicum virgatum]) as viable energy commodities while simultaneously maintaining ecosystem function and biodiversity. However, there is limited research examining the effects of biofuel-focused grasslands on grassland bird reproductive success and conservation. In 2011–2013 we studied the effects of vegetation composition and harvest regimens of switchgrass monocultures and native warm-season grass (NWSG) mixtures on nest success, nest density, and productivity for dickcissels (Spiza americana) in Clay Co. MS, USA. There was no effect of vegetation metrics, harvest frequency, or biofuel treatment on nest survival. However, both vegetation composition and harvest frequencies influenced nest density and productivity. Native warm season grasses contained 54–64 times more nests relative to switchgrass treatments, and nest density and productivity were 10% greater in single harvest plots. Our results suggest semi-natural grasslands can balance biofuel production, ecosystem functionality, and conservation so that biofuels offer an opportunity for wildlife conservation rather than a continued threat to grassland birds.

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1. Introduction

Biofuels are a recent focus of global energy policies aimed at reducing greenhouse-gas emissions and alleviating climate change concerns while bolstering local economies (Farrell et al., 2006; Campbell et al., 2008; Tilman et al., 2009; U.S. EPA, 2011). As such, there is increased interest in the use of perennial native grasses (e.g., switchgrass [Panicum virgatum]) for bioenergy production as they may also maintain ecosystem services including water and soil quality and wildlife habitat (McLaughlin and Kszos, 2005; Parrish and Fike, 2005; Fargione et al., 2009; Hartman et al., 2011; Uden et al., 2014 Fargione et al., 2009; Hartman et al., 2011; Uden et al., 2014). However, there is limited research addressing the effects of semi-natural grasslands (Allen et al., 2011) for biofuel production on the distribution, habitat selection, and demography of wildlife (Murray and Best, 2003; Allen et al., 2011; Mitchell et al., 2012; Dunlap, 2014).

Semi-natural grasslands managed for biofuels may mimic natural grasslands based on overall ecosystem functionality and vegetation structure (Fletcher and Koford, 2002), but there is ongoing debate regarding the most appropriate grass species or harvest strategies to use for energy production while maintaining biodiversity. Switchgrass monocultures often produce more cellulosic ethanol than low-input high-diversity plant mixtures because greater plant species richness decreases biofuel yield (Adler et al., 2009). However, greater structural and species heterogeneity in mixed species plantings supports greater biodiversity and ecosystem functions (Tilman et al., 2006; Adler et al., 2009; Meehan et al., 2010; Werling et al., 2014). Additionally, these mixed species plantings provide resources important for breeding birds including potential nest sites and arthropods for nestling sustenance (Simpson, 1949; MacArthur and MacArthur, 1961; Wiens, 1974; Rotenberry, 1985; McCoy et al., 2001). Biofuel production also requires annual or semi-annual harvests, with a main cutting traditionally during fall or winter months to

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maximize total biomass, and a potential secondary cutting for forage or biomass during the summer (Vogel et al., 2002; Fike et al., 2006; Liu et al., 2015). As such, the timing of these additional harvest events can be detrimental to avian species if they occur during the breeding season (Roth et al., 2005) because they destroy active nests, remove vegetative cover, and reduce food availability (Bollinger et al., 1990; Kershner and Bollinger, 1996; Warren and Anderson, 2005; Perlut et al., 2006). Biomass harvests can also reduce plant height and density in subsequent years (Roth et al., 2005) which may leave nests more vulnerable to detection by predators (Martin, 1993). Additionally, most avian species abandon harvested plots for the remainder of the breeding season (Frawley and Best, 1991), limiting future nest attempts and seasonal productivity.

Habitat manipulations can afford unique opportunities to understand management concurrently with ecological concepts. Animals select breeding habitats by distributing themselves across landscapes to maximize fitness within the constraint of resource availability and predation risk to themselves and offspring (Grinnell, 1917; Hildén, 1965; Jones, 2001; Fontaine and Martin, 2006). Considering animal settlement patterns, the ideal free distribution [IFD] model (Fretwell and Lucas, 1969) predicts that local habitat quality determine species' density, resulting in equal fitness across all individuals regardless of habitat quality. In contrast, the ideal despotic distribution [IDD] model (Fretwell, 1972) suggests breeding birds occupy territories based on competition in addition to resource availability, thereby relegating subordinates into lower quality, less productive habitat, which leads to variation in per capita productivity. Regardless of distribution models used to examine individual fitness, resource rich environments and mixed species plantings support greater densities of breeding birds and greater total production of offspring per unit area (Fretwell and Lucas, 1969; Bakker and Higgins, 2009), thereby contributing more individuals to the overall population. Thus, areas receiving multiple annual harvests or containing switchgrass monocultures would be expected to provide lower quality habitat and concomitant avian productivity than areas receiving single annual harvests or containing native warm-season grass mixtures. This effect would be exacerbated if competitive behaviors resulted in unequal per capita productivity across treatments.

We examined the effects of biofuel treatments on nest success, nest density, and productivity of dickcissels (*Spiza americana*), a polygynous, ground and shrub-nesting grassland bird of conservation concern (Blankspoor, 1970; Temple, 2002). We predicted daily survival rate (DSR) and nest density would be greater in native warm-season grasslands (hereafter "NWSG") than in switchgrass monocultures after accounting for other nest survival covariates including microhabitat and plot-level characteristics, ordinal date, and nest age (Jensen and Finck, 2004; Shaffer, 2004; Grant et al., 2005). We also expected nest survival and nest density in multiple-harvested plots to be lower than single-harvested plots due to increased predation risk or direct failures from mowing and plot abandonment following harvest (Frawley and Best, 1991). As productivity per unit area is a product of reproductive success and nest density, even if nest survival was similar across treatment types, we expected plots with greater nest density to produce more offspring per hectare. However, in accordance with ideal free distribution, individual productivity would be similar across all territories, regardless of treatment. Conversely, if males display an ideal despotic distribution (Zimmerman, 1982), males in higher quality territories will also have greater individual productivity. This could have population-level implications for grassland birds if the potential loss of high quality breeding habitat due to biofuel cultivation reduces overall offspring production while also limiting

the reproductive efforts of dominant individuals that would normally breed there (Haché et al., 2013).

2. Methods

2.1. Study area

This study was conducted from late April to late July 2011–2013 at B. Bryan Farm in Clay Co., Mississippi, on 16 plots (range: 4.73–8.51 ha) configured in a randomized complete block design. B. Bryan Farm is comprised mostly of row crop agriculture, pastureland, and conservation easements situated within the historical range of the Blackland Prairie (Barone, 2005). Eight plots were planted in spring 2010 with a mixture of warm season grasses (e.g. big bluestem [*Andropogon gerardii*], little bluestem [*Schizachyrium scoparium*], indian grass [*Sorghastrum nutans*]) and forb species including Illinois bundleflower (*Desmanthus illinoensis*), wild blue lupine (*Lupinus perennis*), and tickseed sunflower (*Bidens aristosa*) and eight were planted with switchgrass; other species in the seedbank included giant ragweed (*Ambrosia trifida*), broadleaf signalgrass (*Urochloa platyphylla*) and *Sesbania* spp. All plots were mowed in April 2012 prior to green-up to simulate harvest. Additionally, 4 "multiple harvest" plots of each vegetation type were also harvested annually in late-June 2012 and 2013, resulting in 4 unique treatments: native warm-season grass single harvest ("NWSG single harvest"), switchgrass single harvest ("switchgrass single harvest"), native warm-season grass multiple annual harvest ("NWSG multiple harvest"), and switchgrass multiple annual harvest ("switchgrass multiple harvest"). One switchgrass single harvest plot and 1 switchgrass multiple harvest plot failed to establish sufficient vegetation so we limited subsequent analyses to the remaining 14 plots.

2.2. Territory mapping and banding

We conducted weekly visits to all plots and noted arrival dates of male dickcissels to determine the pattern of habitat settlement from 1 May in 2011 and 24 April in 2012 and 2013 to 15 July each year. Once male dickcissels established territories, we used target mist-netting for territorial males by attracting birds with conspecific playback of songs and call notes. After capture, we aged and banded all adult birds with a USFWS aluminum band and unique 3-color band combination for individual identification under approved permits (Mississippi State University IACUC approval #11-020, Mississippi Cooperative Wildlife Research Unit Federal Bird Banding Permit #22456).

We delineated territory areas for all males in the study plots by conducting surveys every 3–10 days from 0530 to 1200 CDT by walking each plot along 100-m gridlines established to ensure systematic sampling effort and to minimize disturbance to dickcissels (Baker, 2011). If birds were present, we monitored birds from $\geq$15 m for at least 20 min and recorded 3–7 unique bird locations/survey with a handheld Global Positioning System (GPS), excluding locations where birds were influenced by observer presence, (e.g. birds engaged in scolding behaviors directed towards the observer). Following biomass harvest on treatment plots in late-June 2012 and 2013, we continued territory mapping and re-sighting efforts across all plots until 15 July. We used fixed kernel density estimators (KDE) and 95% volume contours to estimate territory size (Silverman, 1986; Worton, 1989) for all territorial males present $\geq$3 weeks for use in subsequent analyses using package *adehabitatHR* (Calenge, 2006) in program R 3.1.3 (R Core Team, 2015). We excluded territories from subsequent density analyses if the calculated 95% KDE contained $\leq$25% of the study plots.

2.3. Nest searching and monitoring

From 1 May-9 August 2011 to 2013 we found and monitored nests using structured (systematic rope-dragging or walking), opportunistic, and behavioral searches (Conkling et al., 2015). We searched all 14 plots in 2011–2012, and only NWSG plots in 2013 based on the limited number of nests for all avian species found in switchgrass during previous 2 seasons ($n = 11$, T. Conkling, unpublished results). For bi-weekly structured searches, 3 technicians used a 25-m rope with attached noisemakers to disturb vegetation, walking the entire study area to flush nesting birds. Existing vegetation limited rope-dragging efforts in 2011 (mostly *Sesbania* spp. >2 m tall), necessitating the use of systematic walking by 3–5 technicians spaced at 4 m intervals disturbing the vegetation with hand-held 2-m PVC pipes (2.5 cm diameter). As part of the experimental treatment, all plots were mowed to ~16 cm prior to the arrival of dickcissels in April 2012; this also allowed observers to use rope-dragging for structured searches in 2012 and 2013. Additionally, we found nests opportunistically based on adult behaviors, incidental flushes, or by locating a nest in the absence of adult cues during visits to active dickcissel territories every 3–10 days while conducing other activities (e.g. vegetation sampling, nest checks, and behavioral monitoring). We allocated equal time monitoring birds in all territories ($\geq$30 min each week) to balance search efforts regardless of treatment. During all searches, observers spent $\leq$10 min scanning the vegetation to locate nests after a bird was flushed (Barg et al., 2005).

We recorded the location of each nest with a handheld GPS and marked the nests with flagging >5 m north of the nest. We then monitored all nests at 2–6 day intervals until the nest failed or young fledged (day 9–10 post-hatching) to determine nest fate and calculate daily survival rate. For nests found after hatch date, we aged nest contents based on physical development of nestlings (Temple, 2002) and then back-dated to determine incubation initiation date (12 days incubation, 9 days nestling). When we found nests after incubation began that failed prior to hatch date, we estimated incubation initiation date by assuming the midpoint of incubation (6 days) coincided with halfway between available check dates (Sousa and Westneat, 2012). In 2012 and 2013 we banded nestlings at approximately 6 days old with a USFWS aluminum band and 2-color band combination unique to each nest. We estimated territory productivity as the maximum of the number of fledglings per territory based on the total nestlings present at the last nest check before fledging for successful nests and the maximum number of fledglings observed interacting with an adult bird (e.g. active begging or feeding behaviors) in that territory irrespective of nest. If we observed banded fledglings, we only counted those individuals towards the maximum number of fledglings for their original nesting territory, regardless of their observed location.

We collected nest vegetation measurements about 2 weeks after the estimated hatch date to avoid nest disturbance or prematurely force-fledging nestlings and to reduce variability on the timing of vegetation collection. We measured nest height, maximum vegetation height, litter depth, and vegetation visual obstruction with a Robel pole observed at a distance of 4 m and height of 1 m in each of the cardinal directions (Robel et al., 1970). We calculated distance to nearest edge of grassland habitat using ArcMap 10.1 (ESRI, 2011). We also calculated nest visible height as the difference between nest height and mean visual obstruction. A nest with a positive visible height would be potentially visible from 4 m, whereas a negative visible height indicated that a nest would be obscured by vegetation.

We collected plot-level vegetation data along 5 randomly located 50-m transects to determine structure and species composition among treatments. We first used a geographic information system (ESRI, 2011), to overlay a 50×50 m grid on each study plot and randomly selected 5 grid squares per plot for transect locations established as part of a concurrent study. Each 50-m transect was centered on the grid square midpoint with a randomly assigned transect orientation. We sampled each transect in March 2011 and then monthly from June 2011 to December 2013, but we restricted analyses to samples collected in June each year (prior to midseason harvest) to limit effects of harvest on resulting vegetation measurements. We used the point-intercept method (Firemon, 2007) to quantify vegetation species composition by recording litter depth along with species name and height (cm) for the 3 most common vegetation species at 5-m intervals along the transect (10 measurements/transect). We also classified vegetation structure at 10-m intervals (5 measurements/transect) by recording maximum height of visual obstruction from each of the 4 cardinal directions with a Robel pole (Robel et al., 1970).

2.4. Statistical analyses

We used R 3.1.3 (R Core Team, 2015) to test covariates for multicollinearity based on variance inflation factors (VIFs; Zuur et al., 2009). Nest height VIF was >3, so we removed it from subsequent analyses; after removal, all other VIFs were <1.12, indicating no multicollinearity between the remaining variables. We calculated mean values ($\pm$SE) for nest age at initial discovery (hereafter "age found"), nest visible height, and distance to edge of habitat and plot-level characteristics including first week of territory establishment by males (hereafter "first week"), vegetation visual obstruction, and estimated vegetation species diversity by plot using Shannon's Diversity Index (H'; Hill, 1973) based on the maximum number of species detected from all transects at each plot annually in June. We used analysis of variance (ANOVA; $\alpha = 0.05$), linear mixed models with R package *lme4* (Bates et al., 2015), and Tukey's test ($\alpha = 0.05$) with plot as a random effect to compare mean differences of vegetation metrics among treatments.

2.4.1. Nest survival modeling

We used a Bayesian framework (Royle and Dorazio, 2008) using JAGS 3.4.0 (Plummer, 2013) and R package *R2jags* (Su and Yajima, 2014) to estimate daily nest survival for monitored nests based on vegetation characteristics (visible height, distance to habitat edge), linear and quadratic effects of date, linear and quadratic effects of nest age, year, mean Robel measurement for the plot, and treatment, with plot and search method as random effects to account for potential variation in survival estimates (Conkling et al., 2015). We calculated period nest survival for nests starting on median incubation initiation date (25 May) and multiplied daily survival rate estimates generated for each of 21 days in the nesting period (i.e. incubation to fledging (Temple, 2002)). We standardized all data and used uninformative priors for all parameters and sampled using MCMC procedures with 3 independent Markov chains, 25000 burn in, and 75000 iterations. We examined traceplots and posterior distributions for the effects of interest using Brooks-Gelman-Rubin statistics ($\hat{R}$) <1.05 and evaluated goodness of fit for all models and the proportion of posterior distribution values >0 or <0 when 95% credible intervals overlapped zero using Bayesian *P*-values (Brooks and Gelman, 1998; Schmidt et al., 2010; Gelman et al., 2014).

2.4.2. Plot nest density and productivity

We estimated nest density per ha by treatment per year given the total number of nests observed with contents (eggs or nestlings) using a generalized linear mixed model with a Poisson distribution within the same Bayesian framework outlined above.

We used treatment and year as fixed effects, a random effect of plot, and plot area (ha) as an offset to account for differences in nest density based on survey area. Many analyses estimating densities of animal populations include detection probabilities (MacKenzie, 2006; Royle and Dorazio, 2008; Fiske and Chandler, 2011), although this is often difficult to account for in nest searching (but see Monroe, 2014). Given the complexity of nest detection models (Monroe, 2014), we instead used unadjusted counts of nests found per plot as an index of nest density. As a result, we accounted for potential discrepancies in nest density by equally allotting nest searching efforts using systematic searches among treatments and spent a minimum of 30 min weekly in every identified territory. We estimated mean brood size for each treatment from the number of nestlings present in nests during the last nest visit before fledging (With et al., 2008). We calculated the odds ratio for categorical covariates in the model by exponentiating the resulting parameter coefficients. Finally, we estimated productivity (fledglings/ha) by vegetation treatment and year during each iteration within the Bayesian framework by multiplying the estimates for 21-day period survival and nest density by an estimate of brood size sampled from a normal distribution with treatment-specific means and variance. We used Cohen's D to calculate effect sizes between treatments to assess biological importance (Cohen, 1988; Nakagawa and Cuthill, 2007) by calculating the mean difference between groups, with Cohen (1988) defining effect sizes as small ($d = 0.20$), medium ($d = 0.50$), and large ($d = 0.80$). We also used Cohen's U_3 index derived from calculated effect sizes and corresponding z scores to determine the percentile gain of mean values between treatments (Durlak, 2009). For example, a large effect size of 0.8 corresponds to the 79th percentile under the normal curve, indicating that the mean value for a given treatment is 29 percentiles greater than mean value in the reference treatment (i.e. 50% percentile), whereas a small (0.2) effect size only equals an 8% difference between mean treatment values.

2.4.3. Territory nest density and productivity

To determine if productivity varied at the territory level across treatments in accordance with IDD, we used a Bayesian framework to estimate nest density for each documented territory. We used a generalized linear mixed model with a zero-inflated Poisson distribution with vegetation treatment and year as fixed effects, random effect of plot, and total territorial males per plot as an offset to control for male density as outlined above. We then calculated productivity (fledglings/ha) per territory by multiplying territory nest density by brood size and period survival estimates for each treatment and year. We restricted our territory-level analyses to territories that included ≥25% of the study plots.

3. Results

We monitored 238 nests (99 in 2011, 79 in 2012, 60 in 2013) in 176 dickcissel territories and located 0 to 6 nests per territory (mean = 1.65 ± 0.04); we only found 7 nests (3%) in switchgrass (5 in 2011, 1 in 2012, 1 in 2013). Settlement dates for males establishing territories were similar among treatments ($F_{1,6} = 1.34$, $P = 0.29$; see Table A.1 in Supplementary materials). Predation accounted for 63.8% of apparent nest failures, 11 nests (4.8%) failed due to mowing, 3 (1.3%) nests failed to hatch and were subsequently abandoned by adults, and 8 others (3.4%) were abandoned in the incubation stage for unknown reasons. Only 2 nests (0.8%) were parasitized by a single brown-headed cowbird (*Molothrus ater*) egg, with 1 nest later depredated during incubation, and 1 fledging a cowbird offspring. Nine nests were associated with territorial males but located outside of the plots and were excluded from analyses. The ages of nests found ($F_{3,7} = 0.68$, $P = 0.59$), nest visible height ($F_{3,7} = 2.64$, $P = 0.13$), and distance to edge ($F_{3,7} = 1.88$, $P = 0.22$) were similar among treatment types (see Table A.1 in Supplementary materials). Plot-level vegetation visual obstruction was greater in mature switchgrass treatments compared with NWSG (2013: $F_{3,10} = 28.72$, $P < 0.01$), although this metric varied during plot establishment years (2011: $F_{3,10} = 8.43$, $P = < 0.01$; 2012: $F_{3,10} = 0.46$, $P = 0.72$); (see Table A.2 & Fig. A.1 in Supplementary materials). Additionally, plant diversity was greater in NWSG relative to switchgrass across all years ($F_{3,10} = 26.15$, $P < 0.01$), but was similar between harvest frequencies for each vegetation type (see Fig. A.1 in Supplementary materials).

There was no effect of vegetation metrics, harvest frequency, or biofuel treatment on nest survival. Daily survival rate for breeding dickcissels was best explained by quadratic nest age, quadratic date, year (2012) and age of the nest when found (Table 1). Additionally, the period survival for the 21-day nesting cycle based on median initiation date indicated that overall survival of multiple-harvest treatments was not lower than single harvest treatments even with mid-season harvests destroying active nests. (Table 2). Daily survival rate decreased as nests contents aged, resulting in lower survival for nestlings relative to the egg stage.

Table 1
Model coefficients (±SD), 95% credible intervals, Brooks-Gelman-Rubin statistics (R̂), and Bayesian *P*-values for parameters in MCMC model to estimate nest survival for dickcissel nests in Clay Co., Mississippi, 2011–2013.

Parameter	Estimate	SD	95% Credible Intervals		R̂	Bayesian *P*-value
			Lower	Upper		
Intercept	2.778	0.606	1.674	4.005	1.050	0.997
Age	−1.064	0.115	−1.301	−0.851	1.002	1.000
Quadratic Age	−0.507	0.093	−0.683	−0.320	1.000	1.000
Date	−0.639	0.157	−0.939	−0.331	1.001	1.000
Quadratic Date	0.960	0.199	0.588	1.368	1.002	1.000
Nest Age When Found	0.288	0.098	0.091	0.472	1.000	0.998
Year−2012[a]	−0.823	0.253	−1.333	−0.341	1.001	1.000
Year−2013[a]	−0.085	0.399	−0.860	0.689	1.000	0.590
Nest Distance to Edge	0.121	0.087	−0.050	0.289	1.002	0.922
Visual Obstruction	−0.070	0.164	−0.390	0.256	1.001	0.347
Territory Area (95% KDE)	−0.078	0.085	−0.237	0.093	1.001	0.819
Nest-Visible Height	−0.062	0.108	−0.263	0.162	1.001	0.725
Native Warm-Season Grass (single harvest)[b]	0.059	0.454	−0.938	0.966	1.002	0.419
Switchgrass (multiple harvest)[b]	−0.001	1.037	−1.980	2.198	1.002	0.519
Switchgrass (single harvest)[b]	0.880	0.845	−0.633	2.826	1.001	0.862

[a] 2011 is the reference year. Coefficient refers to change in daily survival rate (DSR) for given year relative to 2011.
[b] Native Warm-Season Grass (multiple harvest) is the reference condition. Coefficient refers to change in relative density for given treatment relative to NWSG-M.

Table 2
Period survival (21-day nesting period) for dickcissel (*Spiza americana*) nests located on median incubation initiation date (25 May) midway through nesting cycle (day 11), period survival, plot productivity (number of fledglings/ha), and territory productivity (# fledglings/ha) in Clay Co., Mississippi, 2011–2013.

Treatment	Year					
	2011		2012		2013	
	Mean	SD	Mean	SD	Mean	SD
Period Survival						
Native Warm-Season Grass (multiple harvest)	0.096	0.106	0.019	0.057	0.086	0.102
Native Warm-Season Grass (single harvest)	0.105	0.109	0.022	0.059	0.097	0.109
Switchgrass (multiple harvest)	0.147	0.194	0.056	0.126	–	–
Switchgrass (single harvest)	0.316	0.230	–	–	–	–
Plot						
Nest Density						
Native Warm-Season Grass (multiple harvest)	1.182	5.714	0.928	4.115	0.667	3.216
Native Warm-Season Grass (single harvest)	2.562	4.590	2.045	3.836	1.445	2.389
Switchgrass (multiple harvest)	0.027	0.039	0.022	0.030	–	–
Switchgrass (single harvest)	0.047	0.068	–	–	–	–
Productivity						
Native Warm-Season Grass (multiple harvest)	0.497	7.855	0.088	1.545	0.260	3.869
Native Warm-Season Grass (single harvest)	0.907	2.306	0.128	0.425	0.462	1.357
Switchgrass (multiple harvest)	0.008	0.023	0.003	0.026	–	–
Switchgrass (single harvest)	0.044	0.126	–	–	–	–
Territory						
Nest Density						
Native Warm-Season Grass (multiple harvest)	0.173	0.049	0.112	0.033	0.114	0.035
Native Warm-Season Grass (single harvest)	0.192	0.047	0.125	0.032	0.128	0.035
Switchgrass (multiple harvest)	–	–	–	–	–	–
Switchgrass (single harvest)	–	–	–	–	–	–
Productivity						
Native Warm-Season Grass (multiple harvest)	0.084	0.102	0.014	0.034	0.042	0.057
Native Warm-Season Grass (single harvest)	0.094	0.113	0.016	0.040	0.050	0.068
Switchgrass (multiple harvest)	–	–	–	–	–	–
Switchgrass (single harvest)	–	–	–	–	–	–

Similarly, DSR declined as the season progressed, although there was a positive effect of quadratic date on survival. Additionally, DSR increased for nests found later in the nesting cycle independent of the effect of nest age ($\beta = 0.288$, 95% CrI: 0.098, 0.472). We also noted a marginal effect of distance to habitat edge (Bayesian *P*-value = 0.92).

The estimated nest density across plots ranged from 0.03 to 2.56 nests per hectare (Table 2). Nest density and productivity were lower in 2013 than in previous years and NWSG plots contained 54.0–64.6 times more nests than switchgrass monocultures of the same harvest frequency (Tables 2 & 3,Fig. 1), providing support that birds chose breeding locations in NWSG based on vegetation heterogeneity and diversity (see Fig. A.1 in Supplementary materials). Additionally, nest density and resulting productivity estimates were 2.4 times greater for NWSG single harvest plots relative to NWSG multiple harvest. The Bayesian *P*-value (0.78) for nest density indicated that the posterior distribution overlapped zero, but Cohen's effect sizes (2011: $d = 0.27$ [95% CI: 0.19, 0.34]; 2012: $d = 0.28$ [95% CI: 0.21, 0.35]; 2013: $d = 0.27$ [95% CI: 0.20, 0.35]) indicated a small practical significance, with a > 10.5% gain in nest density estimates for single harvest plots (2011:$U_3 = 60.5\%$; 2012: $U_3 = 61.1\%$; 2013: $U_3 = 60.8\%$).

Most dickcissel territories were located primarily in NWSG treatments; there was no significant difference between harvest frequencies in either 95% KDE territory area or the proportion of NWSG contained within the 95% KDE (see Table A.2 in Supplementary materials). We only had 2 dickcissel territories with a greater proportion of their 95% KDE territory area within switchgrass treatment plots rather than in NWSG, so we restricted our territory-scale analyses to birds in NWSG treatments. We also excluded 5 territories from subsequent analyses whose 95% KDE contained ≤25% of treatment plots.

Table 3
Model coefficients ($\pm$ SD), 95% credible intervals, Brooks-Gelman-Rubin statistics ($\hat{R}$), and Bayesian *P*-values for parameters in MCMC model to estimate plot nest density (number of nests/ha) for dickcissel nests in Clay Co., Mississippi, 2011–2013.

Parameter	Estimate	SD	95% Credible Intervals		$\hat{R}$	Bayesian *P*-value
			Lower	Upper		
Intercept	−0.369	0.891	−2.230	1.322	1.012	0.697
2012[a]	−0.231	0.153	−0.534	0.073	1.001	0.931
2013[a]	−0.570	0.173	−0.917	−0.239	1.004	1.000
Native Warm-Season Grass (single harvest)[b]	0.881	1.198	−1.421	3.370	1.009	0.780
Switchgrass (multiple harvest)[b]	−3.989	1.719	−7.981	−1.491	1.020	0.997
Switchgrass (single harvest)[b]	−3.288	1.489	−6.652	−0.859	1.019	0.993

[a] 2011 is the reference year. Coefficient refers to change in daily survival rate for given year relative to 2011.

[b] Native warm-season grass (multiple harvest) is the reference treatment. Coefficient refers to change in daily survival rate for given treatment relative to native warm-season grass (multiple harvest).
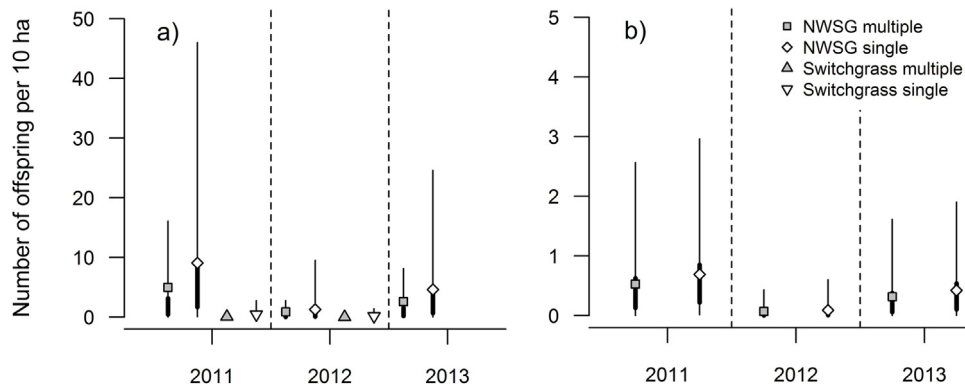
Fig. 1. Mean (symbol) and 50% (thick bar) and 95% CrI (thin bar) for a) plot productivity and b) territory productivity in native warm-season grass (NWSG) multiple harvest (□), NWSG single harvest (◇), switchgrass multiple harvest (△), and switchgrass single harvest (▽) treatments in Clay Co., Mississippi, 2011–2013.

For the 7 nests located in switchgrass, we identified 4 territories associated with nests in switchgrass plots, but most of the 95% KDE territory areas for associated males were located in NWSG treatments (mean proportion = 0.62 ± 0.08). The remaining 3 nests were >50 m from the nearest known location of any territorial male so we were unable to determine the male associated with them. There was no difference in territory nest density between harvest frequencies (Table 4), but there were fewer nests in 2012 and 2013 relative to 2011, in accordance with increasing vegetation structure as all grasses matured (see Fig. A.1 in Supplementary materials). Additionally, per capita productivity did not differ between NWSG single harvest and multiple harvest treatments (Table 4), contrary to predictions based on IDD that individual reproductive success would be greatest in the higher quality habitat.

4. Discussion

Species composition of vegetation did not affect nest survival but there was a negative effect of switchgrass on nest density and productivity. Dickcissels appeared to perceive NWSG as higher quality habitat in accordance to IFD and IDD density-dependence predictions (Svärdson, 1949; Fretwell and Lucas, 1969; Morisita, 1971; Petit and Petit, 1996), establishing territories and building nests in greater densities relative to switchgrass plots. Birds respond positively to increased vegetation structural complexity in high diversity plant mixtures (Simpson, 1949; MacArthur and MacArthur, 1961; Wiens, 1974; Robertson et al., 2011), including those used for biofuels (Robertson et al., 2011; Blank et al., 2014). Although switchgrass and other cellulosic biofuels produce less ethanol than corn, they can offer a suitable alternative to rowcrop production on marginal lands (DeVault et al., 2012) while providing ecosystem benefits including carbon sequestration and grassland bird conservation (Fargione et al., 2009; Werling et al., 2014). However, monocultures of native grass species may not provide quality breeding habitat, especially as grasses mature

(Keyser et al., 2012). Switchgrass monocultures produce more ethanol than NWSG (Adler et al., 2009), but the vegetation heterogeneity in NWSG that limits biofuel production also provides higher quality habitat for breeding grassland birds.

Our small sample size of only 7 nests in switchgrass plots may have limited the ability of our nest survival model to identify vegetation treatment effects. For example, period survival for switchgrass single harvest nests in 2011 (mean = 0.316 ± 0.230) was greater than all other treatment types (Table 2), but this estimate was based on data from 4 total nests, compared with 32 nests in NWSG multiple harvest and 60 in NWSG single harvest plots, respectively. Regardless of model limitations, >97% of nests in our study were located in NWSG and only 2 of 176 males established territories primarily in switchgrass treatment plots, providing support that vegetation species composition had a strong effect on the overall nest density. Additionally, 5 of the 7 total switchgrass nests were found in the initial year of the study, further suggesting that mature grass monocultures might not be used by breeding grassland birds.

Contrary to our initial predictions regarding harvest frequency, multiple harvests did not reduce nest daily survival rates. We observed 11 nest failures attributed to mowing during June harvests, but these failures had minimal influence on the effects of harvest frequency on DSR, likely due to the low number of active nests ($n = 40$; 17% of total nests) in late June 2012 and 2013, and lower nest density in multiple-harvest plots. Perlut et al. (2006) also noted that while mowing was responsible for nest failures at 55% of nests on fields hayed in the middle of the breeding season (21 June–10 July), there was no difference in nest survival compared to unmowed plots until after the nesting season. In contrast, our nest density and plot productivity estimates were greater in single harvest treatments relative to multiple harvest plots. While Bayesian *P*-values for the posterior distribution overlapped zero, this lack of statistical support may be due to the small number of NWSG plots sampled each year. Regardless,

Table 4
Model coefficients (±SD) and 95% credible intervals for parameters in MCMC model to estimate nest density (number of nests/ha) for dickcissel territories in Clay Co., Mississippi, 2011–2013.

Parameter	Estimate	SD	95% Credible Intervals		R̂	Bayesian *P*-value
			Lower	Upper		
Intercept	−1.787	0.286	−2.399	−1.286	1.014	1.000
2012[a]	−0.445	0.174	−0.775	−0.115	1.001	0.992
2013[a]	−0.385	0.187	−0.7721	−0.034	1.000	0.983
Native Warm-Season Grass (single harvest)[b]	0.123	0.370	−0.532	0.954	1.001	0.647

[a] 2011 is the reference year. Coefficient refers to change in daily survival rate for given year relative to 2011.
[b] Native warm-season grass (multiple harvest) is the reference treatment. Coefficient refers to change in daily survival rate for given treatment relative to native warm-season grass (multiple harvest).

we observed a 10.8% annual mean gain in nest densities for single harvest plots; a change in vital rates ≥10% may be biologically important for avian populations (Powell et al., 1999; Donovan and Thompson, 2001; Nakagawa and Cuthill, 2007). Also, our estimates of plot productivity were calculated based only on nest contents at the last nest visit before fledging and did not account for fledgling survival rates (Streby et al., 2014). Fledglings of many grassland birds species including dickcissels have limited mobility and remain near the nest for at least 1–2 weeks post-fledging (Berkeley et al., 2007), making them vulnerable to predation, mowing, or other negative harvest effects that could exacerbate treatment effects on seasonal productivity.

Although we observed no difference in territorial male density between harvest frequencies (T. Conkling, unpublished results), the lower nest densities in multiple harvest plots suggest that dickcissel females perceived a reduction in potential nest sites or food in these locations. It is unclear which habitat cues females use to select breeding habitat (Zimmerman, 1971, 1982; Finck, 1984; Temple, 2002). However, site fidelity for females is rare (Walk et al., 2004; Small et al., 2012; Sousa, 2012), suggesting they may be sensitive to annual changes in vegetation cover, food, availability of potential nest sites, and individual male quality (Orians and Wittenberger, 1991; Germain and Arcese, 2014; Zabala and Zuberogoitia, 2014; Conkling, 2016). In contrast, up to 45% of dickcissel males returned to their same breeding plots regardless of varying habitat conditions or previous productivity (Zimmerman and Finck, 1989; Sousa and Westneat, 2012; T. Conkling, unpublished results). This "always stay" strategy may be advantageous for territorial birds attempting to maximize fitness in non-stable, intermediate grasslands (Switzer, 1993) where existing vegetation structure and arthropods available at territory establishment do not reflect conditions present later in the season (Sergio et al., 2011) or the likelihood of mid-season harvests.

At the individual scale, dickcissels engaged in despotic behaviors to defend territories, but dominant individuals appeared to be distributed equally across single harvest and multiple harvest plots, resulting in similar estimates of per capita productivity among harvest treatments, contrary to predictions based on ideal despotic distribution. Zimmerman (1982) suggested that dickcissel males breeding in preferred habitats experienced increased productivity due to higher orders of polygyny resulting from more females attracted to potential nest sites. Dickcissel populations may demonstrate an ideal despotic distribution as a consequence of increased female density (Zimmerman, 1982), but this effect may be restricted to the core of their breeding range where either quality breeding habitat can support additional females or the overall number of females may be greater, thereby allowing higher orders of polygyny. We only observed low orders of polygyny (≤3 females/territory) and no difference in the number of females per territory between single and multiple harvest treatments (T. Conkling, unpublished results), which may limit variation in per capita productivity between single and multiple harvest plots.

In addition to harvest frequency and year, factors such as individual quality can also increase territory productivity, thereby obscuring site-specific habitat effects of avian fitness (Germain and Arcese, 2014; Zabala and Zuberogoitia, 2014). For example, males establishing territories earlier in the breeding season may have greater productivity than later-arriving males (Lanyon and Thompson 1986; Grzybowski et al., 2005; Joos et al., 2014; Conkling 2016). In turn, arrival date may be influenced by site fidelity or familiarity, age, and conspecific cues, all of which may increase breeding success and seasonal productivity (Greenwood, 1980; Cody, 1985; Zimmerman and Finck, 1989; Switzer, 1993; Pärt, 2001). Accounting for individual metrics such as settlement patterns and site fidelity may help identify additional relationships between habitat covariates and individual productivity (Conkling, 2016).

5. Conclusions

Increasing our knowledge of factors important to nest success or productivity is necessary to understand the impacts that biofuel production in semi-natural grasslands may have on avian populations (Allen et al., 2011). We did not find a treatment effect on nest survival, similar to Conover et al. (2011). However, vegetation species composition and, to a lesser extent, harvest frequency can be important factors driving avian habitat choices and resulting productivity (Perlut et al., 2006; Murray and Best, 2014). Thus, promoting the use of second generation perennial biofuels such as switchgrass improves biodiversity and ecosystem function over monoculture annual plants such as corn, but the actual benefit to avian populations may be limited if monocultures function as poor breeding habitat for grassland birds, one of the most imperiled group of birds in North America (Peterjohn and Sauer, 1999; Askins et al., 2007). Incorporating a diverse forb mixture into biofuel planning or interspersing switchgrass and NWSG plots to maximize biodiversity while still allowing for biofuel production may provide adequate biomass and improved habitat for breeding grassland birds (Tilman et al., 2006). Additionally, altering timing of harvest to early fall or the following spring would have limited effects on nutritional value or combustibility of biomass while minimizing disturbances during the breeding season and potentially providing important migration and overwintering habitat (Adler et al., 2006; Robertson et al., 2011; Gamble et al., 2014; Conkling 2016). Our results also highlight the importance of estimating avian density and nest survival to improve habitat management. Density alone may not accurately reflect productivity or habitat quality of a given patch (Van Horne, 1983; Vickery et al., 1992; Berry et al., 1998; Hughes et al., 1999). By estimating nest density in conjunction with fitness metrics such as nest survival (Van Horne, 1983; Bock and Jones, 2004; Johnson, 2007), researchers can more effectively estimate effects of proposed biofuel vegetation treatments on avian populations of grassland birds. Biofuel production is likely to become a greater focus of land use in the near future. As such, this research provides guidance for management and conservation efforts aimed at balancing biofuel production, ecosystem functionality, and grassland bird conservation so that biofuels become an opportunity for wildlife conservation rather than a continued threat (Robertson et al., 2012).

reflect current FAA policy decisions regarding the control of wildlife on or near airports.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.01.028.

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