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Ecological Determinants of Avian Productivity and Aviation Risk in Semi-natural Grasslands

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Ecological determinants of avian productivity and aviation risk in semi-natural grasslands

By

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Ecological determinants of avian productivity and aviation risk in semi-natural grasslands

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Growing concerns about climate change, foreign oil dependency, and environmental quality have fostered interest in perennial native grasses (e.g. switchgrass [*Panicum virgatum*]) for bioenergy production while also maintaining biodiversity and ecosystem function. However, biofuel cultivation in marginal landscapes such as airport grasslands may have detrimental effects on aviation safety as well as demography and conservation efforts for grassland birds including Dickcissels (*Spiza americana*). In 2011–2013 I studied the response of avian populations to vegetation composition and harvest frequency of switchgrass monocultures and native warm-season grass (NWSG) mixtures at B. Bryan farms in Clay Co. MS, USA. Four treatments incorporating switchgrass and NWSG with single and multiple annual harvesting were established on 16 experimental plots. I examined the relative abundance, aviation risk, and conservation value of birds associated with these treatments, evaluated contributions of habitat attributes and individual male quality towards territory productivity and determined effects of harvest regimens on nest success, nest density, and productivity for Dickcissels.

Avian relative abundance was greater in switchgrass plots during winter months, whereas NWSG was favored by species during the breeding season. Conversely, treatment differences in aviation risk and conservation value were not biologically significant. Only 2.6% of observations included avian species of high risk to aircraft, suggesting that it may be feasible to use semi-natural grasslands at airports to provide grassland bird habitat while concurrently minimizing aviation risk. Regarding individual and habitat quality effects on nest survival and productivity, male song rate was not an effective surrogate for individual quality in demographic models. However, nest survival declined with increasing territory size and territories established earlier in the season had greater territory productivity relative to later arriving males, providing evidence that some metric of individual quality is important for grassland bird reproduction. Additionally, vegetation composition and harvest frequencies influenced nest density and productivity, but not nest survival. Native warm season grasses contained 54–64 times more nests relative to switchgrass treatments, and nest density was 10% greater in single harvest plots. My results suggest semi-natural grasslands can support grassland bird conservation while allowing for biofuel production and aviation risk management in airport landscapes.

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CHAPTER I

GENERAL INTRODUCTION

Recent focus on climate change and global energy production has increased interest in developing biofuels as a viable energy commodity (Devereux et al. 2006; Farrell et al. 2006; Campbell et al. 2008; Tilman et al. 2009; U.S. EPA 2011). Based on standards under the Renewable Fuel Standard program (U.S. EPA 2011), production and demand of biofuels is expected to increase in coming years. However, prevalent global biofuel crops including corn (*Zea mays*), sugar cane (*Saccharum officinarum*), and soybeans (*Glycine max*) often compete for land holdings currently in food production and have negative effects on biodiversity and ecosystem functions. (Landis et al. 2008; Searchinger et al. 2008; Tilman et al. 2009; Fargione 2010; Meehan et al. 2010; Clark et al. 2013). As a result, there is an increasing emphasis on using perennial native grasses (e.g. switchgrass [*Panicum virgatum*]) (Tilman et al. 2006; Robertson et al. 2011; Blank et al. 2014) to generate biomass while maintaining biodiversity and providing ecosystem services such as soil and water quality and carbon sequestration.

These semi-natural grasslands emulate natural habitat, but debate continues over the most appropriate vegetation species composition or harvest frequencies to balance biomass production with biodiversity maintenance (Fletcher Jr and Koford 2002; Allen et al. 2011; Griffith et al. 2011; Hartman et al. 2011; Werling et al. 2014). Switchgrass monocultures may generate more cellulosic ethanol than an equivalent high-diversity grassland (Adler et al. 2009), but mixed species plantings provide greater ecosystem function and biodiversity than their monoculture counterparts (Tilman et al. 2006; Adler et al. 2009; Meehan et al. 2010; Werling et al. 2014). Additionally, biofuel production using perennial grassland species requires multiple harvests (Vogel et al. 2002; Fike et al. 2006) which can have negative effects on wildlife using grasslands, along with reductions to the overall vegetation structure and diversity in subsequent years (Roth et al. 2005). There is limited research examining the effects of biofuel-focused grasslands on habitat selection and reproductive success of wildlife (Murray and Best 2003; Mitchell et al. 2012; Dunlap 2014).

To minimize competition of biofuel cultivation with existing croplands, there is also an increased focus on using marginal agricultural lands and other non-productive human-managed landscapes (Campbell et al. 2008; Gelfand et al. 2013). For example, many airports contain substantial parcels of grassland (average of 297ha per certificated airport) not currently used for crop production (Blackwell et al. 2009; DeVault et al. 2012; DeVault et al. 2013). However, altering land use practices near airports influences animal habitat use and behaviors, potentially increasing risk to aviation (Martin et al. 2013). As such, understanding how habitat structure and composition affect habitat use is important for limiting the potential risk of negative human-wildlife interactions by hazardous species (DeVault et al. 2011; Blackwell et al. 2013; Martin et al. 2013). Additionally, it allows for effective management and conservation of avian populations, including grassland birds, whose populations have declined in recent years due to habitat loss and degradation (Peterjohn and Sauer 1999; Askins et al. 2007).

Habitat manipulations within semi-natural grasslands provide opportunities to investigate ecological concepts including habitat selection and productivity within the context of management practices. Animals select breeding and wintering habitat to maximize individual fitness based on available resources, predation risk, and individual quality (Grinnell 1917; Hildén 1965; Fretwell and Lucas Jr. 1969; Fretwell 1972; Jones 2001; Fontaine and Martin 2006). As such, differences in habitat quality or individual quality can result in variation in individual fitness, especially when competition is present (Andrewartha and Birch 1954; Fretwell and Lucas Jr. 1969; Newton 1998; Sergio et al. 2009; Zabala and Zuberogoitia 2014).

Determining the effects of habitat characteristics and individual quality on avian habitat selection, nest success, and individual productivity is essential to develop effective conservation strategies for avian species within the context of land use and habitat management for aviation safety and bioenergy production. As such, my research objectives were to:

1. Investigate effects of vegetation composition and harvest frequency on seasonal species richness and habitat use of grassland birds.
2. Model relative abundance, aviation risk, and conservation value of birds associated with biofuel crops.
3. Model behavioral expression of individual male quality in grassland birds, using Dickcissels (*Spiza americana)* as a model species relative to temporal and habitat metrics.
4. Determine if Dickcissel nest success and territory productivity are influenced by habitat characteristics, temporal variables, and individual male quality.

5. Evaluate the potential effects of biofuel production on nest success, nest density, and productivity for Dickcissels.

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CHAPTER II

BALANCING AVIATION STRIKE RISK AND GRASSLAND BIRD CONSERVATION IN SEMI-NATURAL GRASSLANDS MANAGED FOR BIOFUELS

Introduction

Growing concerns about climate change, dependency on foreign oil, and overall environmental quality have fostered interest in bioenergy (Farrell et al. 2006; Sagar and Kartha 2007; U.S. EPA 2011). While Corn (*Zea mays*), Sugar Cane (*Saccharum officinarum*), and Wheat (*Triticum aestivum*) are the predominant global biofuel crops, there is an increased focus on using perennial native grasses (e.g., switchgrass [*Panicum virgatum*]) because they provide multiple ecosystem services including carbon sequestration, and wildlife habitat (Parrish and Fike 2005; Fargione et al. 2009; Knight et al. 2010; Hartman et al. 2011). However, bioenergy crop production has drawn concern as it might compete with food production (Campbell et al. 2008). Thus, marginal agricultural land or other non-productive human-managed sites could offer a solution to the land use dilemma. For example, areas such as airport grasslands typically do not produce crops but do provide a substantial land base (Blackwell et al. 2009; DeVault et al. 2012; DeVault et al. 2013a). However, changing land use near airports could affect animal use, subsequently affecting aviation strike risk (Martin et al. 2013).

Current grasslands at certificated airports (those approved for regularly scheduled passenger flights) occupy on average 297 ha per airport (DeVault et al. 2012) and are composed primarily of turfgrass maintained through frequent mowing at a short height (i.e., 15–25 cm) (Dolbeer et al. 2000). While the primary focus of managing wildlife on airport lands is to minimize avian-aircraft collisions (Sodhi 2002; Blackwell et al. 2009; DeVault et al. 2013b), airports converting land cover from turfgrass to native semi-natural grasslands(Allen et al. 2011) could continue to mitigate aviation risk associated with hazardous avian species while also reducing mowing costs, and generating income through biomass production (Fletcher Jr. et al. 2010; Robertson et al. 2012; DeVault et al. 2013a; Martin et al. 2013).

Birds attempt to maximize resource availability by selecting habitat based on vegetation structure or composition that best matches their foraging and flight behaviors or provides suitable breeding locations (Grinnell 1917; Hildén 1965; Fretwell and Lucas Jr. 1969; Fretwell 1972; Stephens and Krebs 1986; Whittingham et al. 2006). However, differences in vegetation structure may affect avian foraging strategies due to variation in real or perceived predation risk (predation risk hypothesis) (Lima and Dill 1990; Butler and Gillings 2004). Taller, dense vegetation can limit visibility of predators and hinder escape for larger-bodied birds and flocking species (Beck and Watts 1997; Whittingham and Devereux 2008; Blumstein 2010). Other avian species may prefer grasslands with variation in vegetation species composition and foliage structure (heterogeneous habitat hypothesis) (Simpson 1949; MacArthur and MacArthur 1961), especially during the breeding season due to greater availability of potential nest sites and arthropods as food for nestlings (McCoy et al. 2001; Hovick et al. 2014).

My objectives were to: (1) investigate the effects of vegetation composition and harvest frequency on species richness and habitat use of grassland birds relating to the predation risk and heterogeneous habitat hypotheses, and (2) relate this to aviation strike risk and conservation value of birds associated with biofuel crops. Avian use of a given habitat influenced by predation risk should vary by vegetation structure relative to species-specific anti-predator strategies. Species dependent on flocking behaviors or powerful escape flights should be more common in shorter vegetation, whereas species more prone to solitary behaviors that are weak fliers or rely on crypsis should select habitat with greater visual obstruction (Lima and Dill 1990; Butler et al. 2005a; Whittingham et al. 2006). Based on the heterogeneous habitat hypothesis, overall bird density and diversity should be greater in Native warm-season Grasslands (hereafter "NWSG") than in switchgrass monocultures, as bird habitat use is positively correlated with increased vegetation structural heterogeneity and habitat complexity present in mixed species plantings (Simpson 1949; MacArthur and MacArthur 1961; Wiens 1974; Robertson et al. 2011b), although this response can vary among species and seasons. I also expected aviation risk and conservation value to demonstrate similar seasonal patterns, with greater risk in more frequently harvested treatments with shorter vegetation favorable to hazardous flocking species (Lima 1993; DeVault et al. 2011). Additionally, I expected greater risk and conservation importance in NWSG during summer based on availability of potential nesting sites and arthropods for breeding birds, especially for species of higher conservation priorities (Panjabi et al. 2012).

Methods

Study Area

I conducted the study from January 2011–December 2013 on 16 adjacent plots (range 5.03–8.41) arranged in a randomized compete block design at B. Bryan Farm in Clay Co. Mississippi. B. Bryan Farm lies within the historical range of the Blackland Prairie (Barone 2005) and consists mostly of row crop agriculture, pastureland, and conservation easements. The region experiences mean daily temperatures from May–August of 25.3˚C and average monthly precipitation of 7.8 cm.

During the spring of 2010, eight plots were planted with a NWSG seed mixture (Table A.1) and eight plots were planted with switchgrass. Additional species prevalent in the existing seedbank included annual ragweed (*Ambrosia artemisiifolia*), broadleaf signalgrass (*Urochloa platyphylla*) and *Sesbania* spp. Treatment plots were harvested once or twice annually, resulting in 4 treatments: NWSG single annual harvest ("NWSG single"), NWSG multiple annual harvest ("NWSG multiple"), switchgrass single annual harvest ("switchgrass single"), and switchgrass multiple annual harvest ("switchgrass multiple"). No harvests occurred in 2011 to allow plots to continue establishing vegetation. Annual harvest occurred on all plots in late-April 2012, whereas excessive precipitation disallowed the winter harvest in 2013. The 8 multiple harvest plots were mowed to ~20cm and baled in mid-June 2012 and 2013.

I defined 5 sampling periods each year (Late Winter: 1 January–15 March, Spring: 16 March–31 May, Summer: 1 June–15 August, Fall: 16 August–31 October, Early Winter: 1 November–31 December) and conducted 3 surveys per period at 10–14 day intervals. Spring surveys were conducted in 2012 and 2013; all other survey periods were sampled for the duration of the study (January 2011–December 2013). I used a variety sampling methods to detect birds including flush transects, point counts, and line transects (Ralph et al. 1993; Butler et al. 2009). I conducted all surveys from sunrise until 3 hours after sunrise during favorable weather conditions (i.e., no precipitation and wind < 16km/h) and recorded percent cloud cover, temperature, average wind speed, and humidity with a Kestrel 3000 pocket weather meter (Nielsen-Kellerman, Boothwyn, PA).

Flush Transects

During Late Winter I used a geographic information system (ESRI 2011), to overlay a 50 x 50 m grid on each study plot and randomly selected 5 grid squares per plot for transect locations (Appendix A) after analyzing preliminary data to determine the necessary number of transects per plot. Each 50-m transect was centered on the grid square midpoint. I randomly assigned transect orientation and started all flush transects from the eastern-most endpoint to prevent observers from facing the sun during surveys. Two observers pulled a 25-m rope with noisemakers (1-liter bottles containing rocks attached to the rope every 6 m) across the vegetation, with a 3rd observer near the center of the rope serving as the data recorder; all observers identified flushed birds to species using visual, aural, and flight cues(Butler et al. 2009). When existing vegetation precluded efficient rope-dragging (vegetation > 1.5m in height), each edge observer walked approximately 12m from the center observer and made noise with hand-held noisemakers to flush any birds. If multiple birds flushed simultaneously, the observer recorded flock size according to Grzybowski (1983b). To avoid double-counting (Grzybowski 1983a, b) individuals, the total number of birds for each transect only included individuals or flocks initially located in the transect that completely left the area during the survey.

Point Counts

During Summer I conducted 5-minute single observer point-counts at the midpoint of 2 previously-defined flush transects in each plot (Buckland et al. 2001). I randomly selected the first flush transect and then chose the second survey location to maximize sampling distance between the two points. I recorded distance to all observed individuals within the plot, identified to species and sex (if possible) based on visual and aural cues. If multiple birds of the same species were detected in a flock (as defined above), I recorded flock size and distance to the center of the flock. I truncated 10% of observations to account for uncertainty of detecting individuals at large distances and to define a fixed survey radius of 100m for subsequent analyses (Buckland et al. 2001).

Line Transects

During Spring, Fall, and Early Winter, I conducted single observer line-transects at each plot to maximize detection of inconspicuous, migratory species as well as facilitate observations of birds in tall vegetation based on methods outlined in Buckland et al.(2001). Using preliminary survey data, I calculated transect length and established one transect for each plot in a zig-zag pattern to maximize transect length while minimizing the potential to double-count individuals, randomly selecting the start corner for each transect. Transect length varied from 650 to 850 m among plots. I walked the length of each transect at 1.6–3 km/h and visually estimated perpendicular distance from the survey line to all observed individuals or song locations within the plot and identified species and sex based on visual and aural cues. If flocks were observed, I recorded flock size and distance to the center of the flock. I also recorded behavior of individuals and flocks when detected and excluded any birds only observed as flyovers from subsequent analyses. I truncated 5% of observations based on recommendations from Buckland et al. (2001) by removing observations > 36m from the transect.

Vegetation Sampling

I collected vegetation data to determine structure and species composition among treatments. I sampled each transect in March 2011 and then monthly from June 2011–December 2013. I collected vegetation measurements using the point-intercept method (FIREMON 2007) to classify species composition at 5-m intervals along each transect (10 measurements/transect); transect locations corresponded to the existing flush transects. At each point I recorded litter depth and species identification and height (cm) for the 3 most common vegetation species. At 10-m intervals I quantified vegetation structure by recording maximum height of visual obstruction (VOR) from each of the 4 cardinal directions with a Robel pole (Robel et al. 1970). I collected VOR each month, but I excluded species and height data from November–February each year because I expected these measurements to be stable during winter dormancy. I used analysis of variance (ANOVA) and Tukey's test ($\alpha = 0.05$) to compare vegetation characteristics among treatments by year and survey period.

Statistical Analyses

Many analytical methods to estimate densities of animal populations incorporate detection probabilities (MacKenzie 2006; Royle and Dorazio 2008), but I was unable to fit these models because of insufficient detections for most species (Blank et al. 2014; Hovick et al. 2014). Furthermore, the species with the fewest detections were often those with the greatest risk to aviation, thus, removing those species in an effort to incorporate detection probabilities would have affected our inference. I assumed detection differences among treatments were minimal because all plots consisted of similar native grass species. Other factors that could possibly affect detection such as weather and observers were controlled through sampling design. I used unadjusted counts as an index of relative density for species with sufficient sample sizes (species detected at > 10% of sites each biological season).

Using R 3.1.0 (R Core Team 2015) I calculated relative density (birds detected per 10ha surveyed) by summing detections across all visits at the plot level divided by total area surveyed, which standardized survey efforts across years and species while accounting for differences in survey area. I was only able to compare density metrics within seasons, but not across survey periods (e.g. Late Winter versus Spring) due to differences in assumptions for each sampling method (Buckland et al. 2001). I determined mean values (± SE) for VOR, avian relative density, aviation risk, and conservation value for each plot by treatment and year. Aviation risk and conservation values for each plot were determined by summing species densities weighted with the relative hazard risk each species poses to aircraft (DeVault et al. 2011) or the relative conservation priority for a given species using Partners in Flight (PIF) regional or global assessment scores (Nuttle et al. 2003), respectively. For relative hazard risk, I categorized detected species not listed in DeVault et al. (2011) with a relative hazard score of 1 (lowest relative score possible). I also included individuals identified only to genus or family group (e.g. unknown sparrows) if there was a relative hazard score available for that group. For conservation values, PIF regional assessment scores for the Southeastern Coastal Plain Bird Conservation Region (BCR) (Beissinger et al. 2000; Panjabi et al. 2012) following Nuttle et al. (2003). PIF calculates scores based on relative extinction risk by region and the resulting rank prioritizes conservation efforts for species in North America—a higher rank indicates species with greater conservation priority. For species not included in the Southeastern Coastal Plain BCR, I calculated conservation values based on PIF global assessment scores. I did not include unidentified birds (e.g. unknown warblers, unknown sparrows) in models to estimate conservation value, as PIF scores were species specific.

I examined bird species composition across treatment types and years with non-metric multidimensional scaling (NMDS) (Faith et al. 1987; Minchin 1987) using relative density of all identified species with sufficient detections using the package *vegan* (Oksanen et al. 2013) in R to create a summary of avian community habitat use. NMDS calculates a distance matrix based on the rank-order correlation in Euclidian distance, allowing for 2-dimensional matrix visualization. I used Bray-Curtis distance metric for dissimilarity and Shepard diagrams and STRESS values to examine goodness of fit and determine the appropriate number of dimensions. I overlaid treatment type on the NMDS plots based on dispersion ellipses with 95% confidence intervals and plotted mean VOR as contour lines to examine species distributions among treatments and vegetation structure. Species in closer proximity to each other in the resulting plots are more similar in distribution than species spaced further apart. I also tested whether species ordination was correlated with treatment type or vegetation structure using the function *envfit*, based on 10,000 permutations for all survey seasons and years.

I modeled relative density, aviation risk, and conservation value using generalized linear mixed models (GLMM) with R package *lme4* (Bates et al. 2015) and linear and mixed models with R package *nlme* (Pinheiro et al. 2013) following model construction and selection procedures outlined in Zuur et al. (2009). I first constructed the most complex model, incorporating fixed effects of treatment, year, and a treatment-year interaction (treatment × year). For density models, I then used likelihood ratio tests to determine the appropriate model distribution (e.g. Poisson, negative binomial). If data were overdispersed, I examined data to determine if a negative binomial model better fit the data, then continued the model selection procedure. Next, I used likelihood ratio tests to determine support for the random effects (block and year), and then fit sequentially more parsimonious models to determine best model fit. When applicable, I examined the proportion of variance explained by the fixed effects in the best-fit models with pseudo R^2 (Nakagawa et al. 2013) for GLMM and McFadden's pseudo R^2 (McFadden 1973) for linear models fitted using generalized least squares. I modeled relative density (number of individuals per 10 ha) of avian species by survey visit with total birds as my response variable, treatment as a fixed effect, year as a repeated measure, total area (ha) surveyed as an offset. I included unidentified species groups (e.g. unknown warblers, unknown sparrows) within the total relative density estimates for each plot if there were sufficient detections (observed at > 10% of survey locations). I modeled overall estimated aviation risk and conservation value using the same model selection procedure while allowing for alternative variance structures for linear models as outlined above.

Results

I recorded 7738 individuals of 57 species across all survey periods and years (Table A.2), including 17 species in Late Winter, 14 in Spring, 26 during Summer, 24 in Fall, and 18 in Early Winter. Forty-four of the 57 species did not have sufficient detections (observed at ≤10% of survey locations across years) and were eliminated from subsequent analyses; I used the remaining data on 2 unknown categories (Unknown sparrows & Unknown warblers) and 13 overall species including 5 species in Late Winter, 6 in Spring, 5 in Summer, 11 in Fall, and 8 in Winter2 for NMDS, aviation risk, and conservation value modelling. For vegetation measurements, VOR differed among treatments and years, with switchgrass plots having greater VOR, especially in 2012 and 2013 (Fig. 2.1). Additionally, VOR in single-harvested treatments was greater than multiple-harvested treatments, although this difference was more pronounced in switchgrass than NWSG, suggesting that the resulting avian community differences should also be more pronounced between switchgrass harvest treatments when compared to NWSG single and NWSG multiple plots.

Avian Community

A greater number of species was observed in NWSG, but more individuals were observed in switchgrass plots, especially multiple-harvest treatments (Table A.2). Savannah Sparrows (*Passerculus sandwichensis*), accounted for 46.8% (*n* = 7738) of all observations, including most observations in multiple-harvest plots. More species were detected during Summer and Fall migration than during Spring or winter seasons, and the number of species declined annually across all treatments as plots reached maturity (Keyser et al. 2012) (Table A.2, Fig. 2.2). Treatment and VOR were correlated with avian species NMDS scores during Late Winter and Spring as plots reached maturity in 2012 and 2013, but not during Fall and Early Winter, except for treatment in 2011 (Table 2.1), providing support that individual species were selecting habitat in winter months based on vegetation structure. For example, Savannah Sparrows and other generalist flock-prone species (including Eastern Meadowlarks (*Sturnella magna*)) (Wheelwright and Rising 2008; Jaster et al. 2012) preferred shorter vegetation of either species composition (Fig. 2.2), whereas Le Conte's Sparrow (*Ammodramus leconteii*), known for solitary behaviors and weak escape flights (Lowther 2005) were associated with greater VOR (Fig. 2.2). Other species during the winter including Song (*Melospiza melodia*) and Swamp (*Melospiza georgiana*) sparrows were primarily found in greater VOR and NWSG plots (Fig. 2.2); these solitary-foraging species are typically associated with woody vegetation and oldfields (Mowbray 1997; Arcese et al. 2002).

There was considerable overlap in treatment dispersion ellipses for all seasons and years, except for Spring 2012. This overlap increased annually as the plots matured, indicating that the overall avian community was similar among treatments, although the number of individuals present varied. During Spring migration, both treatment and VOR influenced habitat use of the avian community, whereas neither factor was important during Fall (Table 2.1, Fig. 2.2). Ellipse spread was reduced in switchgrass treatments relative to NWSG for most years and seasons and during migration (Fig. 2.2), indicating species plotted within the smaller switchgrass ellipses selected that habitat more frequently than NWSG. I lacked sufficient detections in switchgrass treatments during Summer to generate NMDS scores, but 78.0% (n = 832) of all individuals detected and

86.3% (*n* = 682) of observations for species occurring at ≥10% of survey locations during Summer were in NWSG plots, in congruence with the heterogeneous habitat hypothesis.

Relative Density

All GLMM models for relative density incorporated a negative binomial distribution to account for overdispersion and block as random effect, while Summer included a block × year crossed random effect ($L = 15.56$, $df = 5$, $P = 0.008$) (Table 2.2). Overall, relative density declined annually as plots matured across all survey periods (except for Summer) (Tables 2.2 & 2.3, Fig. 2.3). Additionally, by the 3rd year, densities were greater in multiple-harvest plots than single-harvest plots of the same vegetation type, aligning with predictions under the predation risk hypothesis; these density estimates were driven largely by flock-prone species such as Savannah Sparrows (Table A.2). Both Early and Late Winter also included a treatment × year interaction, with more birds detected in switchgrass than NWSG across all years, except for NWSG multiple (2013 only) (Tables 2.2 & 2.3, Fig. 2.3). For Summer, the best-fit density model contained treatment and provided support for the heterogeneous habitat hypothesis, with significantly greater avian relative density in NWSG treatments than either single-harvest switchgrass ($\beta = -1.36$, 95% CI: -1.89, -0.83) and multiple-harvest switchgrass plots ($\beta = -1.58$, 95% CI: -2.14, -1.02) plots (Tables 2.2 & 2.3, Fig. 2.3).

Aviation Risk

Overall, 99.7% (*n* = 7738) of observations included species with a relative hazard score ≤ 10 (maximum hazard score = 100) based on DeVault et al. (2011) classifications. Most birds observed (92.4%) (e.g. sparrows) were considered a "very low" aviation safety hazard, based primarily on small body size or solitary flight behaviors (Dolbeer 2000). All aviation risk models included year (Tables 2.2 & 2.4), with aviation risk declining annually across all survey periods as plots matured and increasing VOR limited predator visibility, thereby restricting the effectiveness of flocking behaviors as an escape strategy. For Spring, the best-supported model only included year effects, with lower aviation risk in 2013 (β = -15.90, 95% CI: -18.66, -13.14). The best-fit models for the other survey periods also included treatment as an additive (Late Winter, Summer, Fall) or interactive effect (Early Winter), respectively (Tables 2.2 & 2.4); however, the treatment type with greater aviation risk varied by survey period. Switchgrass treatments had greater risk during both Late Winter (switchgrass multiple: β = 729.73, 95% CI: 305.62, 1153.81; switchgrass single: β = 528.02, 95% CI: 103.93, 952.12) and Fall (switchgrass single only: β = 29.36, 95% CI: 3.58, 55.15). During Early Winter, switchgrass had a significantly greater aviation hazard score than NWSG plots in 2011 and 2012, but by 2013 the hazard scores were similar across all treatment types (Fig. 2.4). Switchgrass plots had lower hazard scores than both NWSG treatments during Summer (switchgrass multiple: β = -22.65, 95% CI: -40.00, -5.31; switchgrass single: β = -23.54, 95% CI: -40.89, -6.19) (Table 2.4, Fig. 2.4), as most birds favored the heterogeneous NWSG plots during breeding.

Conservation Value

Conservation value was best explained during both Winter survey periods by a treatment × year interaction, while the best-fit model for Summer included additive effects of treatment and year (Table 2.2). During migration periods, the best-fit model for conservation value included year only (Fall) or the null model (Spring). Conservation value declined annually in all models that included year. Additionally, conservation value differed among treatments (Table 2.5, Fig. 2.4), although this treatment effect differed between Summer, and both Winter periods. Switchgrass plots had lower conservation value than NWSG treatments (Table 2.5, Fig. 2.4) during Summer, while there was greater conservation value for switchgrass plots in Late Winter and Early Winter, respectively relative to NWSG (Table 2.5). In 2013, conservation value was greater for multiple-harvested plots during Late Winter (both switchgrass and NWSG) and Early Winter (NWSG only); however 95% CI for estimated Early Winter NWSG treatment means overlapped (Fig. 2.4). Only 5% (*n* = 57) of all species detected (Le Conte's Sparrow, Northern Harrier, Eastern Meadowlark) were considered species of PIF conservation priority based on rank values (Table A.2). Two of these species, Le Conte's Sparrow and Eastern Meadowlark, were detected on 11.8% and 18.2% of all survey visits (*n* = 1215), accounting for 6.9% and 3.7% respectively of total observations (*n* = 7738) whereas Northern Harriers comprised only 0.9% of observations on < 5% (*n* = 59) of survey visits. Of the 3 species, Eastern Meadowlarks were detected across all survey periods, while Le Conte's Sparrows and Northern Harriers were not present during Summer.

Discussion

During Late Winter and Spring, avian species appeared to minimize their perceived predation risk by selecting habitat with vegetation structure in accordance with their species-specific escape behaviors, flight patterns and flocking strategies (Lima and Dill 1990; Lima 1993). Savannah Sparrows and Eastern Meadowlarks, two commonly-detected habitat generalists that forage in loose flocks during the winter (Grzybowski

1983a; Jaster et al. 2012), routinely selected habitats with lower VOR (Fig. 2.2). Not surprisingly, relative densities for these species declined annually as VOR increased with plot maturity (Keyser et al. 2012) (Fig. 2.1), limiting both flocking ability and visibility of predators (Beck and Watts 1997; Whittingham and Devereux 2008; Blumstein 2010). This annual decline also decreased overall aviation hazard scores and conservation value, as Savannah Sparrows alone accounted for 46.8% (*n* = 7738) of all observations.

Alternatively, Le Conte's Sparrow, a PIF species of conservation concern known for solitary behaviors and relying on crypsis rather than flocking or strong escape flights (Lowther 2005), demonstrated a strong preference for greater VOR. These responses to vegetation structure have been noted in other studies on wintering bird use of altered grassland habitats (Beck and Watts 1997; Hovick et al. 2014; Monroe and O'Connell 2014) due to the importance of vegetation for food availability, minimizing predation risk, and providing thermoregulatory cover for energy conservation (Houston et al. 1993; Beck and Watts 1997; Ginter and Desmond 2005; Tsurim et al. 2009). I did not capture birds to measure fat reserves or quantify winter seed availability in the study plots, so it is unclear to what extent food resources and adaptive energy management (Lima 1986; Tsurim et al. 2009) may influence habitat selection choices in addition to predation risk.

Contrary to non-breeding periods when vegetation structure, rather than composition, appeared to be the driving factor towards habitat selection, habitat heterogeneity was more important to grassland birds during Summer. In addition to greater avian densities on NWSG relative to switchgrass plots (Table 2.3, Fig. 2.3), greater than 93% (*n* = 422) of nests found on treatment plots during a concurrent study occurred in NWSG (T. Conkling, unpublished data), suggesting that breeding birds responded positively to the vegetation structural heterogeneity in mixed species plantings. Of the 3 most commonly-observed breeding bird species, Dickcissels (*Spiza* a*mericana*), often associated with habitat containing a high proportion of forbs (Temple 2002), and Red-Winged Blackbirds (*Agelaius phoeniceus*), a marsh and prairie-breeding species (Yasukawa and Searcy 1995), primarily used NWSG plots, whereas Eastern Meadowlarks were observed in all treatment types, though they nested primarily in immature switchgrass plots (T. Conkling, unpublished data) (Keyser et al. 2012). Forb-dominated structurally-complex landscapes (especially NWSG) provide more potential nest sites and abundant food resources, especially during the breeding season, when arthropods (e.g., Orthoptera) are important for breeding birds and nestling nutrition (Patterson and Best 1996; Winter et al. 2005; Mitchell et al. 2012).

Limited research exists on species habitat selection during migration due to difficulties in sampling migrating species (Robertson et al. 2011a; Robertson et al. 2013). Species identification was lower during migration when many species are non-vocal or have cryptic non-breeding plumages; nearly 15% (*n* = 1464) of observations during migration periods included unknown individuals (e.g. unknown sparrows). Additionally, with only 3 surveys over a 20–30 day period during Spring and Fall, I may have inadequately detected some migrating species. As such, these counts may be conservative regarding the total number of individuals and species using the plots during migration. Increasing identification efforts survey frequency to adequately detect all migrating birds based on species-specific migration timings would help mitigate existing data gaps on avian habitat use during migrations.

Many breeding grassland bird species benefit from diverse native-warm season grasslands as opposed to large patches of switchgrass, while the reverse may be true for migrating and wintering birds that select habitat based more on structure than species composition (Fletcher Jr. and Koford 2002; Fletcher Jr. et al. 2010; Blank et al. 2014); this distinction is important to consider for biofuel cultivation. Switchgrass produces more potential ethanol than NWSG (McLaughlin and Kszos 2005), but there is mixed support regarding the benefits of monoculture grass cultivation versus NWSG on avian diversity and conservation (Meehan et al. 2010; Blank et al. 2014; Uden et al. 2014). Growing switchgrass concurrently with NWSG plots instead of as a monoculture allows for biofuel production while still providing multiple cover and habitat options for grassland birds. Additionally, because switchgrass was rarely used as breeding habitat, mid-season harvest of switchgrass plots to optimize biofuel production may have a limited effect on breeding grassland birds.

Conversion of existing airport grasslands to native grasses for both bird habitat and biofuel production does not appear to pose risk to aircraft (Blackwell et al. 2009; DeVault et al. 2013a; DeVault et al. 2013b; Schmidt et al. 2013), supporting the concept of native grasslands as a viable landcover at airports. Most birds (e.g. sparrows) detected (92.4%) pose a "very low" hazard to aircraft based on flight behaviors or body size (Dolbeer et al. 2000; Dolbeer and Wright 2009), and species posing a moderate to extremely high risk to aircraft accounted for < 1% of all observations. Only 2.6% (*n* = 1215) of all surveys yielded observations of high-risk (e.g. classified as "moderate" or greater risk) species. While I did not directly compare aviation risk for turfgrass relative to NWSG or switchgrass, a concurrent study on Bermuda grass (*Cynodon* *dactylon*) fields near the study area in 2012 observed high-risk species on 3.5% (*n* = 57) of all surveys, with these species of moderate or greater risk comprising 8.6% (*n* = 58) of all avian detections (T. Conkling, unpublished data). These values are similar to Schmidt et al. (2013), who documented no elevated aviation risk from avian species for prairie habitat relative to airfield turf on NWSG and airfield grasslands in Ohio.

Model results indicated both aviation hazard and conservation value differed between grassland treatments and years (Fig. 2.4), but these differences are likely not biologically relevant. Treatment was a significant factor in aviation hazard models for every sampling period except Spring, but this was primarily from the large number of sparrows that collectively posed a "very low" aviation risk (DeVault et al. 2011). As such, use of either NWSG or switchgrass plantings do not appear to be detrimental to aviation safety. Aviation hazard scores were greater in NWSG than switchgrass plots during Summer, but maximum relative density for NWSG was < 25 birds/10ha surveyed across all 3 survey visits and all species detected during Summer (Table A.2) posed minimal threats to aircraft. Hazard scores also declined annually across all treatments as the vegetation reached maturity by the third year (Keyser et al. 2012), with the increased vegetation structure limiting numbers of flock-prone species (e.g. Savannah Sparrows). Similar to models for density, conservation value was largely influenced by the number of flocking species using the plots, with conservation value declining as plots matured. Conservation value may be a reliable metric for comparing conservation importance between distinct habitat classes such as pine forest and switchgrass (Loman et al. 2014), but these scores were not useful for comparing similar grassland treatments. Partners in Flight conservation priority species accounted for only 3 of the 57 species detected on surveys (Le Conte's Sparrow, Northern Harrier, Eastern Meadowlark). However, the presence of all 3 species had minimum effect on the weighted conservation value scores that were heavily influenced by densities of low-priority species such as Savannah Sparrows.

Although wildlife management strategies at airports focus on maintaining human safety, my results demonstrate that it may be feasible to use mature native-grass plantings to concurrently minimize aviation risk and provide habitat for grassland birds. Both NWSG and switchgrass provided sufficient vegetative structure to minimize the presence of high-risk, flocking avian species while also providing quality overwintering and breeding habitat for grassland birds. It is also important to consider additional factors that may influence avian habitat use. Although I did not quantify available food (e.g. seed and invertebrate biomass), reductions in habitat structure can improve prey detectability and accessibility, causing birds to modify foraging behaviors and habitat use accordingly to balance predation risk and energy acquisition (Getty and Pulliam 1993; Atkinson et al. 2004; Butler et al. 2005b; Devereux et al. 2006; Whittingham et al. 2006). As such, these behavior modifications may enhance aviation risk if food availability increases avian densities or reduces forager vigilance, thereby slowing response times required to successfully escape approaching aircraft (Blackwell et al. 2013).

Overall, by addressing avian responses specifically within a managed system, this study provides airport professionals with evidence to help make informed decisions regarding the risk produced by native grasses versus traditional landcover strategies at airports. As technological advancements further increase interest in cellulosic biofuels, the benefits from both a risk and cost management perspective are promising for enhancing grassland bird conservation and biofuel production in airport landscapes.

Table 2.1 Correlation (r^2) of treatment and vegetation visual obstruction (VOR)with avian ordination axes from nonmetric multi-dimensional scaling (NMDS)

Parameter	Year	NMDS1	NMDS2	r^2	*P*-value
Late Winter					
Treatment	2011	-0.63	0.78	0.23	0.25
VOR	2011	-0.86	-0.51	0.05	0.75
Treatment	2012	-0.98	-0.18	0.22	0.25
VOR	2012	-0.95	-0.31	0.51	0.02
Treatment	2013	-0.66	0.75	0.59	0.01
VOR	2013	-0.45	0.89	0.49	0.03
Spring Migration					
Treatment	2012	0.10	-1.00	0.81	0.00
VOR	2012	0.55	-0.84	0.46	0.04
Treatment	2013	-0.93	-0.38	0.49	0.02
VOR	2013	-1.00	-0.08	0.47	0.04
Fall Migration					
Treatment	2011	-0.66	0.75	0.43	0.05
VOR	2011	-1.00	0.03	0.24	0.23
Treatment	2012	0.28	0.96	0.11	0.56
VOR	2012	0.25	0.97	0.10	0.58
Treatment	2013	-0.11	0.99	0.32	0.12
VOR	2013	-0.07	1.00	0.22	0.25
Early Winter					
Treatment	2011	-1.00	0.10	0.39	0.07
VOR	2011	-0.88	0.48	0.12	0.51
Treatment	2012	-0.82	0.58	0.21	0.28
VOR	2012	-0.91	0.41	0.14	0.43
Treatment	2013	0.25	0.97	0.12	0.50
VOR	2013	0.26	0.97	0.23	0.24

Table 2.2 Model parameters, random effects, variance structures, and results from Likelihood Ratio (LR) tests and Pseudo R2 values to identify best-fit models for avian relative density, aviation risk, and conservation value by survey period in Clay Co., Mississippi, 2011–2013.

				Lower Model				Upper Model				Pseudo R^2		
Survey Period	Parameters	Random Effects	Variance Structure	Competing Model	df	LR	*P*-value	Competing Model	df	LR	p-value	Marginal	Conditional	McFadden's
Relative Density														
Late Winter	Treatment × Year	Block	-	Treatment + Year	6	19.32	0.004	-	-	-	-	0.94	0.95	-
Spring	Year	Block	-	Null	1	6.72	0.010	Treatment + Year	3	0.04	1.00	0.31	0.75	-
Summer	Treatment	Block × Year	-	Null	3	50.98	< 0.001	Treatment × Year	6	6.76	0.34	-	-	-
Fall	Year	Block	-	Year	2	24.14	< 0.001	Treatment + Year	3	4.36	0.23	0.78	0.81	-
Early Winter	Treatment × year	Block	-	Treatment + Year	6	17.22	0.009	-	-	-	-	0.91	0.93	-
Aviation Risk														
Late Winter	Treatment + Year	-	Year	Treatment	3	26.19	< 0.001	Treatment × Year	6	6.60	0.36	-	-	0.16
Spring	Year	Block	Treatment	Null	1	16.83	< 0.001	Treatment + Year	3	0.64	0.89	0.01	0.66	
Summer	Treatment + Year	Block	-	Treatment	3	14.61	0.002	Treatment × Year	6	4.93	0.55	0.36	0.64	
Fall	Treatment + Year	-	-	Treatment	3	8.30	0.040	Treatment × Year	6	11.63	0.07	-	-	0.17
Early Winter	Treatment × Year	-	-	Treatment + Year	2	46.96	< 0.001	-	-	-	-	-	-	0.34
Conservation Value														
Late Winter	Treatment × Year	-	Treatment × Year	Treatment + Year	6	22.90	0.001	Treatment × Year	6	4.34	0.63	-	-	0.30
Spring	Null	-	Treatment × Year	-	-	-	-	Year	1	1.69	0.19	-	-	0.00
Summer	Treatment + Year	Block	-	Year	2	21.94	< 0.001	-	-	-	-	0.47	0.73-	
Fall	Year	Block	-	Null	2	19.96	< 0.001	Treatment × Year	3	1.05	0.79	0.35	0.51	
Early Winter	Treatment × Year	-	-	Treatment + Year	6	24.69	< 0.001	-	--	-	-	-	-	0.33

Table 2.3 Model coefficients (± SE) and 95% confidence limits for parameters in the best-fit models for avian relative density by survey period in Clay Co., Mississippi, 2011–2013.

			95% Confidence Limits	
Parameter	Estimate	SE	Lower	Upper
Late Winter				
(Intercept)	4.43	0.25	3.94	4.92
NWSG (single harvest)	1.33	0.34	0.66	2.00
Switchgrass (multiple harvest)	1.11	0.36	0.40	1.81
Switchgrass (single harvest)	1.86	0.36	1.16	2.55
2012[b]	1.49	0.33	0.84	2.14
2013[b]	0.52	0.34	-0.15	1.19
NWSG (single harvest) × 2012 [b]	-1.67	0.46	-2.58	-0.76
Switchgrass (multiple harvest)×2012 [b]	-0.86	0.49	-1.83	0.11
Switchgrass (single harvest)×2012 [b]	-1.66	0.49	-2.62	-0.71
NWSG (single harvest)×2013 [b]	-1.87	0.48	-2.81	-0.92
Switchgrass (multiple harvest)×2013 [b]	-0.46	0.50	-1.45	0.53
Switchgrass (single harvest)×2013 [b]	-1.48	0.50	-2.46	-0.50
Spring Migration				
(Intercept)	3.09	0.17	2.75	3.43
2013[c]	-0.45	0.16	-0.75	-0.14
Summer				
(Intercept)	2.84	0.28	2.28	3.40
NWSG (single harvest)	0.09	0.22	-0.34	0.52
Switchgrass (multiple harvest)	-1.58	0.29	-2.14	-1.02
Switchgrass (single harvest)	-1.36	0.27	-1.89	-0.83
Fall Migration				
(Intercept)	3.01	0.12	2.77	3.24
2012 [b]	-0.97	0.19	-1.34	-0.61
2013 [b]	-0.79	0.18	-1.15	-0.43
Early Winter				
(Intercept)	2.73	0.12	2.51	2.96
NWSG (single harvest)	0.09	0.15	-0.21	0.39
Switchgrass (multiple harvest)	0.36	0.16	0.03	0.68
Switchgrass (single harvest)	0.53	0.16	0.20	0.85
2012[b]	-0.87	0.17	-1.21	-0.54
2013[b]	-0.53	0.16	-0.85	-0.22
NWSG (single harvest) × 2012[b]	-0.14	0.24	-0.61	0.34
Switchgrass (multiple harvest) × 2012[b]	0.19	0.25	-0.30	0.68
Switchgrass (single harvest) × 2012[b]	0.17	0.25	-0.32	0.66
NWSG (single harvest) × 2013[b]	-0.70	0.24	-1.17	-0.23
Switchgrass (multiple harvest) × 2013[b]	-0.57	0.25	-1.06	-0.07
Switchgrass (single harvest) × 2013[b]	-0.91	0.26	-1.42	-0.40

[a] Native warm-season grassland-multiple harvest (NWSG-M) is the reference condition. Coefficient refers to change in relative density for given treatment relative to NWSG-M

[b] 2011 is the reference year. Coefficient refers to change in relative density for given year relative to 2011

[c] 2012 in the reference year. Coefficient refers to change in relative density for given year relative to 2012 (no Spring Migration surveys in 2011)

Table 2.4 Model coefficients (± SE) and 95% confidence limits for parameters in the best-fit model for avian aviation hazard score by survey period in Clay Co., Mississippi, 2011–2013.

			95% Confidence Limits	
Parameter	Estimate	SE	Lower	Upper
Late Winter				
(Intercept)	1851.46	539.29	794.46	2908.46
2012[b]	674.67	554.49	-412.10	1761.44
2013[b]	-876.95	532.659	-1920.95	167.04
NWSG (single harvest)	-451.42	200.33	-844.06	-58.79
Switchgrass (multiple harvest)	729.73	216.38	305.62	1153.81
Switchgrass (single harvest)	528.02	216.38	103.93	952.12
Spring Migration				
(Intercept)	137.99	41.60	51.94	224.04
2013[c]	-15.90	1.33	-18.66	-13.14
Summer				
(Intercept)	58.51	7.26	44.28	72.74
2012[b]	-21.55	7.59	-36.40	-6.67
2013[b]	-27.15	7.59	-42.00	-12.27
NWSG (single harvest)	-5.64	8.19	-21.69	10.42
Switchgrass (multiple harvest)	-22.65	8.85	-40.00	-5.31
Switchgrass (single harvest)	-23.54	8.85	-40.89	-6.19
Fall Migration				
(Intercept)	103.774	10.80	82.61	124.94
2012[b]	-82.51	11.28	-104.61	-60.41
2013[b]	-60.80	11.28	-82.90	-38.69
NWSG (single harvest)	-5.42	12.18	-29.29	18.45
Switchgrass (multiple harvest)	9.58	13.16	-16.21	35.36
Switchgrass (single harvest)	29.36	13.16	3.58	55.15
Early Winter				
(Intercept)	318.01	30.78	257.68	378.34
2012[b]	-184.26	43.53	-269.58	-98.94
2013[b]	-130.46	43.53	-215.78	-45.15
NWSG (single harvest)	22.27	43.53	-63.05	107.59
Switchgrass (single harvest)	193.04	47.02	100.89	285.19
Switchgrass (multiple harvest)	125.49	47.02	33.34	217.64
NWSG (single harvest) × 2012[b]	-31.69	61.56	-152.35	88.97
Switchgrass (multiple harvest) × 2012[b]	-33.10	66.49	-163.43	97.22
Switchgrass (single harvest) × 2012[b]	-77.76	66.49	-208.09	52.56
NWSG (single harvest) × 2013[b]	-110.49	61.56	-231.15	10.16
Switchgrass (multiple harvest) × 2013[b]	-165.95	66.49	-296.28	-35.63
Switchgrass (single harvest) × 2013[b]	-259.02	66.49	-389.34	-128.70

[a] Native warm-season grassland-multiple harvest (NWSG-M) is the reference condition. Coefficient refers to change in relative density for given treatment relative to NWSG-M.

[b] 2011 is the reference year. Coefficient refers to change in relative density for given year relative to 2011.

[c] 2012 in the reference year. Coefficient refers to change in relative density for given year relative to 2012 (no Spring Migration surveys in 2011)

Table 2.5 Model coefficients (± SE) and 95% confidence limits for parameters in the best-fit model for avian conservation value in Clay Co., Mississippi, 2011–2013.

			95% Confidence Limits	
Parameter	Estimate	SE	Lower	Upper
Late Winter				
(Intercept)	16.25	5.82	4.36	28.14
2012[b]	69.75	13.71	41.74	97.76
2013[b]	38.00	14.95	7.46	68.54
NWSG (single harvest)	54.25	44.89	-37.43	145.93
Switchgrass (multiple harvest)	32.08	13.45	4.61	59.56
Switchgrass (single harvest)	85.42	16.93	50.83	120.00
NWSG (single harvest) × 2012[b]	-89.75	48.57	-188.94	9.44
Switchgrass (multiple harvest) × 2012[b]	15.58	24.25	-33.94	65.11
Switchgrass (single harvest) × 2012[b]	-37.75	29.23	-97.45	21.95
NWSG (single harvest) × 2013[b]	-85.50	47.21	-181.92	10.92
Switchgrass (multiple harvest) × 2013[b]	-23.33	20.12	-64.43	17.77
Switchgrass (single harvest) × 2013[b]	-99.33	27.01	-154.49	-44.18
Spring Migration				
(Intercept)	22.01	2.23	17.569	24.671
Summer				
(Intercept)	33.34	4.38	24.42	42.26
2012[b]	-10.91	2.73	-16.46	-5.36
2013[b]	-12.84	2.73	-18.38	-7.29
NWSG (single harvest)	-1.03	2.95	-7.02	4.97
Switchgrass (multiple harvest)	-15.42	3.25	-22.03	-8.80
Switchgrass (single harvest)	-16.23	3.25	-22.84	-9.61
Fall Migration				
(Intercept)	17.39	2.05	13.23	21.56
2012[b]	-9.92	2.00	-13.98	-5.86
2013[b]	-8.83	2.00	-12.88	-4.77
Winter2				
(Intercept)	60.35	6.28	47.53	73.17
2012[b]	-40.85	8.88	-58.98	-22.72
2013[b]	-32.57	8.88	-50.70	-14.44
NWSG (single harvest)	-10.45	8.88	-28.58	7.69
Switchgrass (multiple harvest)	25.37	9.59	5.78	44.95
Switchgrass (single harvest)	43.57	9.59	23.99	63.16
NWSG (single harvest) × 2012[b]	9.15	12.56	-16.50	34.79
Switchgrass (multiple harvest) × 2012[b]	-3.45	13.56	-31.15	24.25
Switchgrass (single harvest) × 2012[b]	-31.31	13.56	-59.01	-3.61
NWSG (single harvest) × 2013[b]	-2.13	12.56	-27.77	23.52
Switchgrass (multiple harvest) × 2013[b]	-32.48	13.56	-60.18	-4.78
Switchgrass (single harvest) × 2013[b]	-53.42	13.56	-81.12	-25.72

[a] Native warm-season grassland-multiple harvest (NWSG-M) is the reference condition. Coefficient refers to change in relative density for given treatment relative to NWSG-M

[b] 2011 is the reference year. Coefficient refers to change in relative density for given year relative to 2011

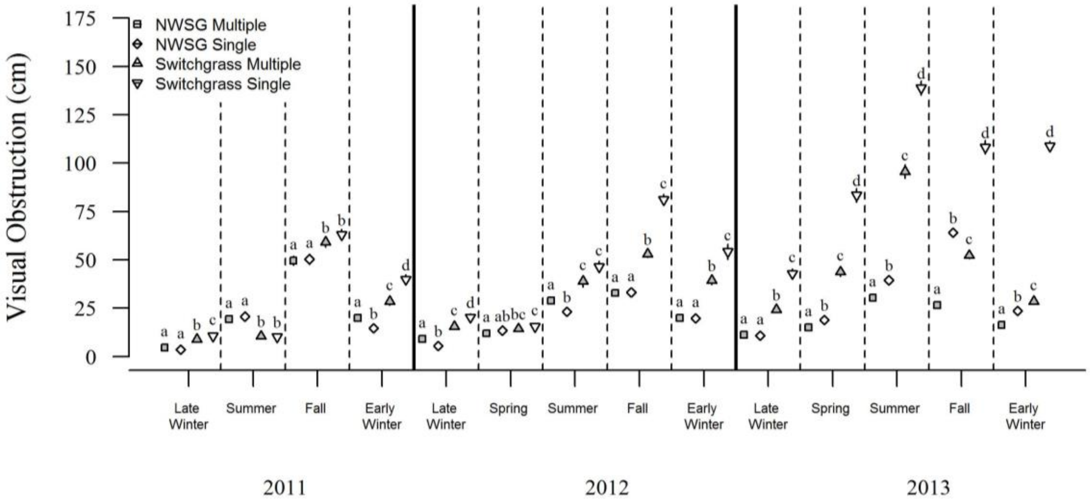

Figure 2.1 Mean and 95% CI visual obstruction by survey period native warm-season grass (NWSG) multiple harvest (□), NWSG single harvest (◇), switchgrass multiple harvest (△), and switchgrass single harvest (▽) treatment types in Clay Co., Mississippi, 2011–2013.

Treatments within a season sharing the same letter (e.g. “a”) were not significantly different (Tukey’s HSD: p-value ≤ 0.05).

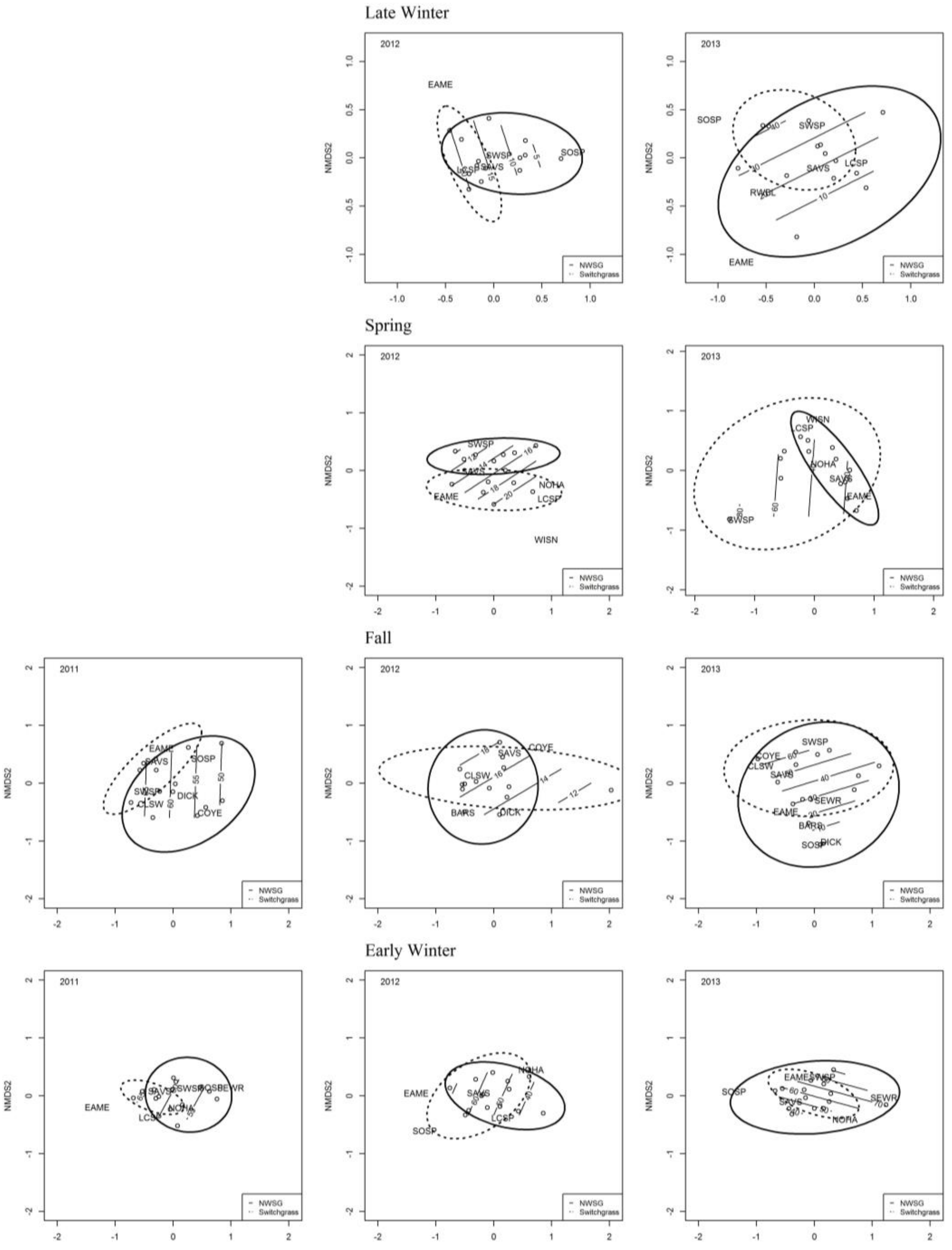

Figure 2.2 Ordination plot from non-metric multidimensional scaling (NMDS) of avian species and dispersion ellipses by native warm-season grass (NWSG) and switchgrass treatments (95% CI) and contour lines for vegetation visual obstruction (cm) by survey type in Clay Co., Mississippi, 2011–2013.

There were not sufficient species detections across all treatment types for 2011 data in Late Winter and Spring survey periods.

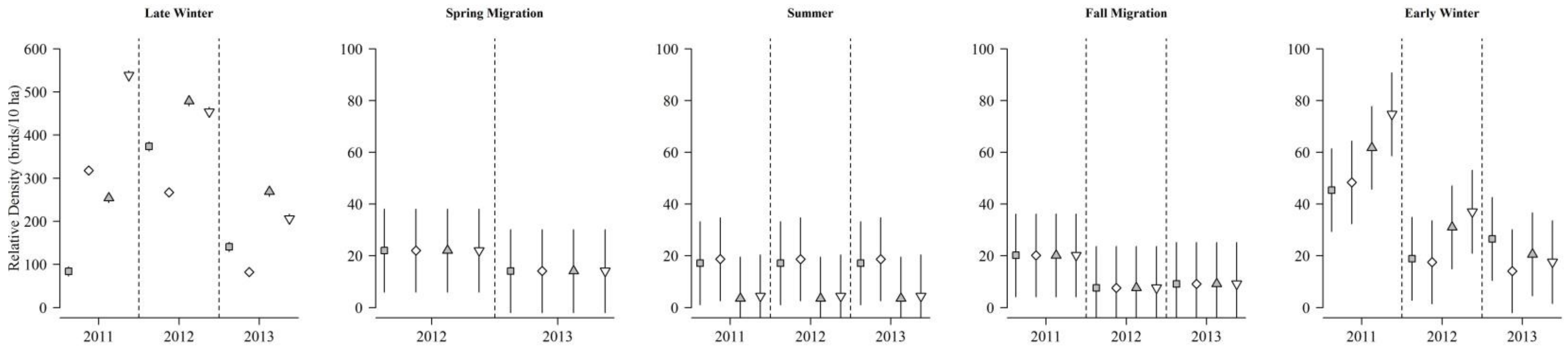

Figure 2.3 Predicted values and 95% CI for avian relative density by survey period for native warm-season grass (NWSG) multiple harvest (□), NWSG single harvest (◇), switchgrass multiple harvest (△), and switchgrass single harvest (▽) treatment types in Clay Co., Mississippi, 2011–2013.

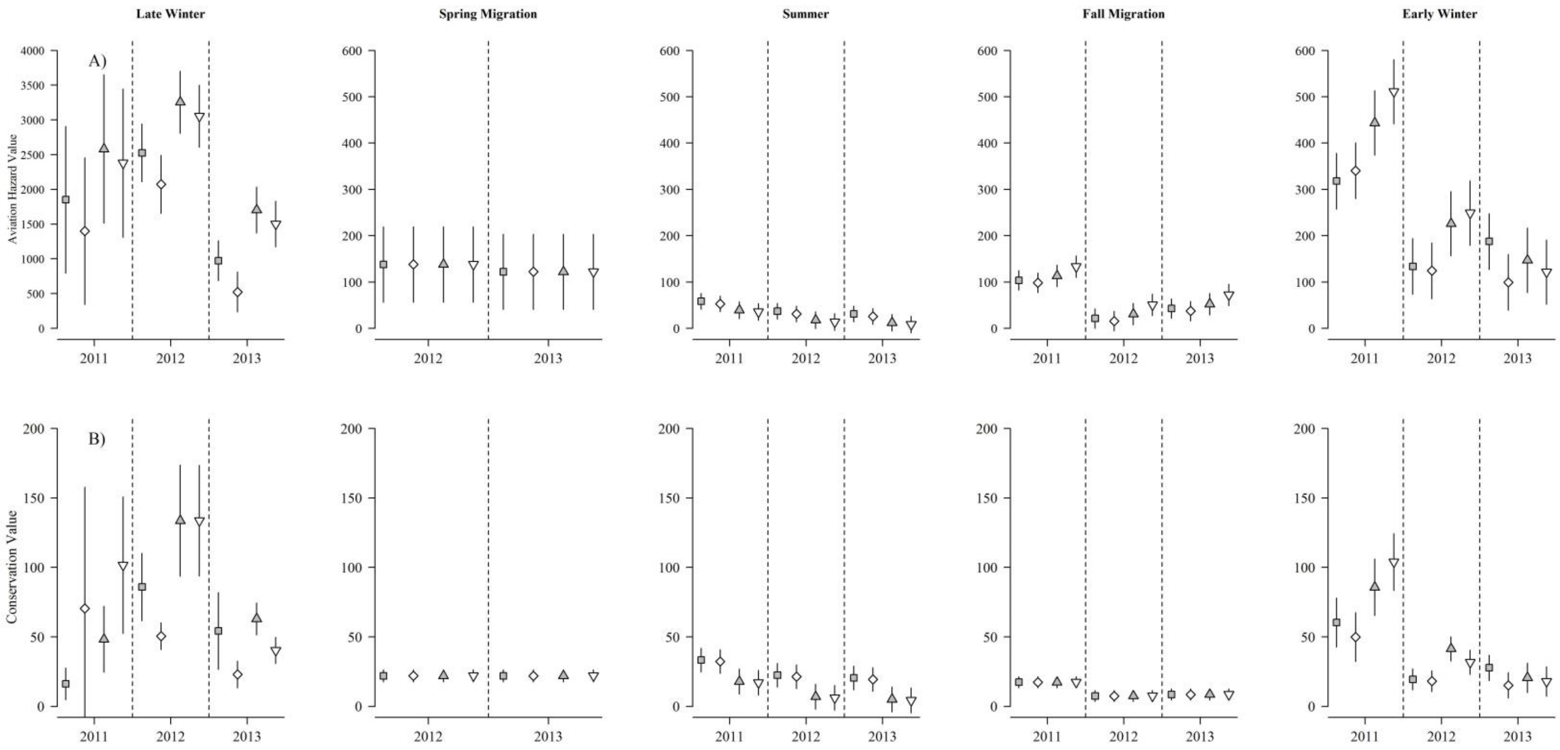

Figure 2.4 Predicted values and 95% CI for: A) avian aviation hazard score and B) conservation value by survey period for native warm-season grass (NWSG) multiple harvest (□), NWSG single harvest (◇), switchgrass multiple harvest (Δ), and switchgrass single harvest (▽) treatment types in Clay Co., Mississippi, 2011–2013.

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CHAPTER III

INFLUENCE OF TERRITORY AND INDIVIDUAL QUALITY ON PRODUCTIVITY IN A POLYGYNOUS SONGBIRD

Introduction

Animals attempt to use resources (Espie et al. 2004; Carrete et al. 2006; Balbontín and Ferrer 2008; Germain and Arcese 2014) to improve reproductive success and survival (Stearns 1992; Peery and Gutierrez 2013). Variation in habitat quality across a species' range due to heterogeneity in food resource availability, predation risk, or suitable breeding locations may affect settlement choices that result in individual variation in breeding success (Andrewartha and Birch 1954; Fretwell and Lucas Jr. 1969; Newton 1998; Sergio et al. 2009). These hypotheses assume that patch quality is determined by available resources and that animals are free to select the highest quality patch available. However, differences in individual quality based on experience, age, body condition (Cody 1985; Brown and Roth 2002) or phenotypic variation (Arcese 2003; Wilson and Nussey 2010) enable dominant individuals to outcompete others for the most productive territories (Coulson 1968; Cody 1985; Sergio et al. 2009; Germain and Arcese 2014), relegating some individuals to sub-optimal habitats where individual fitness may be reduced (Fretwell 1972; Marra 2000). As a result, it may be difficult to separate the contributions of individual and habitat quality on nest success and productivity, especially when competition occurs across heterogeneous landscapes (Zabala and Zuberogoitia 2014).

Accounting for individual quality independent of habitat can allow researchers to more accurately estimate site-specific habitat factors influencing avian productivity (Germain and Arcese 2014). This in turn can improve habitat management strategies for avian species of conservation concern, including grassland birds whose populations have declined across the U.S. in recent years due to habitat loss and degradation (Peterjohn and Sauer 1999; Askins et al. 2007). Based on potential predation risk to offspring (Fontaine and Martin 2006) and the ideal despotic distribution (IDD) model of unequal competition for resources (Fretwell 1972), birds are expected to choose habitats to maximize fitness by selecting territories in low-risk breeding habitat containing more resources, with males defending smaller territories in higher quality habitat. Although habitat metrics including vegetation, food availability, or territory size may quantify territory quality, they do not account for individual variation among territorial males.

Bird song is a sexually-selected trait for territorial defense and mate attraction in many bird species (Catchpole 1982; Reid and Weatherhead 1990) that may also function as an honest signal of territory or male quality because it is a risky and energetically-costly behavior (Hutchinson et al. 1993; Nystrom 1997; Gil and Gahr 2002). Increased song output directly limits time available for foraging while concurrently advertising the male’s location to both conspecifics and potential predators. As such, higher song rates may be indicative of territories with greater food availability or lower predation risk (Hoi-Leitner et al. 1995; Nystrom 1997; Berg et al. 2005). If true, song rate provides a beneficial cue to females selecting potential nesting locations to maximize productivity, because habitat characteristics observed during the settlement period may not be representative of habitat structure or food availability at a later time when nests are active (Searcy 1979; Hoi-Leitner et al. 1995; Sergio et al. 2011). Additionally, song rate may be greater for males with larger territories or conspecific neighbors as males are forced to defend a greater area from potential competitors. However, after controlling for effects of territory resources or size, males singing more frequently during territory defenses may also be superior individuals better able to defend their territories, providing females with additional information regarding male quality (Grafen 1990; Hutchinson et al. 1993; Welling et al. 1997; Sousa and Westneat 2012).

I examined the relative contributions of habitat (nest and territory-scale) and individual quality on nest success and productivity in a grassland environment, using Dickcissel (*Spiza americana*), a polygynous grassland bird (Temple 2002), as a model species. My objectives were to: (1) model behavioral expression of individual male quality relative to temporal and habitat metrics, and (2) determine if nest success and territory productivity are influenced by habitat characteristics, temporal variables, and individual male behavior. Based on the reliability of song as an honest cue of predation risk and food availability (Gil and Gahr 2002)*,* I predicted Dickcissel song rate would be greater in areas with greater food resources, vegetative cover, and would also increase with increasing territory size if males sang more frequently to guard a larger area (Finck 1984). Additionally, if song rate functions as an indicator of individual quality, I expected the number of females to increase with song rate regardless of habitat and temporal factors. In accordance with predation risk to offspring and IDD hypotheses, I expected nest success and territory productivity (number of fledglings produced per territory) to be influenced by the quality of habitat characteristics of the territory (e.g. vegetation structure, arthropod availability, and territory area), rather than individual male quality (e.g. male song rate), after accounting for influential nest survival and productivity covariates such as ordinal date, nest age, nest microhabitat, and territory arrival date (Jensen and Finck 2004; Davis 2005). However, if male quality positively influences either nest success or territory productivity, then the inclusion of male song rate should improve the resulting fit for both models.

Methods

Study Area

I collected data from late April to late July 2011–2013 on 16 8-ha plots (range 5.03–8.41) in a randomized complete block design located at B. Bryan Farm in Clay Co. Mississippi. B. Bryan Farm lies within the historical range of the Blackland Prairie (Barone 2005) and consists mostly of row crop agriculture, pastureland, and conservation easements. In spring 2010, eight plots were planted with a native warm-season grassland (hereafter “NWSG”) seed mixture (Table A.1), and eight were planted with Switchgrass (*Panicum virgatum*). All plots were mowed in April 2012. Additionally, 4 plots of each vegetation type were harvested annually in late-June 2012 and 2013.

Territory Mapping and Banding

Beginning 1 May in 2011 and 24 April in 2012 and 2013, I visited all plots 1-2 times weekly and noted locations of male Dickcissels on each study plot to determine the pattern of territory settlement. Once males established territories, I used conspecific audio playback of songs and call notes to attract birds for targeted mist-netting, which enabled me to uniquely color band territorial males. I aged captured adults and banded individuals with a USFWS aluminum band and unique 3-color band combination under approved permits (Mississippi State University Institutional Animal Care and Use Committee (IACUC) approval #11–020, Mississippi Cooperative Wildlife Research Unit Federal Bird Banding Permit #22456).

I conducted surveys for all territorial males in the study plots every 3–10 days from 0530 to 1200 CDT by walking each plot along 100-m gridlines established to minimize Dickcissel disturbance (Baker 2011) and ensure systematic plot sampling. When birds were present, I followed males for a minimum of 20 minutes at a distance of ≥ 15 m and recorded 3-7 bird locations/survey with a handheld Global Positioning System (GPS), excluding locations influenced by investigator disturbance. I calculated home ranges for all birds present at least 3 weeks with ≥20 GPS points using 95% fixed kernel density estimators (KDE) with least-square cross validation (Rudemo 1982; Bowman 1984) to estimate territory size (Silverman 1986; Worton 1989) in package *adehabitatHR* (Calenge 2006) in program R 3. 0. 3 (R Development Core Team, Vienna, Austria). I obtained daily maximum temperature (˚C) data from the National Oceanic and Atmospheric Administration (NOAA) weather station in Columbus, MS (http://www.ncdc.noaa.gov/cdo-web/).

Song Rate Sampling

I randomly selected 3-5 focal territorial males per plot and collected data on male singing behavior every 7–10 days during territory mapping activities from 15 May–15 July each year. Song rate counts were collected between 0530–1000 CDT. I observed each bird for 10 minutes and recorded total repetitions of standard complete song *dick* and *cissel* phrases (Schook et al. 2008), time of survey, number of neighboring males counter-singing, and number of females and fledglings observed during the territory visit. If the bird departed the territory during sampling or otherwise disappeared from view (e.g., both silent and hidden), I continued with the 10 minute interval, but noted the number of minutes the bird was not visible. If I visited a territory more than once a week, I randomly selected one of the two samples to be used in analyses.

Territory Vegetation Sampling

I collected territory-scale structure and species composition vegetation data approximately 3 weeks after males established territories. I calculated the centroid of the minimum convex polygon (MCP) for each territory with > 20 points using Geospatial Modeling Environment (www.spatialecology.com**)** to establish a 50-m transect centered on each centroid for vegetation sampling. I sampled each transect 3 times about 8–14 days apart and collected vegetation measurements using the point-intercept method (FIREMON 2007) to classify species composition at 5-m intervals along each 50-m transect (10/transect). At each point I recorded the height (cm) and species identification for the 3 dominant vegetation species. At 10-m intervals I recorded visual obstruction from each of the 4 cardinal directions with a Robel pole (Robel et al. 1970). I recorded only visual obstruction on subsequent transect visits because I expected species composition to be consistent across the 20–25 day sampling period.

Arthropod Sampling

I sampled arthropod biomass 3 times in conjunction with territory vegetation sampling visits along each 50-m vegetation transect to quantify territory arthropod biomass commonly consumed by grassland birds (Schartz and Zimmerman 1971; Kobal et al. 1998; Mitchell et al. 2012). I used a modified leaf blower vacuum device (Harper and Guynn 1998; Meyer et al. 2002) and walked along each transect with the vacuum held at maximum vegetation height and collected all samples between 1000 and 1400 CDT either prior to collecting territory vegetation data or ≥2 hours post-vegetation sampling to minimize observer disturbance of arthropods. I placed samples in a kill bucket in the field and transferred samples to a freezer before processing. I identified arthropods to Order and Family when possible, counted the number of individuals per Family, and determined Family total biomass by weighing samples after oven-drying at 60ºC for 48 h and then summing biomass weights across all 3 sampling occasions. I only used Orthoptera total biomass data for subsequent arthropod analyses as this family is the primary food source for nestling Dickcissels (Mitchell et al. 2012).

Nest searching and monitoring

I located and monitored nests during 1 May–9 August 2011 to 2013 using structured (either systematic rope-dragging or walking), behavioral, and opportunistic searches (Conkling et al. 2015). During bi-weekly structured searches 3 technicians walked the entire study area biweekly and disturbed vegetation with a 25-m rope with attached noisemakers to flush nesting birds. When existing vegetation (primarily *Sesbania spp.* > 2m tall) restricted rope-dragging in 2011, 3-5 technicians walked 4 m apart and used hand-held 2-m PVC pipes (2.5 cm diameter) to disturb vegetation. Mowing of all plots to ~16 cm prior to the arrival of Dickcissels in April 2012 allowed rope-dragging on all structured searches for subsequent seasons. I also located nests using behavioral cues or opportunistically by incidentally flushing adults or visually observing nests without adult cues when visiting territories every 3–10 days for song counts, vegetation sampling, and nest checks. For all methods, once birds were flushed observers searched vegetation for ≤10 minutes to locate nests.

I marked all nests with flagging > 5 m north of each nest and recorded nest locations with a handheld GPS. To estimate daily survival rate (DSR) and determine nest fate, I monitored nests every 2–6 days until young fledged or nests failed. I aged nest contests based on progression of physical development for nests found after hatch date (Temple 2002). For failed nests found after incubation commenced, I estimated initiation date as described by Sousa and Westneat (2012). I calculated territory productivity as the maximum number of offspring fledged per territory based on the number of nestlings present during the last nest check before fledging for all nests active within a territory each season or observed fledglings. After each nest was no longer active, I recorded nest height, nest substrate, maximum vegetation height, litter height, and calculated average height of visual obstruction using a Robel pole as observed from a height of 1 m and 4 m from the pole in each of the 4 cardinal directions (Robel et al. 1970) and determined distance to nearest edge of grassland habitat with using ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA). I also calculated nest visible height as the difference between nest height and mean height of vegetation visual obstruction. As such, a nest with a positive visible height would be potentially visible from 4 m, while a nest with a negative visible height would be obscured by vegetation. I collected all nest vegetation measurements ~2 weeks after estimated hatch date when nests were no longer active to reduce variability in the timing of vegetation measurements.

Statistical Analyses

I used R 3.1 (Temple 2002; R Core Team 2015) to determine mean values (± SE) for territory-scale metrics including 95% KDE, visual obstruction, total Orthoptera biomass, mean number of counter-singing males detected during song counts, maximum number of females observed in each territory, and first week of territory establishment, and nest metrics including visible height, nest height, time of day a nest was found (minutes after sunrise), and nest age when found by search method and annual mean daily maximum temperature from May–July each year. I also tested for multicollinearity among covariates in each model by examining variance inflation factors (VIFs, Zuur et al. 2009). All covariates had VIFs < 3.06, providing support that there was no issue with multicollinearity. However, nest height was positively correlated with incubation initiation date ($r = 0.75$), so I removed it from subsequent analyses.

Song Rate

I used a generalized linear mixed model (GLMM) with a Poisson distribution to examine the relationship among total number of songs per season (response variable), territory area (95% KDE), Orthoptera biomass, vegetation characteristics (mean Robel), mean number of countersigning males, the maximum number of females detected within the respective territory during weekly visits, and annual mean daily maximum temperature using MCMC methods within a Bayesian framework using JAGS 3.4.0 (Plummer 2013) and R package R2jags (Su and Yajima 2014). I used minutes monitored per season as an offset in the model to account for a non-constant counting window if birds were not present for the entire 15-week season or weekly 10 minute sampling period. I included a random intercept for each bird. For all models using MCMC methods, I standardized datasets and used flat priors for all terms in the model including Gamma (0.001, 0.001) for inverse of variance terms and Normal (0.01, 0.01) for all other parameters. I then sampled from 3 independent Markov chains for 120000 iterations for each model, with a burn in of 20000 samples. I evaluated traceplots and posterior distributions for the effects of interest using $R < 1.05$ (Gelman et al. 2014). I used Bayesian *P*-values (Schmidt et al. 2010; Gelman et al. 2014) to assess goodness of fit and to examine the proportion of posterior distribution values > 0 or < 0 when 95% credible intervals overlapped zero. In addition to posterior distributions, model output included a scaled mean song rate across the season for each territory for use in the nest survival and fecundity models.

Nest survival modeling

I estimated daily nest survival within a Bayesian framework (Royle and Dorazio 2008) to determine the relative importance of habitat and male individual quality based on vegetation characteristics (visible height, distance to habitat edge), linear and quadratic effects of date, linear and quadratic effects of age, territory-scale metrics including area (95% KDE), mean territory Robel measurement, Orthoptera biomass, year, search method, age (in days) of nest when found (Conkling et al. 2015), and male quality based on mean seasonal song rate derived from the song model. I excluded nests that failed due to anthropogenic causes (e.g. mid-season mowing). I estimated period nest survival by multiplying daily survival rate estimates generated by 21 days in the nesting period (i.e. incubation to fledging; (Temple 2002) for nests starting on the median initial incubation date (21 May).

Productivity modeling

I estimated seasonal productivity by territory with the maximum number of fledglings possible at each successful nest in a territory or the maximum number of fledglings observed with a territorial adult if no monitored nests were successful using a generalized linear mixed model (GLMM) with a zero-inflated Poisson distribution within a Bayesian framework. In addition to covariates and priors mentioned previously, I used Poisson (0.001) priors for the number of fledglings per territory (response variable). I modeled fledglings per territory as a function of territory area (95% KDE), Orthoptera biomass, mean territory visual obstruction, arrival week of the male, maximum number of females within a territory, annual mean daily temperature, and mean seasonal song rates derived from the song rate model. Additionally, I included a random intercept for each bird.

Results

I monitored 176 Dickcissel territories present ≥3 weeks and selected 101 focal territories for subsequent song count, vegetation, and arthropod sampling (Table B.1). Song rate increased with greater territory area (95% CrI: 0.018, 0.450) and maximum number of females present (2 females, 95% CrI: 1.140, 1.816; 3 females, 95% CrI: 0.318, 2.246), but declined with higher mean annual daily maximum temperature (95% CrI: -1.138, -0.551) (Table 3.2). I monitored 134 Dickcissel nests associated with focal territories (57 in 2011, 39 in 2012, 38 in 2013); 68 of the 101 focal territories had ≥1 nest. Nearly 69% of nests failed due to predation. Distance to habitat edge ($F_{2,\,132}$ = 0. 266, *P* = 0. 61) and nest visible height ($F_{2,132}$ = 0. 117, *P* = 0. 73) were similar across years, while the age of nest when found was greatest in 2011 (8.37 ± 1.04) and decreased annually, with nests in 2013 (4.21 ± 0.97) located an average of 4.2 days earlier in the nesting cycle. ($F_{2,\ 132}$ = 10. 16, $P < 0.01$) (Table B.2).

Daily survival rate (DSR) for Dickcissels was best explained by quadratic nest age, quadratic date, and territory area (Table 3.3). DSR declined with age of the nest and linear date, but there was a positive influence of quadratic date on survival. Additionally, DSR was influenced by territory area, as DSR increased for nests located in smaller territories ($\beta = -0.303$, 95% CrI: -0.572, -0.029) (Fig. 3.1), providing support that breeding in higher quality territories improved nest survival. The period survival for the 21-day nesting cycle based on median initiation date was greatest in 2011 (2011: $S = 0.214$, 2012: $S = 0.055$, 2013: $S = 0.139$).

Offspring successfully fledged in 38 territories and from 11 territories independent of monitored nests. The only territory-scale factor that influenced productivity was the first week a territory established (Table 3.4), corresponding to individual quality. Productivity was less in territories established later in the breeding season ($\bar{x}$ = -0. 363, 95% CrI: -0. 769, 0. 006, Bayesian *P*-value = 0.973) (Fig 3.2).

Discussion

Male song rate was a suitable surrogate for individual quality for modeling the effects of temporal and habitat metrics on variation in individual behaviors. However, there was limited evidence for song rate as a suitable metric for quantifying individual quality effects on nest success and territory productivity. Dickcissel males sang more frequently when defending larger territories, likely due to the additional territory defensive behaviors required when guarding a larger area (Finck 1984), even though the number of counter-singing neighbor males had no direct influence on overall song rates

(Table 3.1). Regarding other habitat metrics, song rate can function as a predictor of food availability or predation risk due to vegetation structure, but studies supporting these results focused primarily on forest avian species (Hoi-Leitner et al. 1995; Ritschard and Brumm 2012). I observed no relationship between song rates and vegetation visual obstruction or food availability, suggesting that song rate or the habitat metrics I used may not reliably reflect habitat quality in grassland birds.

Although I found limited effects of temporal or habitat metrics on song rates, males that sang more often also had more than one female in their territories, indicating that even if song rate did not directly provide information about habitat quality, there was some male or habitat cue present that increased female preference. However, this difference in song rate only occurred between monogamous and polygynous males, with no discernable difference in fitness for males with 2 or 3 females. Female breeding success is limited by multiple factors, including availability of nest sites, and food abundance, predation risk, and overall quality of the offspring. If song rate functions as an honest cue for any of these male or territory-related metrics, females may benefit from choosing to breed in a territory occupied by a more vocal male. This study is noteworthy in that most research focused on bird song and individual quality examine the effects of song complexity or repertoire (Lampe and Espmark 1994; Balsby 2000; Reid et al. 2005; Darolová et al. 2012), rather than song frequency (Welling et al. 1997; Manica et al. 2014). While repertoire may be beneficial in species relying on complex songs to attract males, Dickcissel males only produce one song type (Schook et al. 2008), which limits the use of complexity as a quality cue. Hoi-Leitner et al. (1995) obtained similar results with Blackcaps (*Sylvia atricapilla*), noting that females selected males with high song rates. They rationalized that blackcap song output functioned as a cue for nest site quality, with males preferentially defending territories with high vegetation density expected to have lower predation risk.

It is unclear which specific vegetation metrics and male cues female Dickcissels may be using for breeding habitat selection (Zimmerman 1971; Finck 1984; Temple 2002), as previous research found no relationship between male ornamentation or behaviors and number of females in a territory (Finck 1984; Sousa and Westneat 2012). Zimmerman (1982) suggested females primarily select breeding habitat based on potential nest locations. However, if male song rate functions as a surrogate of male quality, females incorporating song rate into breeding habitat decisions could also breed with higher quality males, thereby producing higher quality offspring (Przybylo et al. 2001) in addition to building nests in high quality habitat. This dual-selection strategy could be especially beneficial in non-stationary environments such as grasslands where habitat metrics (e.g. vegetation structure, arthropod availability) during territory establishment differ from those present later in the breeding season (Sergio et al. 2011). Regardless of changes in habitat metrics, females could be knowledgeable of a male's physical quality, allowing birds to maximize fitness and reproduction in the face of varying predation risk or habitat conditions (Switzer 1993). Alternatively, females may use site fidelity for habitat selection choices, returning to breed with males in the same territory as previous years, although this practice may be rare for female Dickcissels (Walk et al. 2004; Sousa and Westneat 2012).

In addition to influential covariates such as ordinal date, nest age, and year, nest survival declined with increasing territory area (Table 3.4), providing support for IDD as nests located in smaller, presumably high-quality territories better defended by males had greater DSR than larger territories. I found no support for effects from other individual habitat metrics including nest location (visible height and distance to edge), food availability, vegetation visual obstruction, or individual quality (song rate), suggesting that territory size (rather than individual habitat metrics) better reflects overall resources abundance, habitat quality, or predation risk in a territory (Calsbeek and Sinervo 2002; Marshall and Cooper 2004; Diemer and Nocera 2014). Additionally, male quality (as quantified by song rate) was not influential on the resulting DSR. My vegetation and arthropod measurements were based on transects established at the midpoint of the territory, rather than the entire territory. As such, these transects may not represent the total food resources or vegetation structure available to breeding birds. Other studies of grassland birds demonstrate mixed results regarding the influence of vegetation and other habitat characteristics on nest survival (Wray and Whitmore 1979; Zimmerman 1982; Walk et al. 2010).

Based on ideal despotic distribution predictions, males occupying smaller territories may also be high quality males as they are able to successfully defend those superior resources (Zimmerman 1971; Fretwell 1972; Zimmerman 1982; Calsbeek and Sinervo 2002) and thus should have disproportionally greater reproductive success. Nests in high-quality, smaller territories did have greater DSR (Table 3.2, Fig. 3.1), but males in these territories did not have more fledglings than their neighbors in larger territories (Table 3.3). Regardless, all males successfully raising ≥1 fledgling benefited from increased fitness resulting from offspring production. Conversely, although females did not engage in despotic behaviors, variation in nest survival due to territory size could produce unequal fitness among females if breeding in smaller, high-quality territories increases their reproductive success. In addition, females building nests in high quality territories may have the additional benefit of mating with competitively superior males (Zimmerman 1982; Finck 1983), thereby maximizing breeding success by producing higher quality offspring (Przybylo et al. 2001).

Contrary to my predictions, arrival date was the only factor to influence territory productivity, with males that established territories earlier in the season having more fledglings per territory than later-arriving males (Table 3.3, Fig. 3.2). Reproductive performance for breeding birds can be influenced by territory quality or age of individuals (Cody 1985; Newton 1998; Pärt 2001b), but early territory settlement dates can also increase seasonal productivity by providing earlier breeding opportunities or more nesting attempts (Lanyon and Thompson 1986; Grzybowski et al. 2005; Joos et al. 2014). Often, older and more experienced birds return to territories earlier in the breeding season, thereby increasing breeding success and fitness relative to younger individuals (Cody 1985; Newton 1998; Pärt 2001a; Smith and Moore 2005). Earlier arrival dates may also correspond to available resources on the breeding or wintering grounds (Cohen et al. 2015).

Additionally, familiarity with resources, neighbors, and relative predation risk may increase the probability of success (Greenwood 1980) and males with preexisting knowledge of a habitat are more likely to monopolize higher quality habitats through site fidelity in subsequent years (Lanyon and Thompson 1986; Zimmerman and Finck 1989; McKellar et al. 2013; Joos et al. 2014). Site fidelity may be more prevalent for breeding birds in non-stable, intermediate environments such as grasslands where the changing vegetation structure makes it difficult to use existing habitat cues at the beginning of the season to determine resource availability or prevailing predation risk a few weeks later. This makes it more advantageous to stay in a familiar territory, regardless of fitness the previous year, resulting in an “always stay” strategy (Switzer 1993). I did not specifically examine the effects of site fidelity or age in my models, as I randomly selected focal birds each year without regard to territory status the previous year. Additionally, I was only able to age captured focal birds to two age categories (Second Year and After Second Year, a common scenario for passerines (Pyle 1997) that restricted my ability to draw any definitive conclusions on the effects of male age on productivity. However, by including individual bird as a random effect in productivity models, I accounted for the influence of repeated measurements of birds across years.

Identifying factors important to nest success or productivity is essential to develop effective management strategies for avian species. My results emphasize the need to include multiple metrics quantifying both habitat quality and individual quality to improve resulting model fit. Although I did not find song rate to be a quality surrogate for individual quality in nest survival or productivity models, the effects of territory area and arrival date on nest survival and productivity, respectively, suggest that some aspect of individual quality is important for reproduction in grassland birds. Incorporating individual quality measurements into avian monitoring practices, especially for species of conservation concern, may provide additional information to quantify high-quality breeding habitat and improve habitat management strategies aimed at species conservation.

Table 3.1 Model coefficients (± SD) and 95% credible intervals for parameters in MCMC model to estimate song rate for Dickcissels in Clay Co., Mississippi, 2011–2013.

			95% Credible Intervals		
Parameter	Estimate	SD	Lower	Upper	$\hat{R}$
First Week	0.130	0.115	-0.094	0.349	1.002
Territory Area (95% KDE)	0.219	0.109	0.018	0.450	1.044
Territory Robel	-0.020	0.115	-0.256	0.200	1.008
Territory Orthoptera	0.139	0.114	-0.096	0.353	1.020
Number of Counter-singing Males	-0.046	0.104	-0.256	0.153	1.007
Number of Females in Territory (2)[a]	1.478	0.169	1.140	1.816	1.014
Number of Females in Territory (3)[a]	1.285	0.494	0.318	2.246	1.003
Mean Annual Temperature	-0.816	0.153	-1.138	-0.551	1.012

[a] 1 is the reference maximum number of females. Coefficient refers to change in productivity for given number of females (2 or 3) relative to territories containing a single female.

Table 3.2 Model coefficients (± SD) and 95% credible intervals for parameters in MCMC model to estimate nest survival for Dickcissel territories in Clay Co., Mississippi, 2011–2013.

			95% Credible Intervals		
Parameter	Estimate	SD	Lower	Upper	$\hat{R}$
Intercept	3.178	0.556	2.108	4.182	1.006
Age	-0.979	0.147	-1.277	-0.716	1.001
Quadratic Age	-0.588	0.116	-0.809	-0.356	1.001
Date	-0.642	0.214	-1.051	-0.227	1.001
Quadratic Date	0.734	0.258	0.242	1.242	1.001
Year-2012[a]	-0.862	0.375	-1.598	-0.105	1.001
Year-2013[a]	-0.342	0.36	-1.025	0.38	1.001
Territory Area (95% KDE)	-0.303	0.14	-0.572	-0.029	1.001
Territory Robel	0.033	0.143	-0.242	0.318	1.002
Territory Orthoptera	0.058	0.14	-0.211	0.345	1.001
Territory Mean Song Rate	0.138	0.134	-0.116	0.394	1.001
Nest-Visible Height	0.164	0.125	-0.077	0.414	1.001
Nest Distance to Edge	-0.096	0.108	-0.309	0.115	1.001
Nest Age When Found	0.137	0.136	-0.133	0.397	1.001

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

[a] Behavioral cues are the reference search method. Coefficient refers to change in daily nest survival for given search method relative to behaviorally-located nests

Table 3.3 Model coefficients (± SD) and 95% credible intervals for parameters in MCMC model to estimate productivity for Dickcissel territories in Clay Co., Mississippi, 2011–2013.

			95% Credible Intervals		
Parameter	Estimate	SD	Lower	Upper	$\hat{R}$
Territory Area (95% KDE)	-0. 061	0. 180	-0. 412	0. 287	1. 001
Territory Robel	0. 033	0. 189	-0. 330	0. 418	1. 001
Territory Orthoptera	-0. 196	0. 176	-0. 546	0. 144	1. 002
First week territory established	-0.363	0.200	-0.769	0.006	1.001
Territory Weekly Song Rate	-0.018	0.176	-0.365	0.321	1.003
Maximum Number of Females (2)[a]	-0.059	0.264	-0.616	0.426	1.001
Maximum Number of Females (3)[a]	0.144	0.567	-1.020	1.258	1.001
Mean Annual Temperature	0.017	0.438	-0.822	0.810	1.002

[a] 1 is the reference maximum number of females. Coefficient refers to change in productivity for given number of females (2 or 3) relative to territories containing a single female.

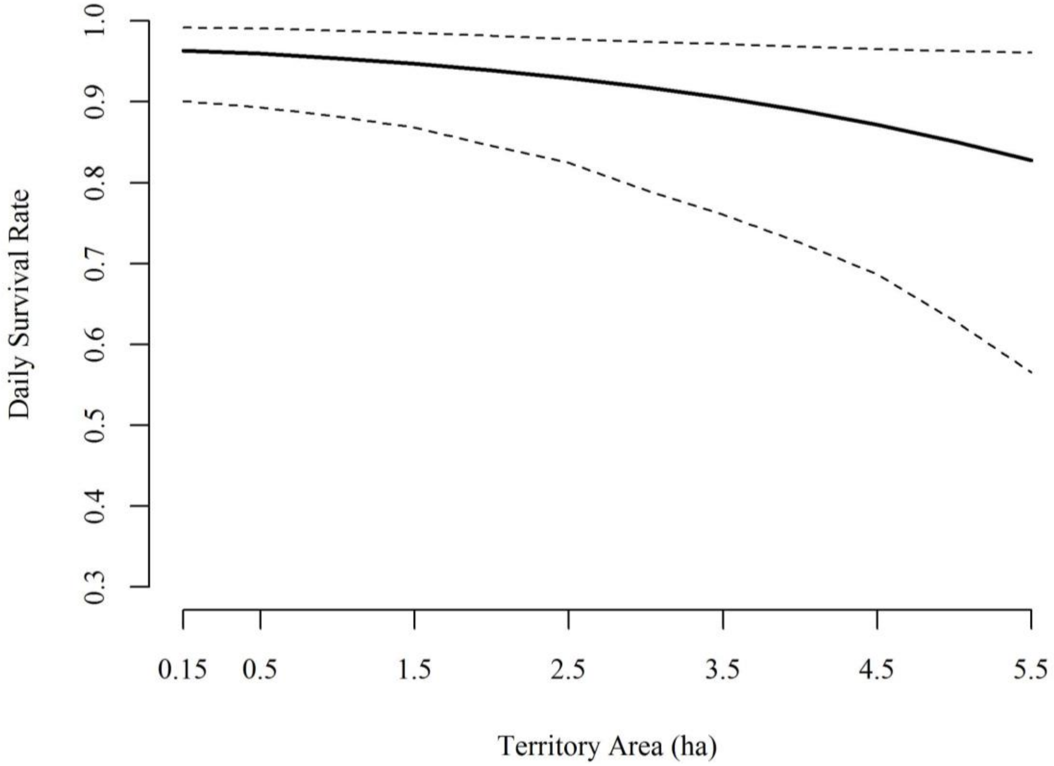

Figure 3.1 Daily survival rate (DSR) and 95% CrI (dashed lines) for Dickcissel (Spiza americana) nests (year = 2011) for territory area (95% KDE) (date held constant at median initiation date (18 May) nest age held constant at day 11, age found held constant at day 8 in Clay Co., Mississippi, 2011–2013.

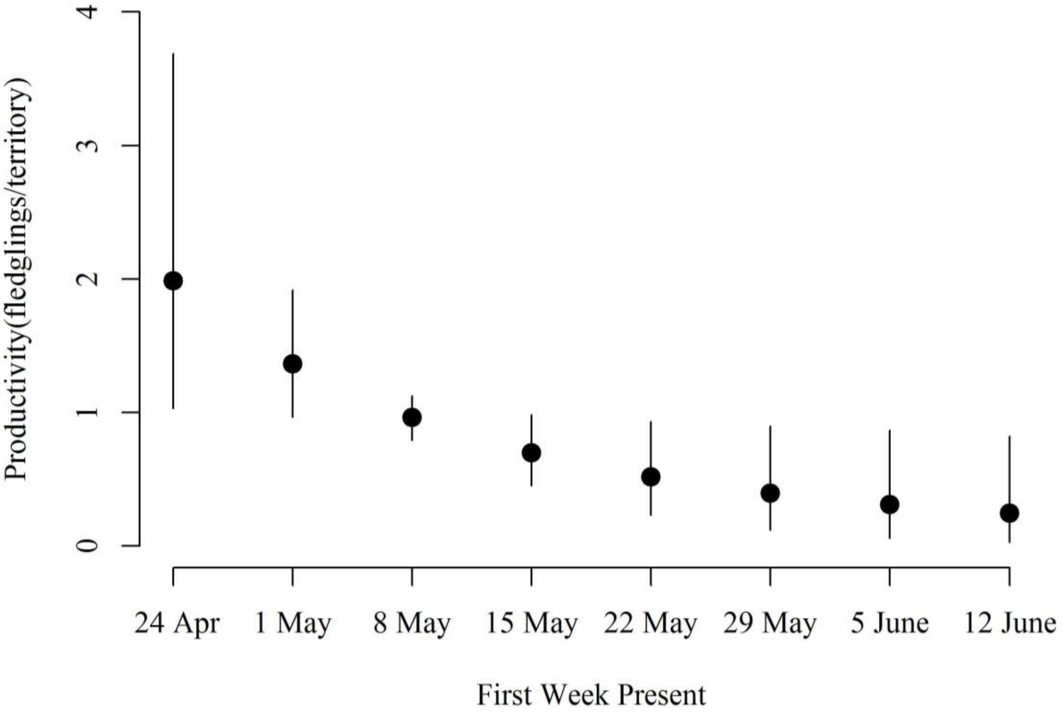

Figure 3.2 Annual territory productivity (fledglings/territory) and 95% CrI (solid lines) for Dickcissel (*Spiza americana*) nests (year = 2011) by first week territory was established in Clay Co., Mississippi, 2011–2013.

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CHAPTER IV

EFFECTS OF CROP TYPE AND HARVEST ON NEST SURVIVAL AND PRODUCTIVITY OF DICKCISSELS IN SEMI-NATURAL GRASSLANDS

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 functions 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). 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 functionality and vegetation structure (Fletcher Jr. 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 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), along with providing 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 (Vogel et al. 2002; Fike et al. 2006) and the timing of harvests can be detrimental to avian species if they occur during the breeding season (Roth et al. 2005) because they remove cover, reduce food availability, and destroy active nests (Bollinger et al. 1990; Kershner and Bollinger 1996; Warren and Anderson 2005; Perlut et al. 2006). Biomass harvest 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 Jr. 1969) predicts that local habitat quality determine species' density, resulting in equal fitness across all individuals regardless of habitat quality. In contrast, ideal despotic distribution [IDD] (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 (Fretwell and Lucas Jr. 1969; Bakker and Higgins 2009), thereby increasing the total production of offspring per unit area and 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.

I examined the effects of biofuel treatments on nest success, nest density, and productivity of Dickcissels (*Spiza americana*), a polygynous, ground-nesting grassland bird of conservation concern (Blankspoor 1970; Temple 2002). I 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). I 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, I expected plots with greater nest density to produce more offspring per hectare, but that individual productivity would be similar across treatments, in accordance with ideal free distribution. However, 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).

Methods

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 NWSG seed mixture (Table A.1) 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 plots of each vegetation type were harvested annually in late-June 2012 and 2013, resulting in 4 unique treatments: NWSG single annual harvest (“NWSG single harvest”), NWSG multiple annual harvest (“NWSG multiple harvest”), switchgrass single annual harvest (“switchgrass single 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 I removed them from subsequent analyses.

Territory Mapping and Banding

Beginning 1 May in 2011 and 24 April in 2012 and 2013 to 15 July each year, I conducted weekly visits to all plots and noted arrival dates of male Dickcissels to determine the pattern of habitat settlement. Once male Dickcissels established territories, I used target mist-netting for territorial males by attracting birds with conspecific playback of songs and call notes to capture territorial males. After capture, I 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).

I delineated territory areas for all males in the study plots by conducting surveys every 3–10 days from 0530–1200 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, I monitored birds from ≥ 15m for at least 20 minutes and recorded 3-7 unique bird locations/survey with a handheld Global Positioning System (GPS), excluding locations influenced by observer presence. Following biomass harvest on treatment plots in late-June 2012 and 2013, I continued territory mapping and re-sighting efforts across all plots until 15 July. I used fixed kernel density estimators (KDE) and 95% volume contours to estimate territory size (Silverman 1986; Worton 1989) for all territorial males present ≥ 3 weeks for use in subsequent analyses using package *adehabitatHR* (Calenge 2006) in program R 3.1.3 (R Core Team 2015). I excluded territories from subsequent density analyses if ≤25% of the calculated 95% KDE was contained within the study plots.

Nest searching and monitoring

From 1 May–9 August 2011 to 2013 I found and monitored nests using structured (systematic rope-dragging or walking), opportunistic, and behavioral searches (Conkling et al. 2015). I 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 seasons. 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.* > 2m tall), necessitating the use of systematic walking by 3-5 technicians spaced at 4m 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 ~16cm 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, I 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). During all searches, observers spent ≤10 minutes scanning the vegetation to locate nests after a bird was flushed (Barg et al. 2005).

I recorded the location of each nest with a handheld GPS and marked the nests with flagging > 5m north of the nest. I then monitored all nests at 2–6 day intervals until the nest failed or young fledged to determine nest fate and calculate DSR. For nests found after hatch date, I 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 I found nests after incubation began that failed prior to hatch date, I estimated incubation initiation date by assuming midpoint of incubation (6 days) coincided with halfway between available check dates (Sousa and Westneat 2012). I 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 number of fledglings observed in the territory irrespective of nest. I collected nest vegetation measurements about 2 weeks after the estimated hatch date to avoid nest disturbance and to reduce variability on the timing of vegetation collection. I measured nest height, maximum vegetation height, litter depth, and vegetation visual obstruction with a Robel pole observed at a distance of 4m and height of 1m in each of the cardinal directions (Robel et al. 1970). I calculated distance to nearest edge of grassland habitat using ArcMap 10.1 (ESRI 2011). I 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 4m, whereas a negative visible height indicated that a nest would be obscured by vegetation.

I collected plot-level vegetation data along 5 randomly located 50-m transects to determine structure and species composition among treatments. I first used a geographic information system (ESRI 2011), to overlay a 50 x 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. I sampled each transect in March 2011 and then monthly from June 2011–December 2013, but I restricted analyses to samples collected in June each year to limit effects of midseason harvest on resulting vegetation measurements. I used the point-intercept method (FIREMON 2007) to quantify 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). I also classified species composition by recording litter depth and species identification and height (cm) for the 3 most common vegetation species at 5-m intervals along each transect (10 measurements/transect).

Statistical analyses

I 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 had a VIF of > 3, so I removed it from subsequent analyses; after removal, all other VIFs were < 1.12, indicating no multicollinearity between the remaining variables. I calculated mean values (± 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. I 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 among treatments.

Nest survival modeling

I 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). I 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)). I 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. I examined traceplots and posterior distributions for the effects of interest using $R < 1.05$ 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 (Schmidt et al. 2010; Gelman et al. 2014).

Plot Nest Density and Productivity

I 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. I 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), I instead used unadjusted counts of nests found per plot as an index of nest density. As a result, I accounted for potential discrepancies in nest density by equally allotting nest searching efforts using systematic searches among treatments and spent a minimum of 30 minutes weekly in every identified territory. I 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). I calculated the odds ratio for categorical covariates in the model by exponentiating the resulting parameter coefficients. Finally, I 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. I 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 ($d = 0.80$). I 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.

Territory Nest Density and Productivity

To determine if productivity varied at the territory level across treatments in accordance with IDD, I used a Bayesian framework to estimate nest density for each documented territory. I 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. I then calculated productivity (fledglings/ha) per territory by multiplying territory nest density by brood size and period survival for each treatment and year.

Results

I monitored 238 nests (99 in 2011, 79 in 2012, 60 in 2013) in 176 Dickcissel territories and located 0 to 6 nests per territory ($\bar{x} = 1.65 \pm 0.04$). Settlement dates for males establishing territories were similar among treatments ($F_{1,6} = 1.34$, $P = 0.29$; Table C.1). 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 (Table A.2). Plot-level vegetation visual obstruction was greater in switchgrass treatments compared with NWSG, and this difference increased annually (2011: $F_{3,10} = 4.53$, $P = 0.03$; 2012: $F_{3,10} = 10.36$, $P < 0.01$; 2013: $F_{3,10} = 70.81$, $P < 0.01$)

(Table C.1 & Fig. C.1). 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 (Fig. C.1).

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 4.1; Table A.2). Daily survival rate decreased as nests contents aged, resulting in lower survival for nestlings relative to the egg stage. 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 ($\beta = 0.287$, 95% CrI: 0.093, 0.486). I also noted a marginal effect of distance to habitat edge (Bayesian *P*-value = 0.92). There was no effect of vegetation metrics, harvest frequency, or biofuel treatment on nest survival. Additionally, the period survival for the 21-day nesting cycle based on median initiation date indicated that overall survival multiple-harvest treatments was not lower than single harvest treatments even with mid-season harvests destroying active nests. (Table 4.2).

The estimated nest density across plots ranged from 0.05 to 2.56 nests per hectare (Table 4.2). 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 4.2 & 4.3), suggesting that birds chose breeding locations in NWSG based on vegetation heterogeneity and diversity (Fig. A.1). 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: $U_3 = 60.8\%$).

I did not have any Dickcissel territories primarily located in switchgrass so I restricted territory-scale analyses to NWSG treatments. I identified 4 territories associated with nests in switchgrass plots, but most of the 95% KDE territory areas were located in NWSG treatments (mean proportion = 0.62 ± 0.04). The remaining 3 nests were > 50m from the nearest known location of any territorial male so I was unable to determine the male associated with them. There was no difference in territory nest density between harvest frequencies (Table 4.3), but there were fewer nests in 2012 and 2013 relative to 2011, in accordance with increasing vegetation structure as all grasses matured (Fig. A.1). Additionally, per capita productivity did not differ between NWSG single harvest and multiple harvest treatments (Table 4.4), contrary to predictions based on IDD that individual reproductive success would be greatest in the higher quality habitat.

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 Jr. 1969; Morisita 1969; 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; Knight et al. 2010; Werling et al. 2014). However, monocultures of native grass species may not provide quality breeding habitat. 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.

Contrary to my initial predictions regarding harvest frequency, multiple harvests did not reduce nest daily survival rates. I 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, my 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, I 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 III 2001; Nakagawa and Cuthill 2007). Also, my 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 I observed no difference in territorial male density between harvest frequencies (T. Conkling, unpublished data), 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; Chapter 3). 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 data). 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. I 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 data), 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; Chapter 3). 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 (Chapter 3).

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). I 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; Chapter 2). My 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).

Table 4.1 Model coefficients (± SD) and 95% credible intervals for parameters in MCMC model to estimate nest survival for Dickcissel nests in Clay Co., Mississippi, 2011–2013.

			95% Credible Intervals			Bayesian
Parameter	Estimate	SD	Lower	Upper	$\hat{R}$	*P*-value
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 4.2 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.

	Year					
	2011		2012		2013	
Treatment	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	0.142	0.172	-	-
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	0.037	0.051	-	-
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	0.016	0.043	-	-
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)	0.053	0.072	0.007	0.023	0.032	0.050
Native Warm-Season Grass (single harvest)	0.069	0.078	0.009	0.025	0.042	0.052
Switchgrass (multiple harvest)	-	-	-	-	-	-
Switchgrass (single harvest)	-	-	-	-	-	-

Table 4.3 Model coefficients (± SD) and 95% credible intervals for parameters in MCMC model to estimate plot nest density (number of nests/ha) for Dickcissel nests in Clay Co., Mississippi, 2011–2013.

			95% Credible Intervals			Bayesian
Parameter	Estimate	SD	Lower	Upper	$\hat{R}$	*P*-value
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).

Table 4.4 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 Lower	Upper	$\hat{R}$	Bayesian *P*-value
Intercept	-1.796	0.281	-2.364	-1.260	1.001	1.000
2012[a]	-0.432	0.175	-0.778	-0.086	1.001	0.993
2013[a]	-0.416	0.189	-0.801	-0.058	1.000	0.990
Native Warm-Season Grass (single harvest)[b]	0.117	0.346	-0.556	0.848	1.001	0.646

[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).

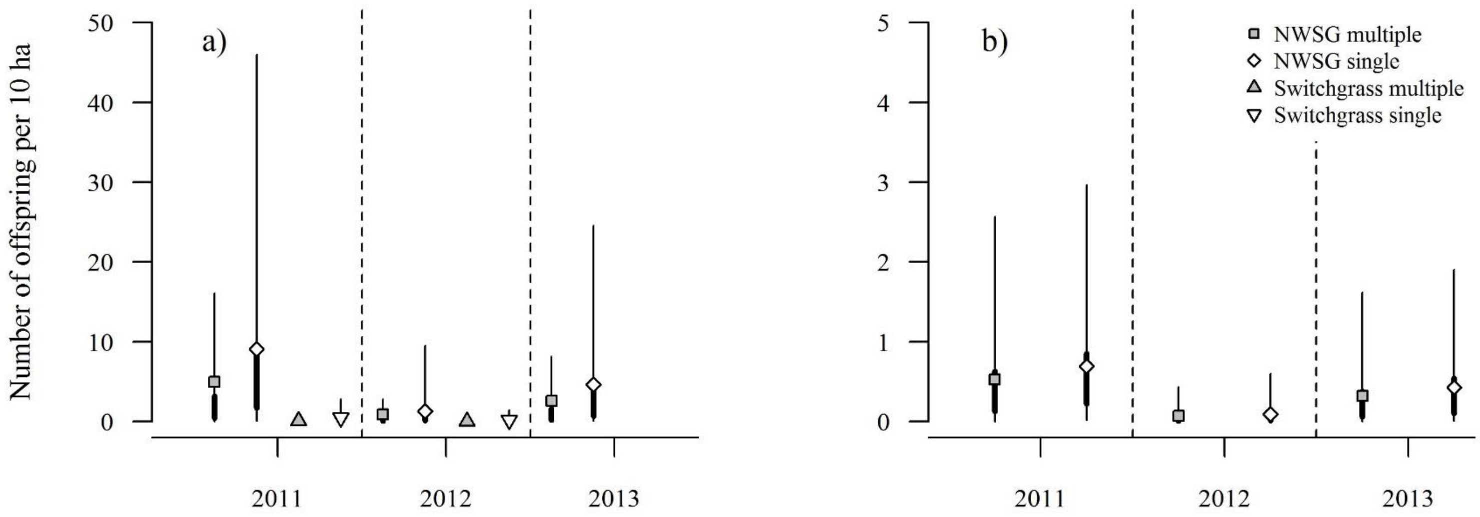

Figure 4.1 Mean and 50% and 95% CrI for a) plot productivity and b) territory productivity in native warm-season grass (NWSG) multiple harvest (□), NWSG single harvest (◇), switchgrass multiple harvest (△), and switchgrass single harvest (▽) treatment types in Clay Co., Mississippi, 2011–2013.

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CHAPTER V

GENERAL CONCLUSIONS

Understanding the effects of habitat manipulation and vegetation species composition on wildlife is important to increase our knowledge of the potential impacts of biofuel cultivation in the coming years. Animals use resource availability, predation risk and individual quality to select appropriate breeding, stopover, or wintering habitat (Grinnell 1917; Hildén 1965; Fretwell and Lucas Jr. 1969; Fretwell 1972; Jones 2001; Fontaine and Martin 2006). As a result, conservation strategies based on these ecological concepts such as predation risk, the heterogeneous habitat hypothesis, and ideal free and ideal despotic distributions that influence habitat selection can improve the effectiveness of land management practices aimed at maintaining biodiversity, biofuel production, and minimizing aviation risk (Blackwell et al. 2009; DeVault et al. 2013a; DeVault et al. 2013b; Schmidt et al. 2013).

In Chapter 2, switchgrass (*Panicum virgatum*) monocultures and diverse semi-natural grasslands provided beneficial habitat to grassland birds. However, treatment effects on relative abundance, aviation risk, and conservation values varied by season, suggesting that year-round metrics of avian populations are necessary to identify patterns of habitat use. Dense monoculture switchgrass provided abundant vegetative cover and structure during winter (Fletcher Jr. and Koford 2002; Fletcher Jr. et al. 2010; Blank et al. 2014), with increasing vegetation structure limiting flocking species that may be hazardous to aircraft (Lima 1993; DeVault et al. 2011). Conversely, breeding birds favored diverse NWSG for building nests and fledging offspring (McCoy et al. 2001; Hovick et al. 2014). Regardless, semi-natural grasslands offered minimal aviation risk, providing support for semi-natural grasslands as a feasible landcover option at airports (Schmidt et al. 2013). Additionally, varied harvest frequencies across a mosaic of switchgrass monocultures and NWSG plots may balance biofuel production with multiple habitat options for grassland birds to increase seasonal avian biodiversity and productivity.

In Chapter 3, I highlighted the effects of individual quality and habitat quality on reproduction in grassland birds. Although there was no support for Dickcissel (*Spiza americana*) male song rate as an appropriate metric to quantify measured habitat metrics, other individually-varying factors including territory size and male arrival date were positively associated with nest survival and productivity, respectively. My results provide evidence that incorporating individual quality metrics independently of habitat in demographic models may allow researchers to better identify site-specific habitat metrics affecting avian productivity (Germain and Arcese 2014) and to direct habitat management efforts accordingly. In Chapter 4, I demonstrated the impacts of vegetation species and harvest frequency of semi-natural grasses managed for biofuel production on Dickcissel nest survival, nest density, and productivity. Vegetation species composition did not influence nest survival, but breeding birds nested 54 –64 times more often in NWSG. As a result, switchgrass monocultures may be better for overall biofuel production (Adler et al. 2009) than NWSG and provide more ecosystem benefits than traditional biofuel crops such as corn (Fargione et al. 2009; Knight et al. 2010; Werling et al. 2014). Switchgrass appears to function as inferior breeding habitat for grassland birds as they lack the vegetation structural complexity in NWSG favored by breeding birds (Simpson 1949; Wiens 1974; Robertson et al. 2011; Blank et al. 2014). Additionally, harvest frequency had a negative effect on nest density and productivity on the plot level, with a 10.8% decline in density for multiple harvest treatments relative to single-harvest plots. However, there were no identifiable treatment effects of harvest frequency on individual Dickcissel territories located in NWSG.

Given the increased interest in the production of cellulosic fuels, my results demonstrate that vegetation composition and harvest strategies inherent to grassland biofuel cultivation strongly influence year-round habitat use and reproductive success of avian species and the resulting aviation risk. As such, my research functions as a proof of concept regarding effective management strategies for avian conservation and mitigation of aviation risk and provides direction for future research efforts aimed at investigating implementation of semi-natural grasslands in airport landscapes.

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APPENDIX A

SUPPLEMENTARY MATERIAL

Table A.1 List of species planted in native warm-season grass (NWSG) plots in Clay Co., Mississippi, USA (2011–2013).

Common Name	Species Name
Big Bluestem	*Andropogon gerardii*
Little Bluestem	*Schizachyrium scoparium*
Indian Grass	*Sorghastrum nutans*
Switchgrass - Alamo	*Panicum virgatum*
Roundheaded Lespedeza	*Lespedeza capitata*
Greyheaded Coneflower	*Ratibida pinnata*
Canada Tick Trefoil	*Desmodium canadensis*
Tickseed Sunflower	*Bidens aristosa*
Illinois Bundleflower	*Desmanthus illinoensis*
Wild Blue Lupine	*Lupinus perennis*

Table A.2 Mean individuals/10 ha surveyed by species across all treatments by season in Clay Co., Mississippi, USA (2011–2013).

				Treatment Type											
				NWSG-Multiple			NWSG-Single			Switchgrass-Multiple			Switchgrass-Single		
Species Name	Scientific Name	RH[a]	PIF[b]	2011	2012	2013	2011	2012	2013	2011	2012	2013	2011	2012	2013
Late Winter															
American Bittern	*Botaurus lentiginosus*			0	0	1.33	0	0	0	0	0	0	0	0	0
American Pipit	*Anthus rubescens*			1.36	0	0	0	0	0	0	0	0	0	0	0
Eastern Meadowlark	*Sturnella magna*	≤	3	0	1.33	0	11.23	0	4.00	0	0	0	0	8.89	0
Field Sparrow	*Spizella pusilla*			0	0	0	7.18	0	0	0	0	0	0	0	0
Grasshopper Sparrow	*Ammodramus savannarum*			1.36	0	0	2.87	0	0	1.78	0	0	0	0	0
Le Conte's Sparrow	*Ammodramus leconteii*	7	3	2.71	45.33	74.67	0	13.33	17.33	1.78	12.89	37.33	0	129.78	7.11
Lincoln's Sparrow	*Melospiza lincolnii*			0	0	0	2.87	0	0	0	0	0	0	0	0
Northern Cardinal	*Cardinalis cardinalis*			0	0	0	4.22	0	0	0	0	0	0	0	0
Northern Harrier	*Circus cyaneus*			0	1.33	1.33	0	1.33	1.33	0	1.78	0	0	0	0
Red-winged Blackbird	*Agelaius phoeniceus*			0	0	0	0	0	0	0	0	26.67	0	0	0
Savannah Sparrow	*Passerculus sandwichensis*	7	1	90.85	274.67	56.00	414.36	144.00	45.33	481.78	487.11	11.33	752.00	282.67	72.89
Sedge Wren	*Cistothorus platensis*			0	1.33	0	0	2.67	0	0	1.78	0	0	0	1.78
Song Sparrow	*Melospiza melodia*	7	1	4.68	1.33	0	2.87	16.00	1.33	0	0	0	0	0	3.56
Swamp Sparrow	*Melospiza georgiana*	7	1	0	97.33	12.00	0	84.00	13.33	0	4.89	13.11	1.78	83.56	126.22
Unknown Sparrow	*Emberizidae*			2.71	9.33	1.33	2.87	28.00	2.67	0	1.78	1.78	0	5.33	5.33
Unknown species (songbird-sized)	*Passeriforimes*			0	0	1.33	0	0	1.33	0	0	0	0	3.56	0
Vesper Sparrow	*Pooecetes gramineus*			0	0	0	26.67	0	0	0	0	0	0	0	0
White-throated Sparrow	*Zonotrichia albicollis*			0	0	0	1.44	0	0	0	0	0	0	0	0
Wilson's Snipe	*Gallinago delicata*			0	0	0	1.44	0	0	0	0	0	0	0	0
Spring Migration															
American Bittern	*Botaurus lentiginosus*			-	0.26	0	0	0	0	0	0	0	0	0	0

Table A.2 (Continued)

Chipping Sparrow	*Spizella passerina*			-	1.38	0	0	0.27	0	0	0	0	0	0	0
Eastern Meadowlark	*Sturnella magna*	8	3	-	0.26	1.23	0	0.27	3.60	0	3.57	0.53	0	1.64	0
Field Sparrow	*Spizella pusilla*			-	0	0	0	0	0.18	0	0	0	0	0	0
Le Conte's Sparrow	*Ammodramus leconteii*	7	3	-	1.84	1.37	0	0.27	0.54	0	3.98	1.59	0	4.99	0
Mourning Dove	*Zenaida macroura*			-	0	0	0	0	0	0	0	0	0	0	0.55
Northern Harrier	*Circus cyaneus*	8	3	-	0.52	0.69	0	0	0.90	0	0	0	0	0.82	0.27
Red-tailed Hawk	*Buteo jamaicensis*			-	0	0.17	0	0	0	0	0	0	0	0	0
Red-winged Blackbird	*Agelaius phoeniceus*			-	0.26	0	0	0.90	0.18	0	1.19	0	0	0	0
Savannah Sparrow	*Passerculus sandwichensis*	7	1	-	23.45	8.42	0	22.68	11.52	0	3.58	11.12	0	14.76	3.69
Sedge Wren	*Cistothorus platensis*			-	0.77	0	0	0.90	0.18	0	0	0	0	0	0
Song Sparrow	*Melospiza melodia*			-	0.52	0.17	0	0	0.18	0	0	0	0	0	0
Swamp Sparrow	*Melospiza georgiana*	7	1	-	13.14	0.69	0	8.37	0.54	0	0.79	2.12	0	0.50	7.38
Unknown Sparrow	*Emberizidae*	7	1	-	4.12	0.17		2.97	0.36		3.18	0.79		3.28	0.82
Wilson's Snipe	*Gallinago delicata*	1	1	-	0	0.69	0	0	0.54	0	0	0	0	2.46	0.27
Summer															
Barn Swallow	*Hirundo rustica*	3	1	0.28	0	0.38	0	0.56	0.19	0	0	0	0.27	0.56	0
Blue Grosbeak	*Passerina caerulea*			0.28	0	0	0	0.56	0	0	0	0	0	0	0
Bobolink	*Dolichonyx oryzivorus*			0	0	0	1.13	0	0	0	0	0	0	0	0
Brown-headed Cowbird	*Molothrus ater*			0	0	0	0	0.19	0	0.55	0	0	0.52	0.56	0
Cedar Waxwing	*Bombycilla cedrorum*			0	0	0	9.38	0	0	0	0	0	0	0	0
Cliff Swallow	*Petrochelidon pyrrhonota*			0	0	0	0	1.13	0	0	0	0	0.27	0.25	0
Common Yellowthroat	*Geothlypis trichas*			0	0	0	0	0.19	0	0	0	0.26	0	0.25	1.26
Dickcissel	*Spiza americana*	1	1	18.77	10.61	8.15	14.25	11.63	10.69	0	0.78	1.30	1.56	1.52	0.76
Eastern Meadowlark	*Sturnella magna*	8	3	3.12	3.50	2.46	3.38	1.52	0.76	3.86	1.38	1.56	4.69	1.12	0
Eastern Towhee	*Pipilo erythrophthalmus*			0.28	0	0	0	0	0	0	0	0	0	0.56	0
Field Sparrow	*Spizella pusilla*			0.62	0.19	0	1.13	0.19	0	0	0	0	0	0	0
Grasshopper Sparrow	*Ammodramus savannarum*			0	0	0	0	0	0	0	0	0	0.78	0	0

Table A.2 (Continued)

Great Crested Flycatcher	*Myiarchus crinitus*			0	0	0	0	0	0	0	0	0.26	0	0	0
Indigo Bunting	*Passerina cyanea*	1	1	0.28	0	0	0.76	0	0.56	0.28	0.52	0	0	0.76	0
Killdeer	*Charadrius vociferus*			0	0	0	0.19	0	0	0	0	0	0	0	0
Mourning Dove	*Zenaida macroura*			1.88	0	0	0.56	0	0.19	0	0	0	0.27	0	0
Northern Bobwhite	*Colinus virginianus*			0.83	0.19	0	0	0	0	0	0	0	0	1.12	0
Northern Cardinal	*Cardinalis cardinalis*			0	0	0	0	0.38	0	0.55	0	0	0	0.25	0
Orchard Oriole	*Icterus spurius*			0	0	0	0	0.19	0	0	0	0	0	0	0
Red-bellied Woodpecker	*Melanerpes carolinus*			0	0	0	0.19	0	0	0	0	0	0	0	0
Red-winged Blackbird	*Agelaius phoeniceus*	1	1	2.29	1.89	3.60	6.38	2.63	3.56	0.28	0.52	1.30	0.78	0.25	1.12
Ruby-throated Hummingbird	*Archilochus colubris*			0	0	0.38	0	0	0	0	0	0	0	0	0
Savannah Sparrow	*Passerculus sandwichensis*			0.28	0	0	0.19	0	0	0	0	0	0.52	0	0
White-eyed vireo	*Vireo griseus*			0	0	0	0	0	0	0	0.52	0	0	0	0
Yellow-billed Cuckoo	*Coccyzus americanus*			0.28	0	0	0.19	0.19	0	0	0	0	0	0.25	0
Yellow-breasted Chat	*Icteria virens*			0	0	0	0.38	0.19	0	0	0.26	0	0	0.56	0
Fall Migration															
American Crow	*Corvus brachyrhynchos*			0	0	0	0	0.18	0	0	0	0	0	0	0
Barn Swallow	*Hirundo rustica*	3	1	0	0.52	1.23	0	0.90	1.98	0	0.26	0.26	0	1.94	0.55
Blue Grosbeak	*Passerina caerulea*			0	0	0	0	0	0	0	0	0	0	0	0.82
Brown-headed Cowbird	*Molothrus ater*			0	0	0	0	0	0	0	0	0	0	0.27	0
Carolina Wren	*Thryothorus ludovicianus*			0	0	0	0	0	0	0.26	0	0	0.27	0	0
Cliff Swallow	*Petrochelidon pyrrhonota*	2	1	0.34	4.64	1.89	4.68	4.50	0	2.12	4.24	0.26	0.82	1.38	4.37
Common Yellowthroat	*Geothlypis trichas*	1	1	4.98	0.52	0.69	5.58	0.36	0.36	0.53	0.53	0.53	0.82	0.55	2.46
Cooper's Hawk	*Accipiter cooperii*			0	0	0	0	0	0	0	0	0	0	0	0.27
Dickcissel	*Spiza americana*	1	1	1.72	0.17	0.86	1.44	0.90	3.60	0	0	0.26	2.46	0.27	0.27
Eastern Meadowlark	*Sturnella magna*	8	3	0.34	0	2.45	0.18	1.26	0.36	1.59	0.79	0.53	2.19	0	0
Grasshopper Sparrow	*Ammodramus savannarum*			0	0	0	0	0	0	0.26	0	0	0	0	0
Great Blue Heron	*Ardea herodias*			0.17	0	0	0	0	0	0	0	0	0	0	0

Table A.2 (Continued)

Indigo Bunting	*Passerina cyanea*			1.23	0	0	0.36	0	0	0	0	0	0	0	0
Le Conte's Sparrow	*Ammodramus leconteii*			0	0	0	0	0	0	0	0	0	0.27	0	0
Lincoln's Sparrow	*Melospiza lincolnii*			0	0	0	0	0	0	0	0	0	0.82	0	0
Northern Harrier	*Circus cyaneus*			0	0	0.17	0.18	0	0	0	0	0	0	0	0
Red-winged Blackbird	*Agelaius phoeniceus*			0	0	0	0	0	3.78	0	0	0	0	0	0.55
Ruby-throated Hummingbird	*Archilochus colubris*			0	0.17	0	0.18	0	0	0	0	0	0	0	0
Savannah Sparrow	*Passerculus sandwichensis*	7	1	3.95	1.37	1.37	5.40	1.98	0.72	16.15	1.85	1.32	1.38	9.18	2.46
Sedge Wren	*Cistothorus platensis*	7	1	0	0	2.45	0	0.18	1.44	0	0.26	1.59	0	0.27	0.82
Song Sparrow	*Melospiza melodia*	7	1	0.34	0	0.17	1.80	0	0	1.59	0	0	1.64	0	0
Sora	*Porzana carolina*			0.17	0.17	0	0	0	0	0.26	0.53	0	0.27	0	0.27
Swamp Sparrow	*Melospiza georgiana*	7	1	6.36	0	0	2.52	0	0.72	7.15	0	0.53	6.12	0	2.73
Unknown Sparrow	*Emberizidae*	7	1	8.25	0.86	1.37	5.40	0.18	5.22	4.24	0.26	0.53	1.66	0.27	6.29
Unknown species (songbird-sized)	*Passeriforimes*			0	0.34	0	0	0.36	0	0	0.53	0	0	0.27	0
Unknown swallow	*Hirudinidae*			0	0.69	0	0	0.54	0	0	0	0	0	1.37	0
Unknown Warbler	*Parulidae*	7	1	0.69	0.52	0.17	0.90	1.44	0	0	0	0	0	1.91	0
Winter Wren	*Troglodytes hiemalis*			0.17	0	0	0	0	0	0	0	0	0.27	0	0
Early Winter															
American Bittern	*Botaurus lentiginosus*			0	0	0	0	0	0	0	0	0	0.50	0	0
American Crow	*Corvus brachyrhynchos*			0	0	0	0	0.90	0	0	0	0	0	0	0
Black Vulture	*Coragyps atratus*			0	0	0	0.27	0	0	0	0	0	0	0	0
Chipping Sparrow	*Spizella passerina*			0	0	0	0.27	0	0	0	0	0	0	0	0
Cooper's Hawk	*Accipiter cooperii*			0	0	0.17	0.27	0	0	0	0	0	0	0	0
Eastern Meadowlark	*Sturnella magna*	8	3	0.26	0.52	0.86	0	0	2.52	0.40	3.18	0.26	9.84	0	0.27
Lark Sparrow	*Chondestes grammacus*			0	0	0	0.27	0	0	0	0	0	0	0	0
Le Conte's Sparrow	*Ammodramus leconteii*	7	3	11.34	2.58	0	2.16	1.98	0	21.46	5.30	0	2.86	2.73	0
Northern Bobwhite	*Colinus virginianus*			0	0	0	0.54	0	0	0	0	0	0	0	0
Northern Harrier	*Circus cyaneus*	8	3	1.84	1.23	0.86	0.54	1.44	0.54	1.99	1.32	0.53	0.50	1.64	0.27

Table A.2 (Continued)

Red-tailed Hawk	*Buteo jamaicensis*			0	0	0	0.27	0	0	0	0	0	0	0.27	0.27
Red-winged Blackbird	*Agelaius phoeniceus*			0	0	0	0.27	0	0	0	0	0	0	0	0
Savannah Sparrow	*Passerculus sandwichensis*	7	1	49.73	8.76	26.80	41.39	9.72	8.28	96.95	21.97	15.35	112.73	12.24	12.58
Sedge Wren	*Cistothorus platensis*	6	1	0.77	0.17	0.86	1.35	0.18	0.72	0	0	0.26	0	0.27	0.27
Song Sparrow	*Melospiza melodia*	7	1	8.25	0.17	0.34	25.92	0.18	0	5.56	0.26	0	6.97	1.91	0
Swamp Sparrow	*Melospiza georgiana*	7	1	11.34	0.86	4.29	11.70	1.80	3.60	11.12	1.32	5.56	2.46	7.65	8.20
Turkey Vulture	*Cathartes aura*			0	0	0	0.27	0	0	0	0	0	0	0	0
Unknown Sparrow	*Emberizidae*	7	1	4.64	7.93	1.72	7.56	6.12	1.80	9.13	11.91	1.85	17.63	14.21	0.55
Unknown species (songbird-sized)	*Passeriforimes*			0.26	0	0	0	0	0	0	0	0	0	0.27	0
Wilson's Snipe	*Gallinago delicata*			0	0.17	0	0	0	0	0	0	0	0	0.27	0

[a] Relative Hazard Score obtained from DeVault et al. 2011; [b] Conservation Rank based off of Partners in Flight (PIF) Scores

APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Table B.1 Mean (± SE) Territory metrics for all focal Dickcissel territories in in Clay Co., Mississippi, 2011–2013.

Year	Number of Territories	Area (ha)	Robel (cm)	Orthoptera Biomass (g)	Number of Counter-singing Males	Maximum Number of Females	First Week	Mean Daily High Temperature (˚C)
2011	34	2.06 ± 0.16	30.31 ± 1.51	0.049 ± 0.006	1.42 ± 0.07	1.76 ± 0.11	3.06 ± 0.22	32.30 ± 4.70
2012	36	1.43 ±0.10	23.35 ± 1.36	0.090 ± 0.009	2.28 ± 0.13	1.72 ± 0.09	2.39 ± 0.13	31.81 ± 3.58
2013	31	1.95 ± 0.19	37.30 ± 2.11	0.034 ± 0.003	2.72 ± 0.11	1.55 ± 0.09	3.52 ± 0.26	29.61 ± 3.93

[a] First week male established territory, with Week 1 corresponding ~24 April (start of territory monitoring) each year.

Table B.2 Nest metrics (± SE) for all nests from focal Dickcissel territories in Clay Co., Mississippi, 2011–2013.

		Age Found (Days)	Nest Visible Height	Distance to Edge (m)
Year	# of Nests	Mean	Mean	Mean
2011	57	8.37 ± 0.77	-15.35 ± 3.14	39 87 ± 3.34
2012	39	7.41 ± 1.04	-11.03 ± 1.41	40.84 ± 4.06
2013	38	4.21 ± 0.97	-13.89 ± 6.44	36.89 ± 4.01

APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table C.1 Plot vegetation visual obstruction (VOR), species diversity (H') and territory metrics for Dickcissel (*Spiza americana*) territories in Clay Co., Mississippi, 2011–2013.

					Territory				
	VOR		Diversity (H’)		# of Territories	First Week		Territory Area (95% KDE)	
Year	Mean	SE	Mean	SE		Mean	SE	Mean	SE
NWSG (multiple harvest)	26.19 A	0.79	1.40 A	0.04	77	3.14 A	0.01	1.82 A	0.01
NWSG (single harvest)	27.78 A	1.38	1.32 A	0.04	99	3.67 A	0.02	1.63 A	0.01
Switchgrass (multiple harvest)	47.44 B	3.56	0.60 B	0.05	-	-	-	-	-
Switchgrass (single harvest)	63.31 C	3.44	0.51 B	0.05	-	-	-	-	-

[a] Treatments within a covariate sharing the same letter (e.g. “A”) were not significantly different (Tukey’s HSD: p-value ≤ 0.05).[b] First week male established territory, with Week 1 corresponding ~24 April (start of territory monitoring) each year.

Table C.2 Nest metrics for Dickcissel (*Spiza americana*) nests in Clay Co., Mississippi, 2011–2013.

		Nest					
		Age Found (Days)		Nest Visible Height (cm)		Distance to Edge (m)	
Year	# of Nests	Mean	SE	Mean	SE	Mean	SE
NWSG (multiple harvest)	91	2.86 A[a]	0.63	-18.36 A	2.39	44.30 A	2.47
NWSG (single harvest)	131	4.37 A	0.51	-15.56 A	2.45	33.06 AB	1.85
Switchgrass (multiple harvest)	3	7.33 A	5.93	-35.25 A	34.13	39.06 AB	12.75
Switchgrass (single harvest)	4	6.75 A	2.10	-0.38 A	2.63	49.33 A	18.75

[a] Treatments within a covariate sharing the same letter (e.g. "A") were not significantly different (Tukey's HSD: *P*-value ≤ 0.05).

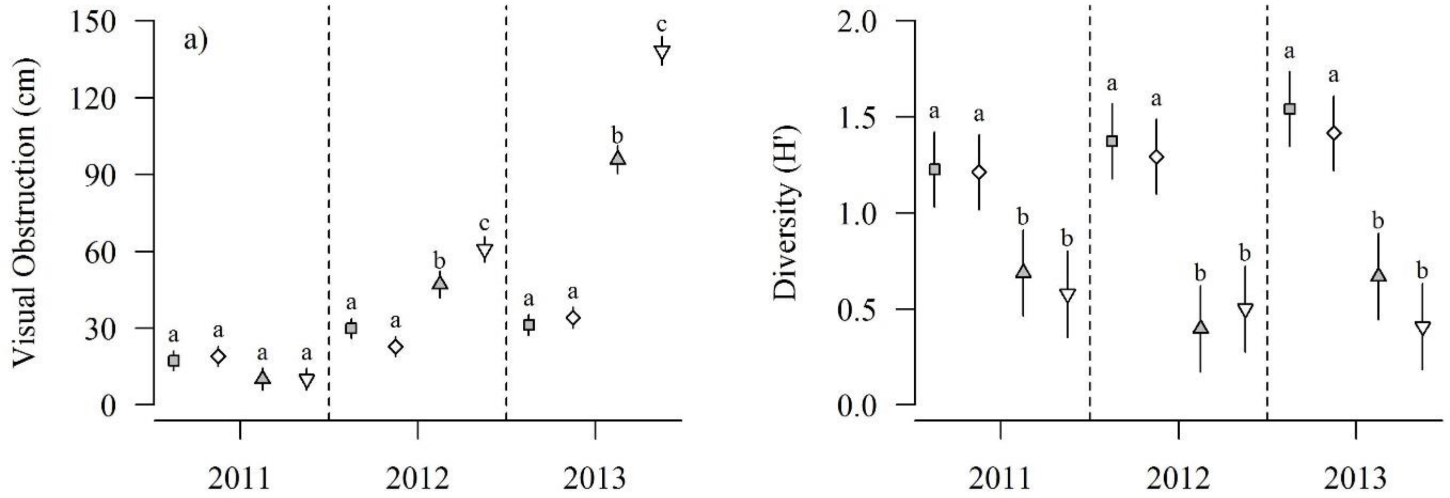

Figure C.1 Model coefficients and 95% confidence limits for parameters in the best-fit models for a) vegetation visual obstruction and b) vegetation species diversity (H’) in NWSG multiple harvest (□), NWSG single harvest (◇), Switchgrass multiple harvest (△), and switchgrass single harvest (▽) treatment types in in Clay Co., Mississippi, 2011–2013.