Effects of conservation practices on bird nest density and survival in intensive agriculture

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ABSTRACT

Nest density and survival of two farmland birds (dickcissel, *Spiza americana* and red-winged blackbird, *Agelaius phoeniceus*) were evaluated in four early-succession conservation practices: (1) large forest block [6–8 year old trees], (2) riparian forest buffer [1–3 year old trees], (3) monotypic switchgrass [*Panicum virgatum*] buffer [no trees], and (4) diverse forb-native grass buffer [no trees] over three years (2005–2007). We modeled daily survival of dickcissel ($n = 733$) and red-winged blackbird ($n = 414$) nests as a function of nest-site, patch, and landscape covariates. Dickcissels nested in greater densities (3.5 times) in large blocks than any buffers, and of non-wooded buffers, they preferred those with diverse vegetation. Dickcissels largely nested in buffers only early in the season. Dickcissel nest success was 22.9% on average and was similar among conservation practices except riparian forest buffers, in which they apparently suffered from high densities of red imported fire ants (*Solenopsis invicta*) and low vegetative cover. Dickcissel nest success related positively to nest height, but negatively to grass cover, horizontal vegetation density, and proximity (<30 m) to row-crop fields. Red-winged blackbirds had low overall nest success (8.6%) across conservation practices, though substantially higher for nests in diverse forb-native grass buffers (23.4%).

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1. Introduction

Global declines of grassland bird populations are largely associated with agricultural expansion and intensification (Teyssèdre and Couvet, 2007). Conservation programs administered by the United States Department of Agriculture (USDA) under farm bill legislation provide economic incentives to create habitat through various set-aside programs, such as the Conservation Reserve Program (CRP). The CRP is a US agri-environmental scheme that provides economic incentives (signup bonus payments, cost-share, and annual rental payments based on county-specific soil rental rates) for producers to take environmentally sensitive land out of production and establish a resource conserving cover which is maintained for a 10–15 year contract period. First introduced in the Food Security Act of 1985 (P.L. 99-198) for soil conservation and commodity control, statutory objectives of the CRP have evolved in subsequent farm bills to target specific resource concerns including water quality and wildlife habitat.

Allocation of land to wildlife habitat entails opportunity costs associated with commodities that would have otherwise been produced, creating an asymmetry in private costs incurred by agricultural producers to provide a public benefit (wildlife populations). Hence, the incompatibility of whole-field practices with agronomic production goals may constrain the size, shape and landscape context of conservation practices. Birds in small, linear patches may be more vulnerable to negative edge or area effects (Gates and Gysel, 1978; Vickery et al., 1994; Winter and Faaborg, 1999). Grassland birds may experience lower nest survival in smaller patches from increased nest predation (Johnson and Temple, 1990). Patch-level effects are complex and can be constrained by features of the larger landscape context (e.g., land-cover composition; Chalfoun et al., 2002; Thompson, 2007; Ribic et al., 2009); hence, understanding bird response to patch design in concert with landscape context is crucial.

Conservation buffers (i.e., strips of non-crop vegetation on the field margin) attract high bird densities and can provide significant avian benefits in intensive agricultural landscapes (Camp and Best, 1994; Conover, 2005; Conover et al., 2009). However, most buffer studies have been limited to game species, avian community structure, or a single conservation practice (Smith et al., 2005; Conover et al., 2009). Furthermore, nearly all of our understanding of bird responses to common buffer practices in Mississippi (ripar-

ian forest buffers (RFB) and filter strips) come from the Midwest US, not the Southeast (Clark and Reeder, 2007; Best, 2000; but see Maul et al., 2005; Smiley et al., 2007). Hence, conservationists lack insight on the relative demographic consequences between conservation buffers and large blocks for birds in agricultural landscapes (Fletcher et al., 2006).

On a local scale, the visual concealment of a nest and its surrounding vegetation complexity can influence nest survival (Chalfoun and Martin, 2009). For example, dickcissel (*Spiza americana*) nest survival has been correlated with dead and live cover, vegetation height, grass cover, and ground cover (Hughes et al., 1999; Winter, 1999). Other nest-site characteristics may influence survival; for example, both dickcissel and red-winged blackbird (*Agelaius phoeniceus*) have shown increased survival in nests higher off the ground (Harmeson, 1974; Dinsmore and Dinsmore, 2007). Spatial processes (e.g., habitat fragmentation, land-cover composition) can also strongly influence nest survival and, in some landscapes, may supersede local-scale effects (Donovan et al., 1997; Thompson, 2007). Furthermore, landscape features can influence habitat use by nest predators in agricultural landscapes (Chalfoun et al., 2002).

Dickcissel and red-winged blackbird nest density and success were evaluated at fine (30 m) and coarse (400 m) spatial scales in four (three buffers and one large block) early-succession conservation practices amid intensive, row-crop agriculture. Both species have previously exhibited population sinks in CRP fields and extant remaining grasslands (McCoy et al., 1999; With et al., 2008) and hence, their reproductive performance may provide insight on whether or not these conservation practices can augment the overall avian benefits provided by the CRP. Based on current understanding of bird ecology in agricultural landscapes, we hypothesized that (1) nest density will be greater in the larger, block patches, (2) nest survival will positively correlate with patch area, vegetative cover, and structural complexity, and (3) nest survival will inversely correlate with distance to an abrupt edge.

2. Methods

This study took place over three years (2005–2007) on a 2630 ha farm located in Coahoma County, Mississippi, USA (34°18′N, 90°34′W), which is in the Mississippi Alluvial Valley (MAV); Bird Conservation Region 26. In 2007, average farm size in Coahoma County was 469.4 ha (USDA, 2009) and mean cropland field size in a 7800 ha region surrounding the farm was 16.8 ha (SD 23.1 ha, range 1–220.5 ha). This farm exemplifies the current MAV landscape, which is dominated by large fields of ditch-to-ditch, row-crop agriculture of primarily cotton (*Gossypium* sp.), corn (*Zea* sp.) and soybean (*Glycine* sp.) that are dissected by a network of drainage ditches, streams, wood lines, and fencerows, with negligible topographic relief. However, the farm differed from the surrounding landscape (83% row-crop) in that it recently established many seminatural vegetation patches to promote wildlife-friendly farming. Land cover types on the study farm included 48% row-crop, 30% early-succession hardwood (still primarily herbaceous), 14% partially forested wetlands, 4% herbaceous conservation buffers, 2% late-succession forest, and 2% herbaceous drainage strips. Soybean was the only farm crop in 2005 and 2007, whereas in 2006 soybeans were double-cropped following a winter wheat (*Triticum* sp.) harvest in May–early June. All row-crop fields on the farm were managed with conventional tillage regimes. Soil associations on the farm were predominantly heavy clays that included sharkey clay (41%), dowling clay (15%), and tunica silty clay (11%) (Soil Survey Staff, 2008).

Four early succession, conservation practices with varying vegetative structure and patch shapes were evaluated to determine bird
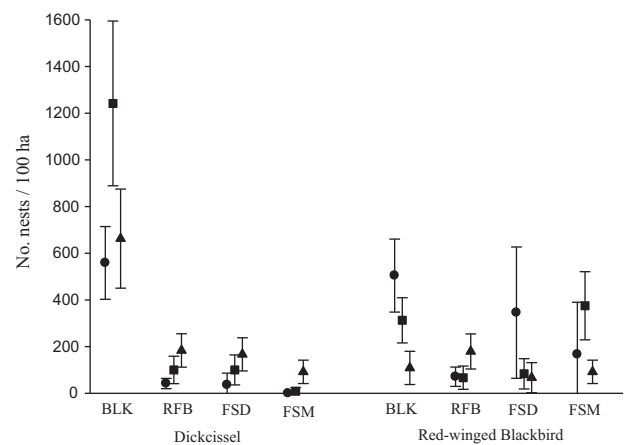
Fig. 1. Relative nest densities (mean ± 95% CI) for dickcissel and red-winged blackbird in early-succession, afforestation blocks (BLK), early-succession, riparian forest buffers (RFB), diverse filter strips (FSD), and monotypic filter strips (FSM) during breeding seasons of 2005 (●), 2006 (■), and 2007 (▲) on an agricultural farm in the Mississippi Alluvial Valley, Mississippi.

nesting activity. Conservation practices included (1) diverse filter strips (FSD) planted with a forb-native warm-season grass mixture, (2) monotypic filter strips (FSM) planted with only switchgrass (*Panicum virgatum*), (3) early-succession, riparian forest buffers (RFB), and (4) early-succession, hardwood afforestation blocks (BLK). Filter strips and RFBs were planted in 2004, established on row-crop field margins adjacent to aquatic features and in similar landscape contexts, and were 30 m and 60 m wide, respectively. At the onset of the study, perennial grass/forb communities were well established in filter strip practices. Hardwood seedlings that were planted in RFBs had not yet emerged above the early-succession herbaceous community and thus, RFBs were dominated by grasses and forbs. BLKs were planted in 1999 and had enhanced woody growth compared to RFBs, but were still primarily herbaceous with scattered shrubs and saplings. All study plots were invaded by local, non-planted vegetation (Conover, 2009). Twenty study plots were selected at random from a pre-determined, farm-wide population of all four conservation practices. Study plot sizes were 200 m × 60 m for BLK and RFB and 200 m × 30 m for filter strips. Sample sizes were less for FSD (*n* = 14) and FSM (*n* = 6) in 2005, the first year of the study. No management beyond establishment had yet occurred on any plots (Fig. 1).

2.1. Nest searching and monitoring

Intensive nest searches were conducted from 15 May to 20 July, 2005–2007. Two to four people searched for nests by systematically walking through each study plot (one person per 2 m wide section) and mildly disturbing the vegetation with 1 m sticks. Hence, every area of each treatment was searched for an equal amount of time during systematic searches. Search protocol changed for FSM in 2007 to a rope-drag technique because the vegetation was too thick and tall to search from within the buffer. The rope was 30 m long and had clusters of three aluminum cans attached every 1 m. However, this remains comparable as the switchgrass in FSM was so thick in all years that nest discovery only occurred by observing flushing birds regardless of search technique (Winter et al., 2003). Nest locations were georeferenced using a Global Positioning System (GeoExplorer II; Trimble Navigation, Sunnyvale, California).

Nests were monitored every 2–4 days, primarily in the afternoon after dew had evaporated to minimize scent trails, with care taken to minimize trampling of vegetation or creating dead-end

trails that may cue nest predators. Nest monitoring data included nest stage (laying, incubation, and nestling), clutch/brood size, nest age (in days), parent behavior, and nest fate. We estimated age during incubation using egg-candling techniques and during the nestling stage using species-specific voucher images (R.R. Conover, unpubl. data). Egg-candling procedures included a 9 cm long piece of 3/4 cm foam pipe insulation, which was directed towards the sun to observe the extent of embryo development through the eggshell (Lokemoen and Koford, 1996). Failed nests were classified as depredated, abandoned, weather-caused, human-caused, or unknown. Nest fate determinations incorporated nest condition (i.e., disturbance), nest-site clues (e.g., feces, feathers, eggshells, etc.), parent behavior (e.g., alarm calls or food carrying), fledgling presence, and nestling age at previous visit. Nests were considered successful at the incubation and nestling stages if ≥1 egg hatched or nestling fledged, respectively. Nest visitation occurred on or after the expected fledging date to increase the accuracy of nest fate determination. We report minimum relative nest density as the number of nests detected per 100 ha. Nest density was compared between buffers adjacent to wooded and non-wooded vegetation to evaluate the effect of nearby mature wooded habitat on nest distributions. These estimates assume all active nests had equal detectability across habitats. This is justified for BLK, RFB, and FSD, which had similar vegetation density, but the high density of switchgrass in FSM may induce some negative bias (Conover, 2009).

2.2. Nest-site characteristics

We measured the surrounding vegetation, including nest height (Harmeson, 1974), nest concealment, vertical and horizontal cover, and live/dead vegetation structure (Hughes et al., 1999; Winter, 1999). Nest height is the distance from the ground to the nest bowl rim, and nest concealment is the percentage of total cover (live or dead) directly above the nest bowl. Nest-site vegetation was quantified in an 8 m diameter, circular plot centered on the nest. Vegetation measurements included vertical cover (visual obstruction reading, VOR), horizontal vegetation density, vegetation structure (percentage of live cover types), and percentage of standing dead vegetation cover. VOR indicated effective vegetation height (where visibility was obstructed by vegetation), which was recorded to the nearest centimeter using a modified-Robel pole placed at the nest site, with the metric calculated as the average of four measurements (one at each cardinal direction) taken at a 4 m distance and 1 m height (Robel et al., 1970; Renken and Dinsmore, 1987). Horizontal density represents the average percentage of total vegetative cover from each of four quadrants within the 8 m diameter circular plot and was visually estimated after walking through each quadrant. Live cover percentages are a subset of horizontal density, and are visually estimated proportions of total live cover that include forb, grass (i.e., grass-like structures), and woody substrates; whereas standing dead vegetation is an independent estimate of the proportion of total dead cover. Nest-site vegetation was evaluated 25 days (±5 days) after nest initiation to standardize potential bias from vegetative growth. Additionally, red imported fire ants (*Solenopsis invicta*; hereafter, fire ant) were surveyed simultaneously with vegetation as they are an invasive predator that can exert significant influence on bird nest survival (Campomizzi et al., 2009). The density (mounds/ha) of fire ant mounds was estimated within 10 m and mound activity was determined by probing the mound surface and observing whether or not fire ants subsequently emerged. Inactive mounds were not recorded. In 2007, we conducted random vegetation and fire ant surveys during the peak of nest initiation (mid–late June) to compare with nest-site vegetation measurements.

2.3. Landscape variables

Landscape context can influence nest success, thus surrounding land cover was characterized at multiple scales (Donovan et al., 1997). Land-cover classes used to define landscape composition included: row-crop, herbaceous, woody (early-, mid-, and late-succession), and developed (i.e., roads and homesteads) classes. Nest locations were georeferenced using a Trimble Geoexplorer III. Nest locations were differentially corrected using local (<100 km) base station data in Trimble Pathfinder Office ©(version 2.90), and exported into ArcGIS ©(version 9.3, ESRI, Redlands, CA). Nest locations were spatially referenced using the North American Datum 1983 and Universal Transverse Mercator Zone 15N coordinate system. The distance of nests from wooded and nearest edges was calculated using the point distance function in ET GeoWizards 9.8 in ArcMAP ©. Wooded edge classifications included mid-late succession (≥15 years old) woody patches and the nearest edge as any land-cover discontinuity. Three years (2005–2007) of digital imagery from the National Agriculture Imagery Program and updated information on USDA-Farm Services Agency conservation practice enrollment provided data to permit accurate land-cover digitization. We used ArcINFO to buffer and clip spatially explicit, land-cover information from Geographic Information System (GIS) vector data at fine (30 m) and coarse (400 m) landscape scales surrounding each nest. Fine scale buffer distance was determined based on the approximate radius of dickcissel and red-winged blackbird breeding territories (Yasukawa and Searcy, 1995; Temple, 2002). The landscape scale's buffer radius was 400 m, as this distance is correlated with predation risk for an open-cup songbird nest relative to landscape-level characteristics (Kus et al., 2008). Land-cover composition, total patch area, and total edge were calculated using FRAGSTATS (McGarigal et al., 2002). Total edge denotes the degree of spatial heterogeneity (i.e., fragmentation) in the landscape, with more edge indicating greater habitat fragmentation (McGarigal et al., 2002).

2.4. Nest survival analyses

Nest survival (i.e., daily nest survival probability) models applied maximum likelihood estimation and a logit link function in Program MARK (White and Burnham, 1999; Dinsmore et al., 2002). Nest survival data were modeled from 13 May to 16 August (96 days) for dickcissel and 10 May to 12 August (95 days) for red-winged blackbird across the three study years combined. Modeling procedures and covariates were identical for both species. We modeled effects of year, nest stage (egg-laying, incubation, and nestling), and patch treatment (BLK, RFB, FSD, and FSM) in MARK as groups. A set of *a priori* candidate models were constructed from combinations of biologically important variables that included nest-site vegetation structure, nest height, overhead concealment, clutch size, and fine and coarse scale spatial characteristics. Vegetation data for late-season nests was imputed using means from comparable nests (same species, year, and vegetation treatment). Imputed values for dickcissel included nest concealment ($n = 24$ total nests; 3% of total nests), nest height ($n = 4$; <1%), and nest vegetation ($n = 42$; 6%). Imputed values for red-winged blackbird included nest concealment ($n = 13$; 3%), nest height ($n = 2$; <1%), and nest vegetation ($n = 8$; 2%).

Hierarchical modeling was performed to account for spatial and temporal variation in nest survival while maintaining a relatively small model set that minimizes the risk of over-fitting the data (Burnham and Anderson, 2002). We constructed models in four hierarchical steps that included (1) additive and interactive effects from year, nest stage, and seasonal time trends (linear and quadratic), (2) patch types, (3) landscape variables (fine and coarse scales) and edge proximities, and (4) local vegetation and nest-site

characteristics, with daily precipitation added to the best model. Step one evaluated daily nest survival rate (DSR) as an interactive and additive function of year and nest stage, and seasonal variation within years as a constant (no time trend), logit-linear time trend, or logit-quadratic time trend. Information theory model selection was applied, with the adjusted Akaike Information Criterion (AIC_c) as the selection tool (Burnham and Anderson, 2002). In the above hierarchical procedure, the best and all competitive ($\Delta AIC_c \leq 2.0$) models were advanced to subsequent steps as reference models. Covariates were added singly to reference models within steps to test for independent effects; combined effects were subsequently evaluated for covariates that competed ($\Delta AIC_c \leq 2.0$) with reference models. We computed the ratio of differences in log-likelihood values as an estimate of the proportion of deviance explained by the best model relative to the global model (Dinsmore et al., 2003). This calculation compared the best model, the global model, and the constant (no covariates) model as an approximate measure of model fit. The constant model represents the Mayfield estimate with only one parameter (Mayfield, 1961), whereas the global model represents the full amount of variation accounted for by all variables, which included year, nest stage, and seasonal effects in addition to all biological covariates for red-winged blackbird. Species-specific seasonal nest survival patterns were analyzed by plotting time-specific nest survival against the most influential environmental variable and conservation practice. This was done using values from the incubation stage in 2007, which represented the middle stage and year values of nest survival, respectively.

Nest success (i.e., probability of surviving an entire nesting period) estimates were calculated from the best approximating models for each species to predict the influence of individual covariates and their combinations. These estimates were calculated based on the range of observed covariate values (Shaffer and Thompson, 2007). All nest success estimates were calculated from the start date of 01 June 2007, which was the peak of nest initiation. Nest success was calculated using empirically-based nesting periods for both species; dickcissel clutch size was 3.83 ± 0.62 and red-winged blackbird was 3.01 ± 0.76 (Conover, 2009). As both species begin incubation with the penultimate egg, dickcissel nesting period was 19 days (two days egg-laying, 10 days incubation, seven days nestling) and red-winged blackbird was 21 days (one day egg-laying, 11 days incubation, nine days nestling).

3. Results

We found and monitored 733 dickcissel nests ($n = 149$, 2005; $n = 340$, 2006; $n = 244$, 2007) and 414 red-winged blackbird nests ($n = 179$, 2005; $n = 147$, 2006; $n = 88$, 2007). Most notably, dickcissel nest densities were 3.6 times higher in BLKs than any conservation buffer in all years. Red-winged blackbird and dickcissel, respectively, both exhibited slightly higher nest densities in RFBs adjacent to non-wooded (nests/100 ha $\pm$ 95% CI; 103.17 ± 60.14, $n = 23$; 65.22 ± 32.40, $n = 23$) than wooded (64.81 ± 41.20, $n = 27$; 37.04 ± 34.14, $n = 27$) vegetation. Red-winged blackbirds exhibited a similar trend in filter strips (93.33 ± 35.21, $n = 75$; 86.67 ± 56.17, $n = 25$), but dickcissel nest densities unexpectedly exhibited the opposite pattern in filter strips (3.11 ± 13.07, $n = 75$; 63.33 ± 30.23, $n = 25$).

Seventy-eight percent of dickcissel nest activity in conservation buffers was initiated before 31 May, with only 5% initiated after 15 June. Dickcissel nest activity in large blocks was initiated more consistently throughout the breeding season (Fig. 2a). Red-winged blackbird nest initiation occurred primarily from 15 May to 15 June in buffer (54% of nests initiated) and large block (70% of nests initiated) treatments (Fig. 2b). Dickcissel continued to nest in large
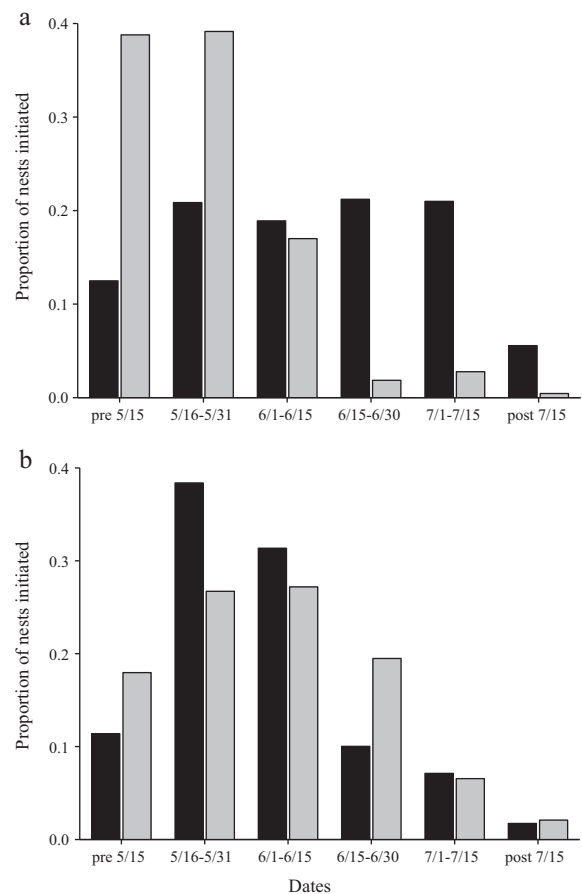
Fig. 2. Total proportions of nests initiated relative to nesting activity in early-succession block (■) and all conservation buffer (▢) practices for dickcissel (a) and red-winged blackbird (b) on an agricultural farm in the Mississippi Alluvial Valley, Mississippi, 2005–2007.

blocks later in the breeding season, whereas red-winged blackbird late-season nesting activity was mostly in buffers (Fig. 2).

Grass cover dominated both filter strip practices although FSD had moderate (26%) forb cover. Forbs were the dominant vegetation in RFB (74%), whereas BLK had relatively equal cover of grasses and forbs (Table S1). Woody cover was at least 20 times greater in BLK and RFB than filter strips, although woody substrates were taller in BLK from advanced maturation. Overhead nest concealment was consistently greater for dickcissel nests (range: 50.8% [FSD]–79.7% [FSM]) than red-winged blackbird nests (21.4% [FSD, FSM]–41.6% [RFB]). Red-winged blackbird nests were higher above ground (65.9 cm [RFB]–89.3 cm [FSM]) and had more dense vertical cover than dickcissels (Table S1).

3.1. Nest survival

Depredation was the leading cause of failure for dickcissel (87.2%) and red-winged blackbird (90.2%) nests. Dickcissel nest outcomes included depredation ($n = 387$), abandoned ($n = 45$), right censored (nest monitoring ended while some nests were still active; $n = 23$), failed from brown-headed cowbird (*Molothrus ater*) brood parasitism ($n = 7$), human-caused failure ($n = 3$), weather-caused failure ($n = 2$), and other failure ($n = 1$). Red-winged blackbird nest outcomes included depredation ($n = 323$), abandoned ($n = 30$), human-caused failure ($n = 3$), weather-caused failure ($n = 1$), and other failure ($n = 1$). Only 2.6% ($n = 17$) of dickcissel nests and 1.0% of red-winged blackbird nests ($n = 4$) were parasitized by cowbirds in all conservation practices across years.
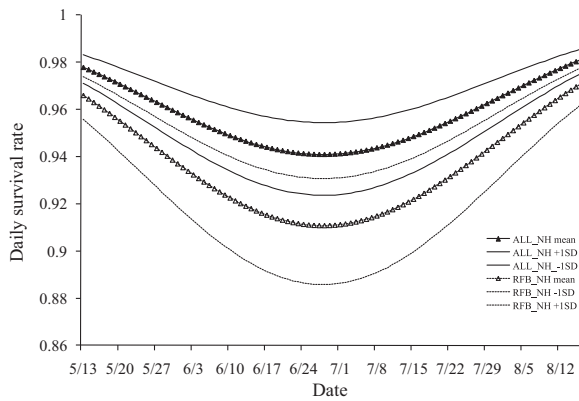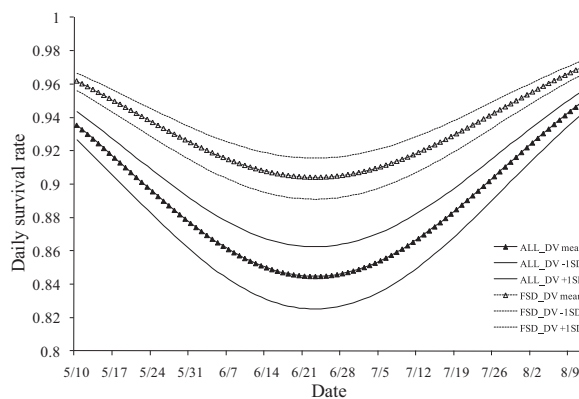
Fig. 3. Dickcissel daily nest survival estimates across the breeding season for all conservation practices combined (ALL; ▲) ±1 SD in nest height (NH; —) and for riparian forest buffers (RFB; △) ±1 SD in nest height (—) amid intensive agriculture in the Mississippi Alluvial Valley, Mississippi, 2005–2007.

Visually confirmed dickcissel nest predation events included fire ants (n = 19), speckled kingsnakes (*Lampropeltis getula holbrooki*, n = 3), and a nine-banded armadillo (*Dasypus novemcinctus*, n = 1). Confirmed red-winged blackbird nest depredation included fire ants (n = 9) and a southern black racer (*Coluber constrictor priapus*, n = 1).

Overall nest success, across all habitats and with average covariates, was 22.9% (95% CI = 10.8%, 36.4%) for dickcissel, and 8.6% (95% CI = 2.3%, 19.8%) for red-winged blackbirds. Nest survival was best explained for both species in model selection step one by the year and nest stage interaction and a quadratic seasonal time trend, which indicated higher nest survival early and late in the season, but lower during peak nest initiation from late-May to mid-June (Figs. 3 and 4). Dickcissel models were largely improved by RFB and BLK conservation practices in step two, by row-crop cover within 30 m in step three, and by horizontal vegetation density, % grass cover, and nest height in step four (Table S2). Red-winged blackbird nest survival models were best explained by FSD in model selection step two, non-significantly by many land-cover covariates in step three, and by dead vegetation cover and nest height in step four.

Dickcissel nest survival was lower for nests in RFB (β_{RFB} = −0.399, SE = 0.182, 95% CI = −0.756, −0.041), within 30 m of row-crop (β_{30Row} = −1.879, SE = 1.365, 95% CI = −4.554, 0.797), and with reduced horizontal vegetation density (β_{HD} = −0.005, SE = 0.002, 95% CI = −0.010, −0.001), and grass cover (β_{Grass} = −0.004, SE = 0.002, 95% CI = −0.007, −0.0003), but

positively related to nest height (β_{NH} = 0.007, SE = 0.002, 95% CI = 0.003, 0.012). The best model for dickcissel explained 15.2% of the proportion of deviance. The worst case scenario (e.g., poorest quality site) for dickcissel nest success as determined using coefficients from the best model was 2.9% (95% CI = 0.4%, 11%) in RFB (i.e., −1 standard deviation (SD) nest height, +1/2 SD grass, +1 SD horizontal density, +1 SD row-crop within 30 m), and 38.4% (95% CI = 21.3%, 54.1%) in all habitats with the best case scenario (i.e., highest quality site or opposite of above).

Red-winged blackbird nest survival was lower for nests in areas with abundant dead vegetation cover ($\beta_{DeadVeg}$ = −0.008, SE = 0.004, 95% CI = −0.016, −0.001), but higher for nests in FSD (β_{FSD} = 0.549, SE = 0.337, 95% CI = −0.111, 1.209) and higher off the ground (β_{NH} = 0.003, SE = 0.002, 95% CI = −0.0004, 0.007). Red-winged blackbird models were minimally improved by adding conservation practice, land-cover, or nest-site covariates and the best model explained 7.9% of the proportion of deviance (Table S2). The worst case scenario (i.e., −1 SD nest height and +1 dead vegetation) for red-winged blackbird nest success was 4.5% (95% CI = 0.8%, 13.9%) in all habitats and the best case scenario was 31.9% (95% CI = 7.8%, 59.9%) in FSD.

Landscape level factors had minimal overall influence on nest survival estimates for either species. Row-crop cover within 30 m of dickcissel nests was the only variable to explain model variation, although we also detected a weak positive effect of patch area.

4. Discussion and implications

We observed greater dickcissel nest densities in BLKs (Fig. 1), which supports our first hypothesis and may be attributed to larger patch area (Vickery et al., 1994; Winter and Faaborg, 1999), local vegetation complexity (Wiens, 1969; Renken and Dinsmore, 1987), and their preference for elevated nests in woody plants (Overmire, 1962). Dickcissels also regularly nested in RFB and FSD but almost completely avoided FSM until 2007 (Fig. 1). Dickcissel nest densities were higher than expected for 2–4 year old RFBs (Twedt et al., 2002), and should continue to increase with woody growth over the next several years (Zimmerman, 1971). Red-winged blackbird nest densities were more variable than dickcissel and they nested frequently in each treatment during at least one year of the study (Fig. 1). Red-winged blackbirds nested most frequently in BLK and FSD in 2005, but densities in those treatments declined annually, suggesting diminished nesting suitability. Their highest nest densities in FSM were in 2006 and in RFB during 2007 (Fig. 1). Overall, nest densities increased annually in all buffers, particularly for dickcissels. Based on the similarity of nest success across conservation buffers and large blocks, we suspect that renesting has a minimal influence on nest density estimates.

The disproportionate amount of early-season nesting activity by dickcissels in buffers may relate to their preference for tall, densely vegetated nest sites with standing dead vegetation perches (Zimmerman, 1971, 1982). Such vegetation characteristics were particularly distinct in filter strips, which are intentionally planted with fast, thick growing vegetation to reduce erosion.

4.1. Nest survival

The average dickcissel nest success of 22.9% exceeds estimates reported in Kansas CRP fields (13.2% and 14.9%; Hughes et al., 1999), is comparable or lower than Missouri tallgrass prairie fragments (19.7% and 39.8%; Winter, 1999), and is lower than Missouri CRP fields that were considered population sink habitats (29.7%; McCoy et al., 1999). The average red-winged blackbird nest success of 8.6% (95% CI = 2.3%, 19.8%) is considerably lower than in Missouri CRP fields considered sink habitats (27.6%; McCoy et al.,

Fig. 4. Red-winged blackbird daily nest survival estimates across the breeding season for all conservation practices combined (▲) ±1 SD in dead vegetation cover (DV; —) and for diverse-planted filter strips (FSD; △) ±1 SD in dead vegetation cover (—) amid intensive agriculture in the Mississippi Alluvial Valley, Mississippi, 2005–2007.

1999). Red-winged blackbird nest success as estimated with aver-aged covariates in FSD (23.4%) was substantially higher than all other conservation practices.

The positive effect of height on dickcissel nest survival may relate to the high apparent frequency of nest depredation by snakes on this farm (Conover, 2009), which supports previous research in Illinois (Harmeson, 1974). Low dickcissel nest success in RFBs (10.6%) provides reason for concern, as it was their preferred buffer practice on the farm and is the most abundant buffer practice in Mississippi (Clark and Reeder, 2007). Our models predict that proper vegetation management could increase dickcissel nest suc-cess to 23% in RFBs, though this may still be inadequate to provide population benefits (McCoy et al., 1999). Many dickcissel nests in RFBs were so conspicuous as to be visible from up to 30 m away (R.R. Conover, pers. obs.), which can increase nest predation (Angelstam, 1986). The relatively low vegetative cover in RFBs may also relate to our result of their having significantly higher mound densities in RFBs than other conservation practices (Allen et al., 2004; Table S1) and that more dickcissel nests were observed depredated by fire ants (20%) in RFBs than any other conservation practice (Conover, 2009).

Both species' nest success exhibited quadratic seasonal trends with lowest survival in mid-season at peak nest activity and the highest survival early and late in the nesting season, (Roos, 2002), which may reflect an association of density dependent predation given the temporal variation of nest densities. The proximity of nests to habitat edges did not influence nest survival as predicted (Suarez et al., 1997) however, this was not wholly unexpected (Jensen and Finck, 2004). This lack of influence by landscape-level factors was previously documented for dickcissel (Hughes et al., 1999) and other grassland birds (Davis et al., 2006), corroborating that dickcissel and possibly red-winged blackbird nest success is largely influenced by local vegetation (Hughes et al., 1999).

This study demonstrates distinct farmland bird benefits for BLKs as well as conservation buffers with increased floristic diversity and structural heterogeneity. Although RFBs provided attractive nest-ing habitat for dickcissel, the combination of high fire ant densities and low dickcissel nest success indicates this conservation practice offers suboptimal reproductive benefits on this farm. Based on high nest densities (especially for dickcissel) and moderate nest suc-cess in BLKs, we recommend establishing large blocks as the basis for conservation management systems that target early-succession birds in the MAV.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2011.02.022.

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