



## Original Article

# Grassland Bird Nest Ecology and Survival in Upland Habitat Buffers Near Wooded Edges

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**ABSTRACT** Upland habitat buffers (i.e., strips of noncrop, herbaceous vegetation) that are established adjacent to wooded fencerows offer landowners an economical option to provide wildlife benefits within intensive agricultural landscapes. However, being located near a wooded edge may increase grassland bird vulnerability to edge effects through reduced nest survival. We examined nesting bird communities in field margins adjacent to wooded field edges with no buffer (i.e., control), narrow (approx. 10-m) buffers, and wide (approx. 30-m) buffers in an intensive agricultural system in the Lower Mississippi Alluvial Valley, United States. Dickcissel (*Spiza americana*) and red-winged blackbird (*Agelaius phoeniceus*) accounted for 97% of nests. Nest density was >7 times greater in wide buffers than in narrow. We modeled nest survival in Program MARK as a function of time (yr and season), nest-site, and local vegetation characteristics. Nest survival was influenced by among- and within-season temporal effects and local vegetation structure, but not by buffer width. Nest success varied substantially between years and within seasons for dickcissel (12.9% and 19.1% early in the seasons of 2003 and 2004, respectively), but not for red-winged blackbird (15.1%). Overall nest-success estimates were similar to noncrop, herbaceous strips elsewhere in the United States, though whether or not these estimates represent population sinks remains uncertain. Based on this research, we advocate integrating upland habitat buffers within intensive agricultural landscapes and emphasize the use of wide buffers when grassland-nesting birds are a conservation priority. © 2011 The Wildlife Society.

**KEY WORDS** *Agelaius phoeniceus*, agriculture, conservation buffers, dickcissel, Mississippi Alluvial Valley, nest survival, red-winged blackbird, *Spiza americana*, upland habitat buffer.

The large-scale conversion of North American grasslands to agriculture is strongly associated with numerous grassland bird population declines (Peterjohn and Sauer 1999, Brennan and Kuvlesky 2005). Many grassland birds have survived by exploiting the noncrop, weedy patches that remained on farm field margins (Warner 1994). These remnant patches are threatened by intensive agricultural practices (e.g., field consolidation, ditch-to-ditch cropping) that remove such noncrop vegetation to maximize crop yield. Based on European studies, loss of these remnant idle areas could pose an additional significant threat to U.S. farmland bird populations (Donald et al. 2001). The U.S. Department of Agriculture's (USDA) National Conservation Buffer Initiative (NCBI) partially aims to mitigate this threat by establishing multiple conservation buffer practices (e.g., strips of noncrop vegetation) on agricultural field margins (Best 2000, Clark and Reeder 2007). Such buffers are designed to achieve specific environmental benefits such as sediment trapping, nutrient capture, water-quality enhancement, and provision of wildlife habitat.

Upland habitat buffers are an NCBI practice; they are planted with diverse, native herbaceous flora to provide habitat for grassland birds and other wildlife in an agricultural matrix. These buffers are typically located in areas of lower crop yield and, thus, often have nominal impact on whole-farm profitability (Barbour et al. 2007, Stamps et al. 2008). Previous research has confirmed that upland habitat buffers receive extensive use by breeding and nonbreeding bird communities (Smith et al. 2005; Conover et al. 2007, 2009), but little information exists on the importance of patch characteristics on bird productivity in buffers (Conover et al. 2011). Such an evaluation is particularly important because upland habitat buffers are typically established adjacent to wooded vegetation, which can facilitate negative edge effects (Fletcher and Koford 2003, Bollinger and Gavin 2004).

Edge effects related to nest success may include elevated diversity, activity, abundance, and search efficiency of nest predators (Gates and Gysel 1978, Paton 1994, Major et al. 1999, Woodward et al. 2001), as well as brood parasitism (Johnson and Temple 1990). If edge effects reduce fitness by decreasing nest activity and survival, buffers may function as population sinks (Heske et al. 1999). These effects are often stronger near wooded edges and specifically on abrupt, agri-

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culture-wooded edges (Suarez et al. 1997, Saracco and Collazo 1999, Jensen and Finck 2004). Wider buffers have more core habitat (more area/unit length) than narrow buffers, which translates into a more gradual edge that can attract more birds (Helzer and Jelinski 1999, Winter and Faaborg 1999, Ribic et al. 2009). Area can be positively correlated with vegetative diversity and heterogeneity (Rodenhouse and Best 1983), which could increase nest densities and reduce nest predation pressure by providing enhanced nest-site diversity (Shalaway 1985, Martin 1993). Consequently, wider buffers may be more suitable and attractive for some grassland-nesting birds, but whether that translates to increased productivity for grassland-nesting birds remains largely unanswered.

Dickcissel (*Spiza americana*) and red-winged blackbird (*Agelaius phoeniceus*) are grassland-nesting birds that utilize buffers during the breeding season in southeastern agricultural systems (Smith et al. 2005, Conover et al. 2007). Because some USDA conservation practices provide habitat in which some populations are not self-sustaining (Ryan et al. 1998, McCoy et al. 1999), understanding how grassland-nesting birds respond to upland habitat buffers is crucial to assist land managers in designing farm-wide, conservation-management systems that benefit a broad suite of grassland birds.

We investigated the nesting bird community in row-crop agriculture that had no buffer (i.e., control), or had buffers that were established within the previous 3 yr at initial width treatments of narrow (10 m) or wide (25–45 m). Specifically, we report on the association of buffer width on dickcissel and red-winged blackbird nest density and survival, seasonal nesting patterns, and nest-site characteristics. We hypothesized that 1) field margins with upland habitat buffers would attract greater nesting activity than margins without buffers, and 2) dickcissel and red-winged blackbird nest survival would be greater in wide than narrow buffers.

## STUDY AREA

The study site included 7 farms in Sunflower County, north-west Mississippi, USA, which was located in the Mississippi Alluvial Valley (MAV; Bird Conservation Region 26). Farms were all geographically located within 12 km. This landscape had nominal topographic relief and was dominated by large row-crop fields (i.e., cotton and soybean) that were fragmented by a network of drainage ditches, streams, and fencerows. This region was historically bottomland-hardwood forest but was cleared, drained, and largely converted to agriculture by the end of the 20th century (King et al. 2005). Hence, upland habitat buffers represented the establishment of semi-natural vegetation in a landscape nearly devoid of noncrop vegetation. Soil associations were primarily Dundee silt loam or Forestdale silt loam, which were stratified alluvium soils of fine to coarse texture that were washed in by the Mississippi River, had poor to moderate drainage, and varied widely in acidity levels (Powell et al. 1952). Average precipitation over the 3 study yr was higher during June (20.1 cm) than in May (8.7 cm) or July

(10.1 cm). Average summer rainfall was also lower during 2002 (19.1 cm) than 2003 (39.2 cm) or 2004 (58.5 cm).

## METHODS

### Upland Habitat Buffers

We investigated bird nesting activity within 200-m-long sections of field margins that had no (i.e., control), narrow, and wide upland-habitat buffers during the summers of 2002–2004. Sites with no buffers were representative of conventional farming practices in the MAV, in which the field margins were turn rows (nonvegetated areas in which farm machinery turns around) or row-cropped. All buffers were established in spring 2002. Narrow buffers were established at 10 m wide ( $8.8 \pm 2.2$  m,  $\bar{x} \pm 95\%$  CI,  $n = 89$ ), whereas wide buffers ranged from 25 m to 45 m wide ( $32.0 \pm 17.3$  m,  $\bar{x} \pm 95\%$  CI,  $n = 26$ ). We calculated average buffer width as the mean of 5 independent measurements at equidistant intervals (50 m). Upland habitat buffers were within similar landscapes, situated between large ( $171.14 \pm 34.20$  ha;  $\bar{x} \pm$  SE) row-crop fields, typically soybean (*Glycine* sp., 58%), cotton (*Gossypium* sp., 16%), or milo (*Sorghum* sp., 10%), and wooded fencerows that buffered riparian zones. We randomly selected buffered and non-buffered field margins from an initial population of buffers on cooperating landowner properties. Although we instructed landowners not to disturb (i.e., mow, burn, apply chemicals, drive on, or disk) buffers, some buffer degradation occurred. This resulted in slightly decreased sample sizes, which were supplemented using buffers from the sampling frame that were not selected in the initial random sample. Hence, the number of buffers differed among 2002, 2003, and 2004 ( $n = 19, 21,$  and  $21$  no buffer;  $38, 27,$  and  $24$  narrow buffer; and  $8, 7,$  and  $11$  wide buffer, respectively). Only 7 of 11 wide buffers in 2004 were used for nest density estimates, as the other 4 buffers were planted in 2003 and did not yet have mature vegetation suitable for nesting birds.

Upland habitat buffers were planted with Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and partridge pea (*Chamaecrista fasciculata*). Other local vegetation that commonly colonized buffers included maretail (*Conyza canadensis*), seashore vervain (*Verbena litoralis*), Bermuda grass (*Cynodon dactylon*), johnsongrass (*Sorghum halepense*), goldenrod (*Solidago* spp.), common ragweed (*Ambrosia artemisiifolia*), giant ragweed (*A. trifida*), poison ivy (*Toxicodendron radicans*), curly dock (*Rumex crispus*), and *Rubus* spp. Buffers with substantive grass competition during the establishment year were treated with the selective herbicide Imazapic (Plateau<sup>®</sup>, 0.29 L/ha) to control competition and promote growth of planted species. Herbicide applications had relatively minor effects, aside from competition control, on total vegetative composition or structure and tended to reduce heterogeneity among planted buffers.

### Nest Searching and Monitoring

We conducted intensive nest searches from 15 April to 31 July, 2002–2004. We searched for nests in all buffers with proportionally equal effort on a weekly basis except control

(i.e., nonbuffered) margins, which were searched less intensively (every 3 weeks) to reduce damage to row-crops. Nest searches entailed 2–3 people pacing systematically through each buffer while mildly disturbing the vegetation with 1-m sticks and searching for nests by visual observation or flushing the attending parent. All buffers were searched with equal effort in proportion to their area to justify comparisons of relative nest density among treatments. The location of each nest was mapped using compass bearings and natural landmarks, and marked inconspicuously with a small piece of orange flagging placed below the herbaceous vegetation canopy and 5 m north of the nest to avoid attracting predators. We monitored each active nest every 2–4 days using care not to alter the nest site (e.g., trampling vegetation) or create dead-end trails that may interfere with the nest outcome (Martin 1993). Nest data included nest stage (laying, incubation, and nestling), age, clutch or brood size, parental activity, cowbird parasitism, and nest fate. We estimated embryo age during incubation by observing eggs through a 10-cm piece of foam pipe insulation (Lokemoen and Koford 1996) and during the brooding stage using voucher images (R. R. Conover, unpublished data). We declared a nest successful in the incubation and nestling stages if  $\geq 1$  egg hatched or nestling fledged, respectively. We determined nest outcome based on parental behavior, fledgling presence, nest condition, and other clues (e.g., predator tracks, eggshell fragments). Causes of nest failure were classified as depredated, abandoned, brood parasitism, weather-caused, or human-caused. Clutch size is reported as the maximum number of host eggs/nestlings counted. We quantified the number of clutches initiated per 2-week period throughout the breeding season.

### Nest-Site Characteristics

We characterized red-winged blackbird and dickcissel nest sites by measuring nest height, nest concealment (from directly overhead), distance to wooded and agricultural (i.e., row-crop) edges, and quantifying the immediately surrounding vegetation. Nest height (cm) was measured from the ground to the nest rim and nest concealment was the cumulative percentage of nest cover from directly above. Distances to edges were measured by walking premeasured paces to the nearest wooded and row-crop edges. We evaluated vegetation surrounding nests in a 4-m-radius circular plot centered on each nest. Vegetation measurements included vegetation structure (proportions of live forb, grass, woody, and crop cover), proportion of standing dead vegetation, horizontal density (HD), and vertical cover. Vegetation structure was visually estimated in each of 4 quadrants and subsequently averaged for each nest vegetation plot. Horizontal density was also visually estimated, but represented the average overall ground cover from each quadrant in the plot. Crop cover was negligible in all plots and, therefore, omitted from analyses. We estimated vertical cover by averaging 4 (i.e., each cardinal direction) visual obstruction readings (VOR; cm) that indicated the effective vegetation height (i.e., ht at which a nest would not be visible) and were recorded from 1 m above the ground using

a modified Robel pole (Robel et al. 1970, Renken and Dinsmore 1987). Structural heterogeneity of vegetation was determined using the coefficient of variation (cv) for estimates of both vertical cover (VORcv) and horizontal density (HDcv). We surveyed nest vegetation within 7 days after nests became inactive to minimize nest disturbance but capture representative vegetation measurements.

### Nest Survival Analyses

We modeled the daily nest survival rate (DSR) for dickcissel and red-winged blackbird nests during 2003 and 2004 using maximum-likelihood estimation and a logit link function in the nest survival module of Program MARK (Dinsmore et al. 2002). Nest survival data across both years were modeled from 4 May to 13 August for red-winged blackbird and 7 May to 15 August for dickcissel. We used a hierarchical model-selection approach to account for spatial and temporal variation in nest survival and maintain a parsimonious model set to minimize over-fitting the data (Burnham and Anderson 2002). Model construction proceeded in 4 hierarchical steps that included 1) additive and interactive effects from year, nest stage, and seasonal time trends (linear and quadratic), 2) buffer width and distance to edges (agricultural, wooded, and nearest), 3) local vegetation (VOR, VORcv, HD, HDcv, vegetation structure), and 4) nest-site characteristics (nest concealment, nest ht, nest plant ht, and clutch size). Step one evaluated DSR as an additive and interactive function of year, nest stage, and seasonal variation within years as a constant (no time trend), logit-linear time trend, or logit-quadratic time trend. We used information theoretic approaches for model selection and the adjusted Akaike Information Criterion ( $AIC_c$ ) as our model selection tool (Burnham and Anderson 2002). The best and all competitive ( $\Delta AIC_c \leq 2.0$ ) models from the previous model-selection step 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 ascribed statistical significance to model coefficients if their 95% confidence intervals did not include zero. 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 model as an approximate measure of model fit. The constant model represents only one parameter and no covariates; whereas, the global model represents the full amount of variation documented by all measured variables, which included year, nest stage, seasonal effects, and 29 biological covariates.

We portrayed seasonal nest-survival patterns for dickcissel in each year by plotting time-specific nest survival relative to the best-, average-, and worst-case scenarios for covariates retained in the best approximating model. Best-case scenarios were calculated by adding one standard deviation to coefficients with positive  $\beta$  values and subtracting one standard deviation from coefficients with negative  $\beta$  values. The

opposite calculations were performed to estimate worst-case scenarios. Standard deviations reflected variation in the vegetation parameter, not the  $\beta$  values.

Nest success estimates differ from DSR in that they represent the probability of a nest surviving an entire nesting (laying, incubation, and nestling) period. We calculated nest success using the range of observed covariate values from the best approximating model for each species to predict the influence of individual covariates or combinations (Shaffer and Thompson 2007). Nest success estimates were standardized to start on 1 June 2004 for red-winged blackbird, the approximate peak of clutch initiation for both species. Dickcissel nest survival varied seasonally; therefore, we calculated estimates for early (12 May–31 May), middle (01 Jun–20 Jun), and late (21 Jun–10 Jul) times in the season. We calculated nest success with empirically based nesting period estimates for both species, because they varied slightly from published reports. The dickcissel nesting period was 20-day intervals (2 days egg-laying, 10 days incubation, 8 days nestling) and red-winged blackbird was 21-day intervals (1 day egg-laying, 11 days incubation, 9 days nestling; Conover 2005). These values account for incubation beginning with the laying of the penultimate egg for both species.

We also calculated the number of fledglings per successful nest based on visual and behavioral evidence (see above for evidence to determine nest outcome) and if a nest was deemed successful, we assumed that all nestlings not in the nest had successfully fledged unless evidence indicated otherwise. Relative nest density (nests/ha) was estimated directly as the number of nests found in a season per total buffer area searched that season.

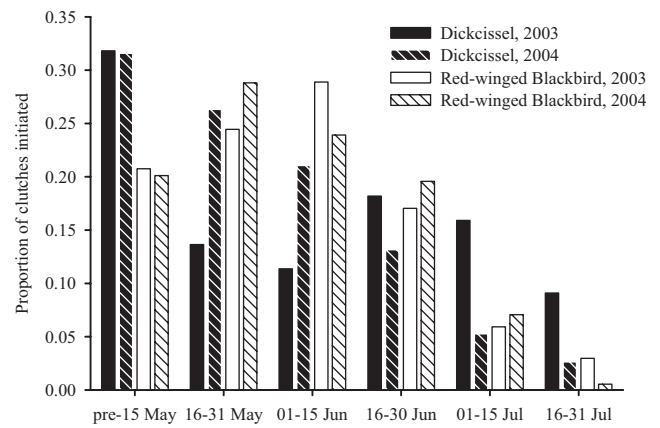
## RESULTS

### Nesting Community

We found 434 nests of 8 bird species in narrow and wide buffers over 3 breeding seasons (2002–2004). Red-winged blackbird (77.7%,  $n = 337$ ) and dickcissel (19.4%,  $n = 84$ ), were the most common nesting species, while the other 3% of nests included indigo bunting (*Passerina cyanea*,  $n = 5$ ), northern cardinal (*Cardinalis cardinalis*,  $n = 2$ ), yellow-billed cuckoo (*Coccyzus americana*,  $n = 2$ ), northern mockingbird (*Mimus polyglottos*,  $n = 2$ ), blue grosbeak (*Guiraca caerulea*,  $n = 1$ ), and mallard (*Anas platyrhynchos*,  $n = 1$ ). Dickcissel, indigo bunting, northern cardinal, red-winged blackbird, and northern mockingbird nested in both narrow and wide buffers, whereas blue grosbeak, yellow-billed cuckoo, and mallard nested only in wide buffers, albeit rarely. We did not find a single nest in any control field margins during all years, although we did frequently observe birds carrying nesting material into agricultural fields.

### Nest Activity and Site Characteristics

Most dickcissel nests were initiated during early and mid-May, whereas nests of red-winged blackbirds were primarily initiated from mid-May to mid-June (Fig. 1). Dickcissel nesting activity was disproportionately greater early in the season during the third year postestablishment (Fig. 1). Nests were mostly found in the incubation ( $n = 235$ ;



**Figure 1.** Seasonal nesting activity as indicated by proportions of initiated clutches of dickcissel (*Spiza americana*; black) and red-winged blackbird (*Agelaius phoeniceus*; white) during 2003 (solid) and 2004 (striped) in row-crop agricultural field borders on wooded edges in the Mississippi Alluvial Valley, Mississippi, USA.

54%) and laying or construction stages ( $n = 151$ ; 35%), compared to nests found in the nestling stage ( $n = 48$ ; 11%). We found 20 total nests in 2002 when vegetation was initially planted, 183 in 2003, and 231 in 2004. This translated to annual buffer nesting densities that increased substantially from 2002 ( $1.08 \pm 0.64$ , nests/ha  $\pm$  95% CL), to 2003 ( $8.91 \pm 6.22$  nests/ha), and 2004 ( $11.59 \pm 7.37$  nests/ha). Dickcissel relative nest density in wide buffers was  $4.23 \pm 7.35$  (nests/ha  $\pm$  95% CL) in 2003 and  $3.54 \pm 6.29$  in 2004, with only one nest found in narrow buffers during each 2003 and 2004. Red-winged blackbird nest densities were also substantially higher in wide buffers ( $12.50 \pm 19.44$  and  $14.47 \pm 23.49$ ) in 2003 and 2004, respectively, than in narrow buffers ( $0.78 \pm 0.33$  and  $3.47 \pm 1.28$ ). Over 2003 and 2004, relative nest densities were considerably higher in wide ( $17.67 \pm 19.21$  nests/ha) than narrow ( $2.38 \pm 0.67$  nests/ha) buffers. Effective nest-day sample sizes were 692 days for dickcissel and 2,658 nest days for red-winged blackbird.

Dickcissel nests were lower to the ground and more concealed than red-winged blackbird nests. Both species nested slightly closer to the agricultural edge than wooded edge and in areas of similar amounts of dead vegetation, forb, grass, and woody cover (Table 1). Red-winged blackbird nests in wide buffers had, on average, greater overhead nest concealment, vertical cover, and forb cover compared to their nests in narrow buffers.

### Nest Survival

Seventy-eight percent ( $n = 338$ ) of all nests failed, primarily from depredation (88.5%,  $n = 299$ ), abandonment (6.5%,  $n = 22$ ), weather (2.7%,  $n = 9$ ), human activity (1.8%,  $n = 6$ ), and brood parasitism ( $<1.0\%$ ,  $n = 2$ ). No nests experienced brood parasitism by brown-headed cowbirds (*Molothrus ater*) in 2002, but a similar parasitism rate (6%) occurred in both 2003 and 2004. Of 283 total fledglings over 2003 and 2004, only 3 were cowbirds. Dickcissel hosted only 4 cowbird eggs, with 2 (50%) fledging. Red-winged

**Table 1.** Local vegetation and nest-site characteristics (mean  $\pm$  95% CI) as measured for dickcissel (*Spiza americana*) and red-winged blackbird (*Agelaius phoeniceus*) in narrow and wide agricultural field borders that were adjacent to wooded edges in the Mississippi Alluvial Valley, Mississippi, USA, 2003–2004. Note: % cover does not sum to 100% because row-crop cover is not included.

Nest variable <sup>a</sup>	Red-winged blackbird						Dickcissel			
	2003		2004				2003		2004	
	Wide		Narrow		Wide		Wide		Wide	
	127		33		151		43		37	
<i>N</i>	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI
Clutch	2.83	0.16	2.91	0.28	2.99	0.13	3.84	0.27	4.00	0.40
Nest ht (cm)	84.03	4.57	87.33	5.60	100.01	5.76	57.55	8.98	50.82	8.62
NC %	52.06	5.53	45.97	9.90	55.04	5.41	71.93	9.17	77.86	8.92
NPH (cm)	150.60	7.22	157.82	9.86	155.82	6.23	126.06	13.20	119.79	14.09
VOR (cm)	129.08	7.54	95.35	8.55	115.42	7.52	119.75	14.03	87.13	11.91
HD %	96.88	0.76	93.19	2.79	95.44	0.84	97.05	1.22	97.06	0.94
Grass cover %	23.68	4.13	62.82	8.77	24.37	2.54	16.23	4.99	32.85	7.38
Forb cover %	75.96	4.15	34.42	7.78	72.49	2.81	82.77	5.03	61.58	6.63
Woody cover %	0.28	0.16	1.88	1.82	1.61	1.17	1.00	0.73	4.34	2.19
Dead vegetation %	15.02	1.90	21.85	5.35	17.06	3.51	16.84	3.84	12.98	4.16
Richness	10.04	0.53	10.00	1.07	12.47	0.63	11.21	0.81	12.75	1.36
DAE (m)	17.64	2.21	4.64	0.52	16.51	1.85	15.04	4.05	15.57	2.72
DWE (m)	22.67	2.72	5.49	1.20	18.95	1.93	25.76	4.26	17.21	3.27

<sup>a</sup> NC = overhead nest concealment; NPH = nest plant ht; VOR = visual obstruction reading; HD = horizontal vegetation density; Richness = plant species richness; DAE = distance to agricultural edge; DWE = distance to wooded edge.

blackbirds were less hospitable, with only 1 of 15 cowbird eggs (7%) fledging successfully.

Red-winged blackbird DSR was best explained by nest stages ( $\beta_{\text{egg-laying}} = -0.765$ , 95% CI =  $-1.237, -0.294$ ;  $\beta_{\text{incubation}} = -0.043$ , 95% CI =  $-0.346, 0.261$ ;  $\beta_{\text{nestling}} = 0.837$ , 95% CI =  $0.068, 1.066$ ), dead vegetation ( $\beta_{\text{DV}} = 0.006$ , 95% CI =  $-0.002, 0.014$ ), clutch size ( $\beta_{\text{clutch}} = 0.240$ , 95% CI =  $0.073, 0.406$ ), and nest plant height ( $\beta_{\text{NPH}} = 0.005$ , 95% CI =  $0.002, 0.008$ ; Table 2). The best approximating model explained 7.5% of the variation in red-winged blackbird nest survival. Red-winged blackbird nest success did not vary significantly among or within year and averaged 15.09%. The number of fledglings/nest for red-winged blackbirds did not significantly vary, including ( $\pm$ SE)  $2.46 \pm 0.13$  ( $n = 61$ ) fledglings per successful nest overall, with  $2.30 \pm 0.34$  in narrow buffers ( $n = 10$ ) and  $2.49 \pm 0.14$  in wide buffers ( $n = 51$ ).

Dickcissel DSR was best explained by lower nest survival in 2004 ( $\beta_{\text{year}} = -2.499$ , 95% CI =  $-4.642, -0.357$ ), quadratic seasonal time trend ( $\beta_{\text{TT}} = 0.234$ , 95% CI =  $0.093, 0.375$ ; Fig. 2), plant species richness ( $\beta_{\text{rich}} = -0.177$ , 95% CI =  $-0.268, -0.085$ ), grass cover ( $\beta_{\text{grass}} = 0.019$ , 95% CI =  $0.001, 0.036$ ), and VORcv ( $\beta_{\text{VORcv}} = 2.242$ , 95% CI =  $0.228, 4.257$ ; Table 2). Dickcissel had  $3.13 \pm 0.26$  fledglings per successful nest ( $n = 23$ ). The best approximating model explained 10.4% of the variation in dickcissel nest survival. Dickcissel nest success varied among and within years, with considerably lower survival during the middle of the nesting season in 2004 (Fig. 2).

## DISCUSSION

Upland habitat buffers provide scarce noncrop vegetation in the agriculture-dominated MAV, and although they are known to benefit many early succession birds (Marcus

et al. 2000, Puckett et al. 2000, Smith et al. 2005), their impacts on nesting passerines has not been addressed. In this study, buffers provided attractive nesting habitat for dickcissel and red-winged blackbirds, but low to moderate nest-survival rates highlight the potential for improvement through habitat management.

## Nest Activity

Narrow and wide upland-habitat buffers adjacent to wooded edges in the MAV provided substantially more attractive nesting habitat for early succession birds than control (i.e., nonbuffered) margins. We found no nests in any nonbuffered margins, which provides compelling support for our first hypothesis that field margins with upland habitat buffers would be more attractive to nesting birds. This complete lack of nesting activity in the control margins was unexpected and we speculate this resulted from the close proximity to a wooded edge in concert with inadequate nest-site vegetation structure. Nest activity in buffers varied seasonally, with most dickcissel nests being initiated early in the season. Wide upland-habitat buffers attracted relatively high (17.67 nests/ha) nest densities but narrow buffers were low (2.38 nests/ha) compared with Iowa (USA) grassed waterways (10.9 nests/ha; Bryan and Best 1994), Iowa roadside buffers (11.8 nests/ha; Camp and Best 1994), and rights-of-way strips in Illinois (USA; 8.89 nests/ha; Warner 1992).

Red-winged blackbirds nested readily in narrow buffers, but dickcissels largely avoided them. Despite low nesting activity in narrow buffers, their ability to attract a diverse and abundant bird community (Conover et al. 2009) demonstrates their potential to benefit birds nesting in adjacent habitats.

**Table 2.** Final model selection results from dickcissel (*Spiza americana*) and red-winged blackbird (*Agelaius phoeniceus*) nest survival in agricultural field borders adjacent to wooded edges in the Mississippi Alluvial Valley, Mississippi, USA, 2003–2004.

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	w <sub>i</sub> <sup>c</sup>	K <sup>d</sup>	Deviance
<b>Dickcissel</b>				
<i>S</i> year × <i>TT</i> + rich + grass + VORcv	0.00	0.07	9	248.13
<i>S</i> year × <i>TT</i> + rich + grass + VORcv + clutch	0.66	0.05	10	246.73
<i>S</i> year × <i>TT</i> + width + rich + grass + VORcv	0.85	0.05	10	246.92
<i>S</i> year × <i>TT</i> + rich + grass + HD + VORcv	0.99	0.04	10	247.05
<i>S</i> year × <i>TT</i> + DNE + rich + grass + VORcv	1.12	0.04	10	247.19
<i>S</i> year × <i>TT</i> + rich + grass + HD + VORcv + clutch	1.33	0.04	11	245.33
<i>S</i> year × <i>TT</i> + rich + grass + VORcv + NC%	1.36	0.04	10	247.42
<i>S</i> year × <i>TT</i> + rich + grass + VORcv + NH	1.53	0.03	10	247.60
<i>S</i> year × <i>TT</i> + width + rich + grass + HD + VORcv	1.62	0.03	11	245.62
<i>S</i> year × <i>TT</i> + width + rich + grass + VORcv + clutch	1.64	0.03	11	245.64
<i>S</i> year × <i>TT</i> + DNE + rich + grass + VORcv + clutch	1.85	0.03	11	245.86
<i>S</i> year × <i>TT</i> + DNE + rich + grass	1.96	0.03	9	250.09
<i>S</i> year × <i>TT</i> + rich + grass + VORcv + NC% + clutch	1.98	0.03	11	245.99
<b>Red-winged blackbird</b>				
<i>S</i> stage + DV + clutch + NPH	0.00	0.05	6	1,170.67
<i>S</i> stage + <i>TT</i> + DV + clutch + NPH	0.20	0.05	8	1,166.84
<i>S</i> stage + DNE + DV + clutch + NPH	0.48	0.04	7	1,169.14
<i>S</i> stage + T + DV + clutch + NPH	0.51	0.04	7	1,169.16
<i>S</i> stage + clutch + NPH	0.72	0.04	5	1,173.39
<i>S</i> stage + DNE + width + DV + clutch + NPH	0.79	0.03	8	1,167.43
<i>S</i> stage + <i>TT</i> + rich + DV + clutch + NPH	1.06	0.03	9	1,165.69
<i>S</i> stage + <i>TT</i> + DNE + DV + clutch + NPH	1.08	0.03	9	1,165.71
<i>S</i> stage + DNE + width + clutch + NPH	1.26	0.03	7	1,169.91
<i>S</i> stage + DNE + clutch + NPH	1.36	0.03	6	1,172.03
<i>S</i> stage + T + clutch + NPH	1.55	0.02	6	1,172.22
<i>S</i> stage + T + DNE + width + DV + clutch + NPH	1.58	0.02	9	1,166.21
<i>S</i> stage + T + DNE + DV + clutch + NPH	1.60	0.02	8	1,168.24
<i>S</i> stage + <i>TT</i> + clutch + NPH	1.73	0.02	7	1,170.38
<i>S</i> stage + <i>TT</i> + rich + clutch + NPH	1.80	0.02	8	1,168.44
<i>S</i> stage + <i>TT</i> + DNE + rich + DV + clutch + NPH	1.83	0.02	10	1,164.44
<i>S</i> stage + rich + clutch + NPH	1.85	0.02	6	1,172.51
<i>S</i> stage + T + rich + DV + clutch + NPH	1.87	0.02	8	1,168.52
<i>S</i> stage + <i>TT</i> + width + rich + DV + clutch + NPH	1.97	0.02	10	1,164.58

<sup>a</sup> Models are ranked by ascending AIC<sub>c</sub>. *TT* = quadratic seasonal trend; rich = plant species richness; grass = total grass cover; VORcv = visual obstruct on reading coeff. of variation; clutch = clutch/brood size; width = field border width; HD = horizontal vegetation density; DNE = distance to nearest edge; NC = overhead nest concealment; NH = nest ht; stage = nest stages (egg-laying, incubation, nestling); T = linear seasonal trend; DV = dead vegetation cover; NPH = nest plant ht.

<sup>b</sup> Denotes the difference of AIC<sub>c</sub> (Akaike's information criteria adjusted for small sample size) between candidate models. AIC<sub>c</sub> of the best model for red-winged blackbird is 1,182.70 and for dickcissel is 266.39.

<sup>c</sup> AIC model wt.

<sup>d</sup> No. of parameters.

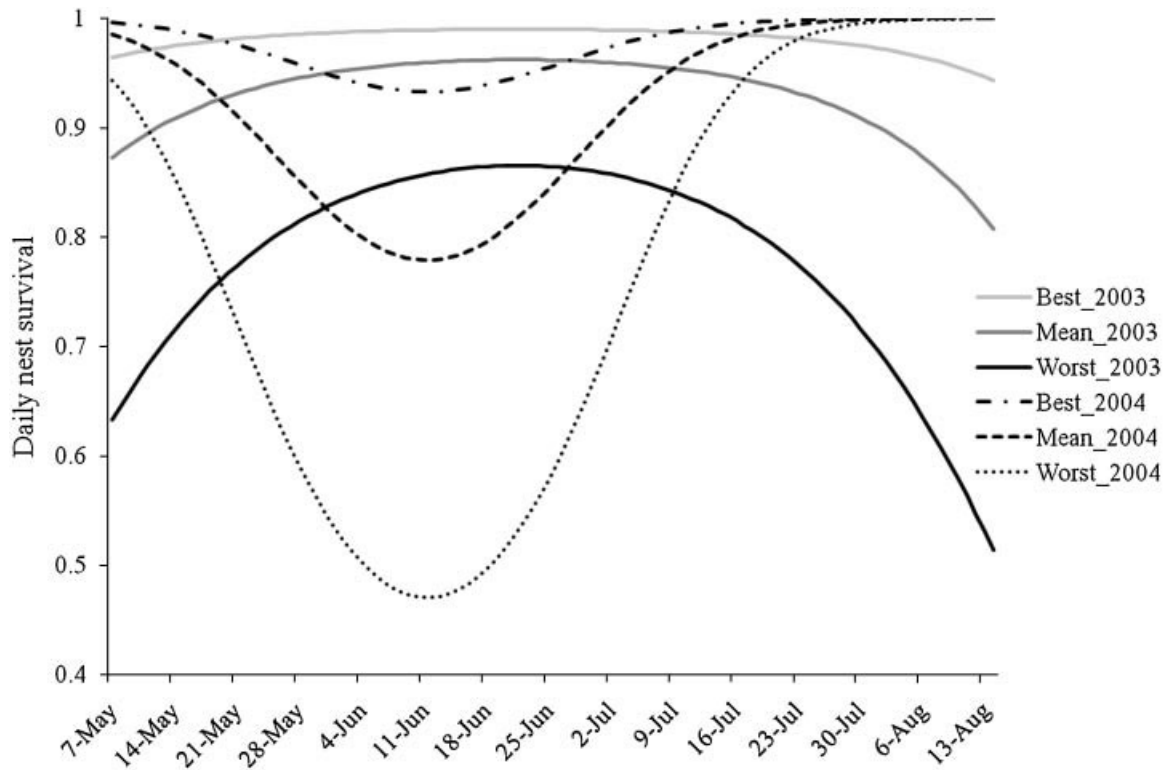
The extensive use of wide buffers by nesting dickcissels and red-winged blackbirds is promising, though both patch size and vegetation structure might limit their value for area-sensitive species such as grasshopper sparrows (*Ammodramus saviannarum*; Conover 2009). Both wide and narrow buffers provided nesting habitat for dickcissel, red-winged blackbird, indigo bunting, northern cardinal, and northern mockingbird. Additionally, yellow-billed cuckoo ( $n = 2$ ) and blue grosbeak ( $n = 1$ ) nested only in wide buffers, albeit rarely.

### Nest Survival

The seasonal increase of red-winged blackbird DSR likely corresponded to the concomitant increase in vegetation height and density (Bryan and Best 1994) and, hence, greater visual obstruction of nests (Chalfoun and Martin 2009). Seasonal trends of dickcissel DSR were more ambiguous, with the middle of the season having the highest DSR in 2003 but the lowest in 2004. We speculate the high survival

in 2003 relates to predator naïvetè in a novel vegetation patch, but that predators identified it as a viable food source by 2004. This speculation was anecdotally substantiated by our documentation (using a motion-sensitive camera) of a raccoon (*Procyon lotor*) depredating a red-winged blackbird nest 1 night, with many red-winged blackbird and dickcissel nests ( $n = 23$ ) in the same buffer being similarly depredated on 2 subsequent nights (R. R. Conover, personal observation). Hence, predator activity may be related to bird nest survival in this situation, but in a nonlinear manner that may be associated with density-dependence (Nams 1991).

Red-winged blackbird nest-survival models were largely influenced by nest stage and clutch size, which do not provide much insight into how to manage this species. Nest plant height and dead vegetation cover were also important variables for nest survival, which may illustrate the importance of vegetation structure on red-winged blackbird nest success. Higher survival for nests in taller plants may relate to reduced access or visibility by nest predators (Brown and Goertz



**Figure 2.** Dickcissel daily nest-survival patterns varied annually, seasonally, and with management case-scenarios for nest-site characteristics of Dickcissel nests in field borders in the Mississippi Alluvial Valley, Mississippi, USA, 2003–2004. Best-case scenarios were calculated by adding one standard deviation (SD) to coefficients with positive  $\beta$  values and subtracting one SD from coefficients with negative  $\beta$  values (–1 SD richness, +1 SD grass, +1 SD vertical cover heterogeneity). The opposite was done to estimate worst-case scenarios (+1 SD richness, –1 SD grass, –1 SD vertical cover heterogeneity). The mean represents unmanipulated model estimates.

1978), though we did not find evidence for these effects specifically. We speculate the positive influence of dead vegetation may relate to increased invertebrate food source, but this remains untested and this result contrasts previous reports (Warren and Anderson 2005, Conover et al. 2011). Dickcissel nest-survival models were more complex, varying with a year  $\times$  season interaction and several vegetation characteristics, which included plant species richness, grass cover, and vertical cover heterogeneity. The inverse relationship of survival to plant species richness may have been an artifact of greater grass-cover dominance suppressing floral colonization. Enhanced dickcissel nest survival and activity early in the nesting season may be associated with cover provided by tall, dense residual vegetation of dead grasses (Zimmerman 1971). Conover et al. (2011) reported greater use of buffer habitats by nesting dickcissels early in the nesting season. The combination of early season selection and higher early season success suggests that buffers may provide greatest benefits during the period before crops close canopy when other available nesting habitat is scarce. Dickcissel nest survival related positively to grass cover, possibly from the dense visual obscurity provided by grasses (Chalfoun and Martin 2009). Vertical cover heterogeneity was a particularly important explanatory variable, substantiating the known preference of dickcissels to nest in areas with moderate proportions of forbs and grasses (Zimmerman 1982, Temple 2002). The importance of cover heterogeneity to

dickcissel nest survival reveals that dense, homogeneous cover may not provide optimal benefits.

Buffer width did not have a substantial influence on nest survival of either species, but was clearly important for initial settlement, particularly by dickcissels. This refutes our second hypothesis and potentially indicates that narrow and wide buffers were under similar nest predation pressure as they relate to edge effects.

Dickcissel nest success varied substantially by year, season, and vegetation. This variability makes interpretation difficult because they had exceptionally high success in 2003, but very low in 2004. Despite the large variation in seasonal dickcissel nest success, our early season estimates (12.9% and 19.1% in 2003 and 2004, respectively) were comparable to those in Kansas Conservation Reserve Program (CRP) fields (13.2% and 14.9%; Hughes et al. 1999) as well as old fields (14.3%) and prairies (15.2%) in Kansas, USA (Zimmerman 1982), but lower than in Missouri (USA) CRP fields (29.7%; McCoy et al. 1999) or Iowa grassed waterways (22.0%; Bryan and Best 1994).

Red-winged blackbird average nest success (15.1%) was higher than found in Iowa grassed waterways (8.4%; Bryan and Best 1994), but lower than Iowa roadsides (26.0%; Camp and Best 1994) or Missouri CRP fields (27.6%; McCoy et al. 1999). Given that our nest success estimates are substantially lower than those in population sink habitats (McCoy et al. 1999), it is imperative that

upland-habitat buffer vegetation be managed to increase nest success for these species in the MAV.

## MANAGEMENT IMPLICATIONS

Despite commonly voiced concerns that conservation buffers may have limited value as nesting habitat because of low survival, nest success during this study was not substantively lower than previously reported for other habitats. Conover et al. (2011) similarly reported nest survival in buffers comparable to large block habitats. However, greatest conservation benefits are likely to be achieved by establishing upland habitat buffers at maximized widths ( $\geq 30$  m) and with substantive vegetation cover and structural heterogeneity to benefit nesting dickcissels and red-winged blackbirds among intensive agriculture in the MAV. Even narrow (approx. 10-m) buffers provide greater benefits than non-buffered field margins and likely represent an important ancillary component to a whole-farm management regime that targets nesting songbirds. Residual standing vegetation from the previous year provides crucial vegetative cover for early season nesting activity and, thus, should remain undisturbed except when periodically managing to maintain early succession vegetation.

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