SONGBIRD NEST SURVIVAL IS INVARIANT TO EARLY-SUCCESSIONAL RESTORATION TREATMENTS IN A LARGE RIVER FLOODPLAIN

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ABSTRACT.—We monitored songbird nest survival in two reforesting, ~50-ha former cropland sites along the Missouri River in central Missouri from 2001 to 2003. Sites were partitioned into three experimental units, each receiving one of three tree planting treatments. Nest densities varied among restoration treatments for four of five species, but overall nest survival rates did not. Nest survival varied with day-of-year and with incidence of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Nest survival was higher early and late in the season, and parasitized nests experienced lower nest survival, despite few complete losses directly attributable to parasitism. Probability of parasitism was inversely related to distance to the nearest tree, and was much lower than in old field study sites in the same region. High cowbird parasitism frequencies are usually associated with landscapes low in forest cover, yet these sites in an agriculturally-dominated bottomland landscape experienced low (~0.8–24%) cowbird parasitism. The assumed negative relationship between landscape-level forest cover and cowbird parasitism needs further study in habitats other than forest. *Received 1 September 2008. Accepted 26 November 2009.*

Studies of nest predation have noted variation in nesting success among habitat types within the same species or suites of species (McCoy et al. 1999, Lloyd and Martin 2005), or variation in nesting success among regions or fragment sizes (Donovan et al. 1995, Robinson et al. 1995). These differences could be attributed to predators, which are known to vary across regions (Thompson et al. 1999, Pietz and Granfors 2000). Predator identities may vary across habitat types within the same landscape or region (Chalfoun et al. 2002), although predator differences may not be reflected in differences in nesting success (Thompson and Burhans 2003).

Nest predation is considered the largest cause of nest loss (Ricklefs 1969, Martin 1992), and Brown-headed Cowbird (*Molothrus ater*) brood parasitism, which also affects nest success, may also vary by region, landscape, or habitat type (Robinson et al. 1995, Burhans 1997, Burhans and Thompson 2006). Much of our present understanding about the interactions of habitat and landscape features affecting cowbird parasitism comes from studies in upland forested habitats (Brittingham and Temple 1983, Robinson et al. 1995, Donovan et al. 2000, Thompson et al. 2000).

We monitored songbird nesting success at two sites having three contiguous 16.2-ha habitats of former cropland along the Missouri River. The habitats varied in densities of planted oaks (*Quercus* spp.) and in presence of a homogenous herbaceous cover crop. The treatments were sufficiently large to attract reasonable numbers of species of nesting birds across the different habitat types. Habitats were physically adjacent to one another, so that any differences in predation within the site should have been attributable to variation in habitat type only, and not to factors such as region, landscape context, or fragmentation. Our specific goals were to examine: (1) whether nesting success varied among the planted habitat types, and (2) whether frequencies of cowbird parasitism varied among habitat types.

METHODS

Our central Missouri, USA research sites were managed by the Missouri Department of Conservation and were in predominately agricultural floodplain landscapes surrounded by agriculture or early-successional vegetation originating from floods of the mid-1990s. Plowboy Bend Conservation Area (38° 48′ 05″ N, 92° 24′ 17″ W) was a row-crop agriculture/floodplain ecosystem west of the Missouri River's main channel within a levee-protected floodplain. The surrounding landscape within a 5-km radius (Driscoll and Donovan 2004) centered on Plowboy Bend was ~24% cropland,

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26% grassland, 34% forest, and 15% water (based on circa-2000 TM satellite data interpreted by the Missouri Resources Assessment partnership; www.cerc.usgs.gov/morap). Smoky Waters Conservation Area (38° 35′ 09″ N, 91° 58′ 03″ W) was 72 km southeast of Plowboy Bend between the main channels of the Missouri and Osage rivers (a major tributary of the Missouri River). The surrounding landscape within a 5-km radius was ~24% cropland, 23% grassland, 33% forest, and 18% water. The floodplain at Smoky Waters is subject to occasional flooding and has not been protected since a levee was breached in the 1993 and 1995 floods. Smoky Waters was flooded for 3 weeks in June 2001, and Plowboy Bend was flooded for 1 week during the same time period; Smoky Waters was also flooded for 1 week in early May 2002.

The three 16.2-ha restoration treatment units at each site were cleared of herbaceous vegetation and disked in autumn 1999. Two of the three units were planted with swamp white oak (*Quercus bicolor*) and pin oak (*Q. palustris*) at a 9 × 9-m spacing (Dey et al. 2001, Shaw et al. 2003). Redtop grass (*Agrostis gigantea*) was planted in one of the two units, producing a low, dense ground cover that substantially reduced invasion of other herbaceous and woody vegetation. We refer to the combination of planted oaks and redtop grass as the ''redtop'' treatment. The ''no redtop'' treatment contained the same oak plantings, but without seeded ground cover, and had diverse mixtures of invasive herbaceous and woody growth compared to redtop habitats. The remaining unit at each site served as a ''control'' and was not planted to either oak or redtop (Shaw et al. 2003). Structurally, vegetation in the control treatments was most similar to that in the no redtop treatments except for the absence of oaks. Planted oaks included conventional 1-year old, not transplanted bare root seedlings, but also included ''RPM®'' (Root Production Method) oaks. These oaks were grown with a special root-pruning method and attained heights of ≥1.5 m within the first year of planting (Grossman et al. 2003, Dey et al. 2004). Both sites received the same three plantings in the same arrays but, at Plowboy Bend, the three units adjoined each other in a ''pyramid'' fashion, whereas at Smoky Waters they were adjoined linearly (redtop, no redtop, control).

Nest Monitoring.—We searched for and monitored nests from late April to early August during 2001–2003. Nests were located by systematically searching potential nest sites and by observing behavior of adult birds (Martin and Geupel 1993). We devoted equal time to searching in each treatment unit, alternating searches among the three habitats according to visit and time of day within each site.

We marked nest locations with plastic flagging placed ≥3 m from the nest. We focused on Dickcissel (*Spiza americana*), Field Sparrow (*Spizella pusilla*), Indigo Bunting (*Passerina cyanea*), Red-Winged Blackbird (*Agelaius phoeniceus*), and Song Sparrow (*Melospiza melodia*) because they were the most common nesters at the sites. We monitored nests on average every 3–4 days except during flooding in 2001 and 2002. We found nests of the five focal species in building (22%), laying (20%), incubation (46%), and nestling (12%) stages.

We visited nests in early morning on the expected fledging date (based upon observed date of hatching or estimated age of nestlings) to look for evidence of fledging, such as fledgling begging calls, observation of fledglings, parents carrying food to fledglings, or parents chipping rapidly nearby. Nests found empty prior to this date were considered depredated unless we observed evidence of premature fledging. Nests were considered ''successful'' if they fledged at least one chick; fates of nests where we did not observe these activities were classified as ''unknown'' for the last interval between visits; this interval was censored to not bias the analysis (Stanley 2004). We approached nests and viewed their contents at the maximum distance possible (~2 to 4 m) to ascertain status, and were careful not to leave ''dead end trails'' leading to the nest (Martin and Geupel 1993). Interval fates other than ''successful'' and ''depredated'' included ''abandoned'' and ''flooding.'' Nest failures due to cowbird brood parasitism were from parental desertion (eggs remaining in abandoned parasitized nest) or complete brood loss after parasitism (starvation of host chicks or complete absence of host chicks or eggs in parasitized nests) and were classified as ''cowbird.'' ''Disturbance'' included cases where nests were tipped or removed from the substrate, presumably due to wind or animal trampling, but the nest contents remained on the ground.

Vegetation Measurements.—We used vertical density-board measurements taken between 20 June and 8 July in 2002 from 72 systematically

placed locations in each treatment. Vegetation data were collected in other years, but we chose 2002 data because samples were most complete in that year, and because 2002 represented a temporal midpoint in the study. Percent cover of vertical vegetation was estimated using a nine-increment density board (2.25 m tall $\times$ 0.25 m wide). Percent cover of living and dead vegetation was estimated at each 0.25-m increment from a distance of 15 m. We estimated percent cover in each increment for forb, grass, and woody vegetation, combining them to generate an estimate of mean total percent cover for each board measurement. Grand means were calculated for each sample over all of the 0.25-m increments for each vegetation type of interest (forb, grass, and total vertical vegetation). We focused on grass cover, forb cover, and grass height because visually these differences appeared to distinguish treatments from each other (despite the presence of planted oaks, woody cover was negligible within all treatments because the young seedlings were small). We added a category for ''grass cover <0.25 m'' using only the grass scores from the lowest increment to quantify low dense grass cover, which appeared to visually distinguish redtop treatments from other treatments in the field. We also added ''Mean grass height,'' which was the last-recorded increment having grass cover on the vertical density board. We randomly chose 68 of the 72 vegetation samples in each site X treatment combination due to inconsistent numbers of samples taken in each treatment.

We measured the distance from ground to the bottom of the nest cup (±0.01 m; hereafter nest height) upon finding each nest because nests were, at times, toppled after predation. Nest height was measured in 0.01-m increments with marked sticks that were carried daily for nest-searching. We obtained the spatial coordinates (Universal Transverse Mercator) after termination of nesting using a Trimble Geoexplorer Global Positioning System (GPS) unit with an accuracy of 5–7 m. We measured the distance between each nest and the nearest tree (≥3 m in estimated height) using a Geographic Information System (GIS) to compare nest locations with locations of previously mapped trees and forest patches.

Data Analysis.—We used a general linear model (Proc MIXED, SAS Version 9.1, 2003) with an LSMEANS statement to calculate means and standard errors for each vegetation variable of interest. We included site as a random effect to account for differences between the two sites. We used Likelihood Ratio Tests to assess overall model significance against a null model that included only the intercept; we performed multiple comparisons tests for differences in least squares means among the three treatment types using a Bonferroni adjustment if the overall model was significant ($P \leq 0.05$).

We investigated whether nest densities varied among restoration treatments by comparing observed numbers of nests in each habitat to expected numbers under the assumption of no difference among restoration treatments. We used Chi-square goodness-of-fit tests to assess statistical significance ($P < 0.05$).

We used the logistic-exposure method (Shaffer 2004) to estimate and analyze nest survival. This approach uses a generalized linear model with binomial distribution (interval nest fate = 0 if failed and 1 if successful) and logit link function to model daily nest survival in terms of covariates potentially affecting nest survival (Dinsmore et al. 2002, Shaffer 2004). We treated each interval between nest checks as an observation, thereby allowing time-dependent covariates such as nest stage to change from one interval to the next during the nesting cycle (Shaffer 2004). We did not include observation days of building stage nests in the analysis. Intervals between nest observations were usually >1 day and varied in length, and we used the modified logit link function: $g(\theta) = \log_e (\theta^{1/t}/[1 - \theta^{1/t}])$, where θ is the interval survival rate and t is the interval length in days (Shaffer 2004). The effective sample size, which follows from the model likelihood, is the sum of the total number of days that all nests were known to have survived and the number of intervals that ended in failure (Rotella et al. 2004). We used the GENMOD procedure in SAS (SAS Institute 2000) to estimate parameters of the logistic-exposure models.

We developed *a priori* candidate models involving (1) covariates related to our hypothesis about effects of the restoration treatment on nest survival, and (2) additional covariates that we believed might explain variation in nest survival (below).

— Restoration treatment, which was defined as control, redtop, or no redtop.
— Nest height, which has been positively related to nest survival for some of the same species in other studies in the region (Burhans et al. 2002, Burhans and Thompson 2006).

— Nesting stage, for which we considered the stage (laying, incubation, nestling) confirmed at the terminal visit of the interval to be the stage for that interval; e.g., if a nest transitioned from incubation to the nestling stage during an interval, a value of ''nestling'' was assigned to that interval.

— Day-of-year, which may reflect seasonal variation in predator activity or abundance. We included both linear and quadratic terms (day-of-year, [day-of-year]^2), the latter term to account for non-linear nest survival over the season in models with ''day-of-year'' (Grant et al. 2005).

— Cowbird parasitism, which presumably affects nest predation because of increased begging calls and nest visits by hosts and/or cowbirds, which alerts predators to the presence of nests (Dearborn et al. 1998, Hauber 2000).

— Year, site (Plowboy Bend or Smoky Waters), bird species, and site were included as categorical covariates to account for additional unexplained variation.

We considered models that corresponded to the covariates and reflected our hypotheses about relationships of habitat and other factors to nest survival: (1) day-of-year, (2) cowbird parasitism, (3) nest height, (4) nesting stage, and (5) habitat. Each model also included species, year, site, and year × site to reflect our study design and to reduce the chance of statistical confounding. We also considered a model that included only species, year, site, and year × site, and a global model that included all covariates.

Nests were considered ''successful'' for the relevant interval if at least one young fledged. We considered complete nest losses due to nest predation, flooding, unknown weather events, or apparent trampling by animals, abandonment, or cowbird parasitism to be ''failed'' nesting attempts. Only one nest fledged a cowbird but not host young; it was considered ''successful'' for the interval for which it fledged the cowbird.

We evaluated support by comparing multiple models, fit to the same data, using an information-theoretic approach (Burnham and Anderson 2002). We considered the model with the lowest value for Akaike's Information Criterion (AIC) to be the best approximating model for the data, and considered models within two AIC units of the best model to represent potential best models (Burnham and Anderson 2002). However, we report 95% confidence intervals (CIs) for each parameter estimate based on model-averaging to account for model-selection uncertainty (Burnham and Anderson 2002). We used model-based methods (Shaffer and Thompson 2007) to estimate nest survival (including 95% CIs) in relation to covariates.

We computed species-specific period survival to show model-based relationships over the entire nest period in terms of the covariates by raising daily survival to a power equal to the average length of the nest cycle for each species (Field Sparrow = 23 days; Dickcissel = 25.5 days; Indigo Bunting, Red-winged Blackbird, Song Sparrow = 27 days; Ehrlich et al. 1988; D. E. Burhans, unpubl. data). We realize this average does not correspond to the exact nest cycle for each species, but it is close for most of the species, and our goal was to simplify graphic interpretation of model-based results. We show model-based relationships between 26-day period survival rates and covariates other than species by weighting the daily survival rate estimate for each species by the proportion of observed nests of that species. We computed model-averaged survival estimates for a given covariate by holding remaining covariates at their mean value. We calculated period mortality due to a specific cause (abandonment, predation, parasitism, disturbance) by multiplying the model-based average period mortality rate (1 − average period survival) by the proportion of nests in that category; for example, if the average period mortality over all nests was 0.75 and the proportion of abandoned nests was 0.10, period mortality due to abandonment would be estimated as 0.10 × 0.75 = 0.075.

We used logistic regression to model the probability of cowbird parasitism, including only nests initiated by the second week of July, as cowbirds typically do not lay after this time in this region (Burhans 1997). We included bird species in each of the models similar to the nest survival models. Models included: (1) species only, (2) habitat (redtop, no redtop, control) and species, (3) site (Plowboy Bend or Smoky Waters) and species, (4) year and species, and (5) a global model with all of the above covariates. We also considered (6) a model incorporating distance to the nearest tree (≥3 m in estimated height; range = 1–263 m.). Parasitism probability has been negatively associated with distance to the nearest tree in other studies (Clotfelter 1998), presumably because female cowbirds are known to survey for

TABLE 1.   Distribution of nests across restoration treatments for five songbird species in lower Missouri River floodplains, 2001–2003. Chi-square tests (df = 2, all tests) were used to assess whether nest number and densities varied with restoration treatment.

| Species | Restoration treatment | | | χ^2 | P |
	Redtop	No redtop	Control		
Dickcissel	22	37	8	18.84	<0.001
Field Sparrow	23	5	22	12.28	0.002
Indigo Bunting	5	31	25	18.23	<0.001
Red-winged Blackbird	70	143	40	66.55	<0.001
Song Sparrow	9	15	8	2.69	0.26

host nests from trees (Hauber and Russo 2000, Saunders et al. 2003).

RESULTS

We analyzed data from 463 nests representing an effective sample size of 4,773. This represented 67 Dickcissel nests (daily survival estimate assuming constant survival = 0.941; CI = 0.913–0.960), 50 Field Sparrow nests (0.958; 0.930–0.975), 61 Indigo Bunting nests (0.957; 0.934–0.972), 253 Red-winged Blackbird nests (0.951; 0.936–0.962), and 32 Song Sparrow nests (0.933; 0.888–0.961). Estimated daily survival rate of all species combined under the assumption of constant survival was 0.950 (CI = 0.939–0.959) and average period survival over the entire nesting cycle was 0.26. Thus, average period mortality across the entire nest cycle from all sources was 0.74. Predation (215 losses) accounted for 63% of period mortality. Flooding (18 losses; 5%); abandonment, including that attributable to cowbirds (11 losses, 3%); and unknown (weather or animal trampling) events (9 losses, 3%) accounted for additional mortality. Complete nest losses due to cowbird parasitism occurred only through abandonment with desertions at one Field Sparrow nest and three Indigo Bunting nests (1%). Nests were not equally distributed among restoration treatments for all species except Song Sparrow (Table 1).

The best approximating model of nest survival was that with parasitism (Table 2; model-estimated period survival for parasitized nests: 0.10, CI = 0.00–0.40; unparasitized nests: 0.27, 0.19–0.35). Day-of-year and global models also received support (Table 2). We found only weak support for differences in nest survival attributable to restoration treatment (Table 2, Fig. 1B). The site × year and species covariates were not related to specific hypotheses, but we include graphs of the model-averaged values to show the considerable variation (Fig. 1C, D).

Cowbird Parasitism.—We analyzed 426 nests for probability of cowbird parasitism. Cowbird

TABLE 2.   Candidate models of daily nest survival for five songbird species in lower Missouri River floodplains, 2001–2003. Models with a lower ΔAIC and a greater Akaike weight (w_i) have greater support; K is the number of parameters in the model.

Model	Variables	K	AIC	ΔAIC	w_i
Parasitism	Year × Site, Year, Site, Species, Parasitism[a]	11	1380.73	0	0.52
Day-of-year	Year × Site, Year, Site, Species, Day-of-year[b]	12	1382.06	1.34	0.27
Global	Year × Site, Year, Site, Species, Parasitism[a], Day-of-year[b], Nest height, Nesting stage, Habitat	18	1383.98	3.33	0.10
Species	Year × Site, Year, Site, Species	10	1385.29	4.55	0.05
Nest height	Year × Site, Year, Site, Species, Nest height	11	1386.74	6.01	0.03
Nesting stage	Year × Site, Year, Site, Species, Nesting stage (laying, incubation, nestling)	12	1387.51	6.79	0.02
Restoration treatment	Year × Site, Year, Site, Species, Restoration treatment (redtop, no redtop, control)	12	1388.28	7.56	0.01
Null		1	1420.55	39.76	0.00

[a] Unparasitized = 0; parasitized = 1.
[b] Includes day-of-year, (day-of-year)^2.

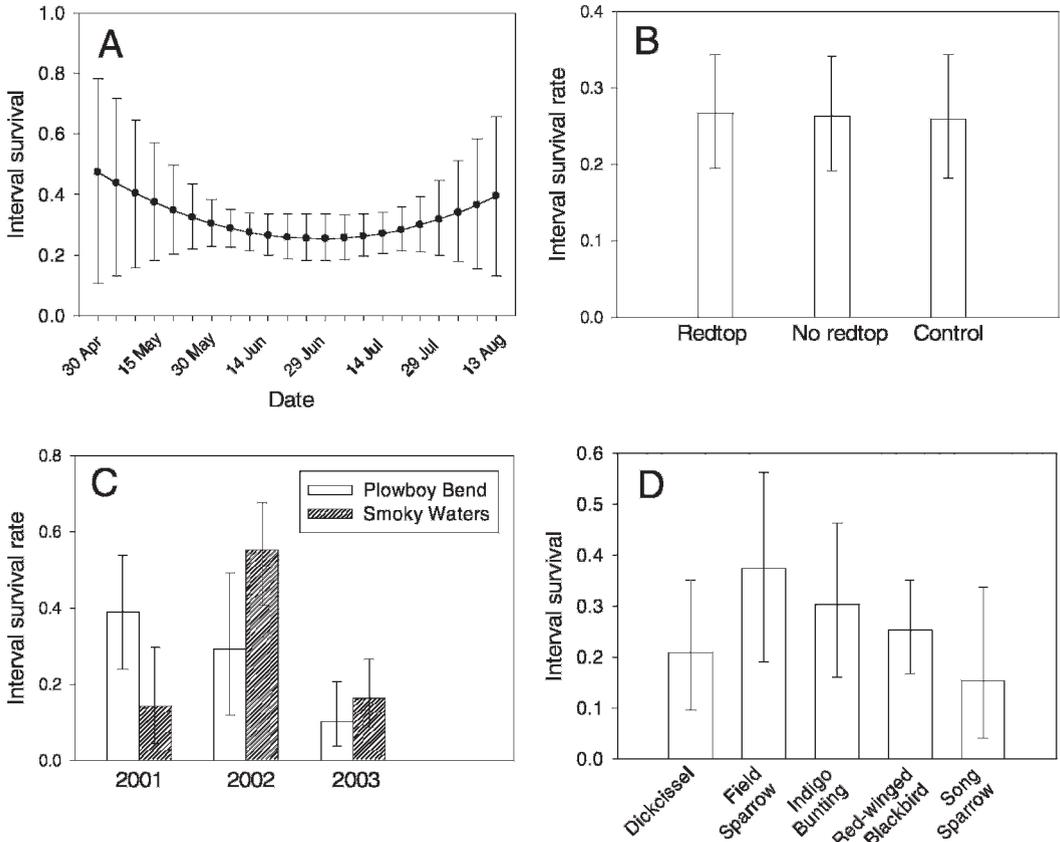FIG. 1. Model-averaged interval survival estimates (±95% confidence intervals) for covariates (A) day-of-year, (B) restoration treatment, (C) site × year, and (D) species from Missouri River floodplain reforestation sites, 2001–2003.

parasitism frequency was 24.0% for Indigo Buntings ($n = 55$ nests); other species were rarely parasitized (Dickcissel 5.1%, $n = 59$ nests; Field Sparrow 4.6%, $n = 44$ nests; Red-winged Blackbird 0.8%, $n = 239$ nests; Song Sparrow 3.5%, $n = 29$ nests). The best-supported model included distance to nearest tree and species (Table 3). Probability of parasitism decreased with distance to the nearest tree (Fig. 2).

Vegetation.—Mean forb cover varied overall among treatments ($\chi^2 = 13.1$, df = 2, $P < 0.05$; Table 4). Mean forb cover was lower in redtop versus no redtop treatments ($t = 12.64$, df = 2, adj. $P = 0.019$), but did not differ in pairwise multiple comparisons between other treatments. Grass cover <0.25 m varied overall among treatments ($\chi^2 = 8.1$, df = 2, $P < 0.05$; Table 4) but did not differ in any multiple-comparisons tests between pairs of treatments.

DISCUSSION

We found little support for our principal hypothesis about variability in nest survival due to differences in floodplain restoration treatments. Nest densities generally varied among habitat-treatment types and mean forb cover was lower in redtop treatments; the model relating nest survival to restoration treatment had the weakest support of any model except the null model.

Twedt et al. (2002) working in Mississippi and Louisiana also evaluated songbird nest survival in relation to different floodplain restoration treatments. Their study considered plantings with a wider range of ages (2–10 years) and tree heights (~3–15 m), and they also found no differences in nest survival among treatments. Daily nest survival of Indigo Bunting, Red-winged Blackbird, and Dickcissel in their treatments with nest sample sizes ≥31 ranged from 0.919 to 0.948 (Twedt et al. 2002).

TABLE 3. Candidate models for incidence of cowbird brood parasitism in lower Missouri River floodplains, 2001–2003. Models with a lower ΔAIC and a greater Akaike weight (w_i) have greater support; K is the number of parameters in the model.

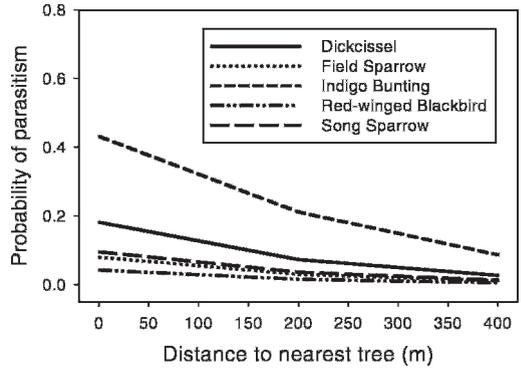| Model	K	AIC	ΔAIC	w_i
Distance to nearest tree, species	6	130.89	0.00	0.95
Global, all variables	11	136.88	5.99	0.05
Species only	5	141.96	11.07	0.00
Site, species	6	143.91	13.02	0.00
Year, species	7	144.54	13.65	0.00
Restoration treatment, species	7	145.87	14.98	0.00
Null	1	169.36	38.48	0.00

FIG. 2. Model-based probability of cowbird parasitism in relation to distance from nearest tree for songbird species using Missouri River floodplain reforestation sites, 2001–2003.

Daily nest survival rates at our sites were comparable to other studies in central Missouri, but were both higher and lower than sites in northern Missouri. Average daily survival for Field Sparrows in a study at old-field sites <30 km away (Burhans et al. 2002) was 0.936 ± 0.004 (SE) compared with 0.958 from model-based estimates in the present study. Daily nest survival for Indigo Buntings at those same old fields was 0.955 ± 0.003 compared to our model-based estimate of 0.957. In contrast, daily survival of Indigo Buntings nesting in riparian forests and buffer strips in northeastern Missouri was 0.90 (Peak et al. 2004). Our model-based Field Sparrow (0.330) and Dickcissel (0.203) interval survival rates (Fig. 1D) were lower than Mayfield success rates for Field Sparrows (0.472 ± 0.6 SE) and Dickcissels (0.297 ± 0.2) in Conservation Reserve Program sites in northern Missouri (McCoy et al. 1999).

A negative relationship between cowbird parasitism and nest survival was evident from the best model (Table 2), although only four complete nest losses, via nest abandonment, were directly attributable to cowbird parasitism. Nest abandonment attributed to cowbird parasitism has been noted frequently for Field Sparrows at more heavily-parasitized locations (Strausberger and Burhans 2001), but has rarely been documented for Indigo Buntings after clutch initiation (reviewed in Burhans et al. 2000). We may have incorrectly attributed bunting abandonments that were due to death of parents or other disturbances to cowbird parasitism. That would not affect the outcome of the logistic-exposure survival analysis, however, because these nests would still be categorized as parasitized. Parasitized nests could

have experienced lower survival if predators were attracted to them because of more frequent and louder begging calls by cowbird offspring (Dearborn 1999) or more frequent visits by host parents (Dearborn et al. 1998). However, we had few parasitized nests that survived sufficiently long to contain cowbird nestlings. A final explanation could be that both nest predators and cowbirds tended to find the same nests.

Considerable variation in nest survival among years, sites, and dates was obvious from our most-supported models of daily survival. Nest survival in an earlier study of Field Sparrow and Indigo Bunting in Missouri old-field habitats (Burhans et al. 2002) was similarly higher in early May and August and lower in June and early July. Temporal patterns in nest survival likely reflect unmeasured variables such as within-season differences in predator activity or among-year differences in predator foraging patterns or abundance. Flooding may have contributed to important yearly mortality differences, particularly at one site. Sixteen nests were lost to flooding at Smoky Waters in 2001 and 2002 with 15 of those lost in 2001, whereas only two nests were lost to flooding at Plowboy Bend, both in 2001 (Fig. 1C). We did not detect a strong effect of nest height on nesting success, although two other studies from the same region found nest survival increased with increasing nest height (Burhans et al. 2002, Burhans and Thompson 2006). The model-averaged parameter estimate for nest height (0.03, CI = −0.10–0.15) suggested a weak positive effect, but the range of heights in the present study (0–2.10 m) was lower (0 to 5.5 and

TABLE 4.   Least-squares means (±95% CI) for vegetation measurements from bottomland restoration sites in lower Missouri River floodplains, 2002. Vegetation variables (expressed as proportions), except for mean grass height, are mean cover values across four vertical board measurements taken for each sample.[a]

Vegetation variable	Restoration treatment		
	Redtop	No redtop	Control
Mean grass cover	0.21 ± 0.16	0.16 ± 0.16	0.26 ± 0.16
Mean forb cover	0.05 ± 0.10	0.27 ± 0.10	0.16 ± 0.10
Mean total vegetation	0.27 ± 0.22	0.43 ± 0.22	0.42 ± 0.22
Mean grass height, m	0.80 ± 0.40	0.67 ± 0.40	1.07 ± 0.40
Grass cover <0.25 m	0.81 ± 0.29	0.23 ± 0.29	0.43 ± 0.29

[a] Sixty-eight samples were taken for each treatment in each site.

0 to 3.6 m, respectively). The reduced range of nest heights in our study may not have been sufficient to reveal an effect, given the positive influence of extraordinarily tall nests on survival in Burhans et al. (2002).

Probability of cowbird parasitism decreased with distance to the nearest tree (Fig. 2). This finding is in agreement with those of Clotfelter (1998), Hauber and Russo (2000), and Saunders et al. (2003). Johnson and Temple (1990) found that parasitism frequencies in open prairie habitats were higher near wooded edges, which presumably contained trees for perches, than far from wooded edges. Twedt et al. (2002) found higher parasitism frequencies in stands with tall cottonwood (*Populus* spp.) trees compared to younger stands with shorter trees in Mississippi and Louisiana floodplain restoration sites.

Our sites experienced low parasitism compared to more forested (~70%) sites in the region (Burhans et al. 2000, Burhans and Thompson 2006) despite having low (~33%) landscape-level forest cover. Field Sparrows experienced parasitism of 11.3% (n = 443 nests) in a study of cowbird parasitism in old fields within 30 km of our sites (Burhans and Thompson 2006) compared to 4.6% in this study; Indigo Buntings experienced parasitism frequencies of 48% (n = 295 nests) in old fields compared to 23.6% in this study. Dickcissels were parasitized at 9.6% (n = 242 nests; Winter 1999) in southwestern Missouri prairie fragments compared to 5.1% at our sites; Dickcissels at other sites in the Midwest have been parasitized at frequencies of 60–85% (Zimmerman 1983). Landscapes with low forest cover such as ours are usually associated with high cowbird abundance and parasitism (Robinson et al. 1995, Donovan et al. 2000, Thompson et

al. 2000). We observed Brown-headed Cowbirds only rarely during 5 years of breeding point counts at these sites (D. E. Burhans and B. G. Root, unpubl. data), whereas cowbird detections were an order of magnitude higher on point counts at old field sites 30 km distant during the same period (Burhans and Thompson 2006). Old fields and large river floodplains are different habitats, and may be prone to different levels of parasitism (Robinson and Herkert 1997), possibly because of differences in vegetation structure. Twedt et al. (2002) similarly worked at sites having low landscape-level forest cover (36%), but noted lower cowbird numbers in stands having short trees at their restoration sites. Cowbirds could be abundant in these large river landscapes, but possibly select habitats within them that have more or taller trees (Twedt et al. 2002). Studies have shown that regional and landscape effects such as forest cover constrain parasitism at more-local scales (Donovan et al. 2000, Thompson et al. 2000). However, most landscape-level studies have used forested habitats to document parasitism frequencies and cowbird numbers (e.g., Robinson et al. 1995). Several studies have looked at variation in cowbird numbers and parasitism among habitats (Hahn and Hatfield 1995, Strausberger and Ashley 1997, Robinson et al. 1999), but the relationship between landscape-level cowbird abundance and allocation of cowbirds among habitats deserves further work. Much of our understanding about landscape determinants of cowbird parasitism comes from work in the 1980s–2000s in upland forested habitats (Brittingham and Temple 1983, Robinson et al. 1995, Donovan et al. 2000, Thompson et al. 2000). Birds using forested bottomlands, abandoned bottomland fields, and grasslands within large

floodplain agricultural landscapes may differ from forests in habitat preference by cowbirds, and require different management considerations.

We do not have data for livestock presence, but low parasitism in our study could be explained by the apparent scarcity of cattle operations in proximity to our sites. Nesting studies have shown decreases in parasitism with distance from grazed habitats (Goguen and Matthews 1999, 2000) despite cowbirds' ability to commute between breeding and feeding areas (Thompson 1994).

We found differences in habitat use by the species in the restoration treatments, but our data did not show that nest survival varied with planting treatment. Our findings and those of Twedt et al. (2002), who also studied agricultural floodplains low in regional forest cover, indicate that further study of interactions between landscape- and habitat-level patterns in Brown-headed Cowbird abundance and parasitism frequencies are warranted.

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