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SPECIES RICHNESS AND NESTING SUCCESS OF MIGRANT FOREST BIRDS IN NATURAL RIVER CORRIDORS AND ANTHROPOGENIC WOODLANDS IN SOUTHEASTERN SOUTH DAKOTA

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Abstract. Forest fragmentation is thought to be partially responsible for declines in many Neotropical migrant birds due to the combined effects of higher rates of brood parasitism and increased predation near forest edges. A majority of the forested habitat in the northern prairie region is found in riparian corridors, but this native habitat has been much reduced from its historical extent. However, additional woodland nesting habitat has been established within the last century in the form of isolated woodlots on farms. We compared abundance, species richness, and nesting success of migrant forest birds breeding in native riparian corridors and anthropogenic woodlots. The two habitats had similar bird abundances but native riparian woodlands were more species-rich than woodlots. We located a total of 650 nests, with 320 nests of 15 species in woodlots and 331 nests of 25 species in riparian corridors. Nesting success was not significantly different between the two habitats for all species combined or for individual species with ≥15 nests in each habitat. Nests above 5 m were more successful than lower nests, but distance to woodland edge did not influence nesting success. Nests initiated in the middle and late portions of the nesting season were more successful than early season nests, significantly so in woodlots. Thus, anthropogenic woodlots were as suitable as natural habitats for successful nesting. However, many of the Neotropical migrants occurring in riparian habitats were absent from woodlots, which suggests that riparian corridors are especially important habitats for breeding birds in the northern prairie region.

Key words: edge effects, forest fragmentation, Neotropical migrant, nesting success, parasitism rates, woodlots.

Riqueza de Especies y Éxito Reproductivo en Aves Migratorias de Bosque en Corredores Ribereños Naturales y en Parches de Bosque Antropogénicos en el Sureste de Dakota del Sur

Resumen. Se cree que la fragmentación de los bosques es parcialmente responsable por la disminución de varias especies de aves migratorias neotropicales debido a los efectos de borde que incrementan la tasa de parasitismo de nidos y la depredación. La mayoría de los hábitats boscosos en la región de la pradera norteña se encuentran en corredores ribereños, pero este tipo de hábitat nativo ha sido reducido en gran medida en comparación con su extensión original. Sin embargo, durante el siglo pasado se establecieron zonas boscosas adecuadas para la nidificación en forma de parches de bosque aislados dentro de granjas. Comparamos la abundancia, la riqueza de especies y el éxito de nidificación de aves migratorias de bosque que se reprodujeron en corredores ribereños nativos y en parches de bosque antropogénicos. Los dos hábitats presentaron abundancias de aves similares, pero las zonas boscosas nativas tuvieron más especies que los parches de bosque antropogénicos. Localizamos un total de 650 nidos, de los cuales 320 correspondientes a 15 especies estuvieron dentro de los parches de bosque y 331 correspondientes a 25 especies en los corredores ribereños. El éxito reproductivo no fue significativamente diferente entre los dos tipos de hábitat cuando el análisis incluyó a todas las especies ni cuando las especies que tuvieron un número de nidos mayor a 15 se analizaron individualmente. Los nidos localizados a más de 5 m de altura fueron más exitosos que aquellos localizados a menores alturas, pero la distancia a la orilla del bosque no influenció el éxito de anidación. Los nidos iniciados a la mitad y al final de la temporada de nidificación fueron más exitosos que los iniciados al principio de la temporada, especialmente en los parches de bosque. Por lo tanto, los parches de bosque antropogénicos fueron tan adecuados como los hábitats naturales para producir nidadas exitosas. Sin embargo, muchas de las aves migratorias neotropicales localizadas en los

hábitats ribereños no fueron registradas en los parches de bosque, lo cual sugiere que los corredores ribereños son hábitats especialmente importantes para la reproducción de las aves en la pradera norteña.

INTRODUCTION

Recent declines in many Neotropical migratory bird species have been documented at breeding grounds in North America (Robbins et al. 1989, Askins et al. 1990, DeGraaf and Rappole 1995). These declines have been attributed to a variety of factors including habitat fragmentation on wintering and breeding grounds, as well as loss of habitat necessary for migratory stopover (Robbins et al. 1989, Terborgh 1989, Finch 1991, Moore et al. 1993). In addition to reducing available forested habitat for breeding, forest fragmentation is generally associated with decreased nesting success in woodland-nesting birds. This reduction is mainly due to the combined effects of a higher rate of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*, Brittingham and Temple 1983, Robinson et al. 1995) and increased predation near forest edges compared to the interior (Wilcove 1985, Yahner and Scott 1988, Martin 1992). In addition, woodland patch size may affect other factors associated with nest success, such as food abundance and forest age structure. Burke and Nol (1998) showed that food abundance increases with forest patch size, and increased food resources may improve nesting success (Zanette et al. 2000). Smaller forest patches also tend to support more first-year breeding males (Zanette 2001), which could lead to lower nesting success because of reduced foraging efficiency or less effective parental care in inexperienced birds (Gochfeld and Burger 1984, Marchetti and Price 1989, Desrochers 1992).

Most of the results documenting reduced nesting success in small woodland patches are from eastern deciduous forests, and whether these findings are applicable to deciduous woodland habitats in the northern prairie region has not been established. A majority of the forest habitat in the northern prairie region is found in relatively narrow and disjunct riparian corridors (Van Bruggen 1996), as opposed to the once vast and contiguous deciduous forests of eastern North America. These riparian corridors provide woodland habitat necessary for breeding Neotropical migrants characteristic of eastern deciduous forests (Tallman et al. 2002), although habitat structure and vegetation composition may vary among different river systems. The riparian zones in the northern prairie region are generally linear in nature and are embedded within a matrix of grassland or agricultural habitats. This landscape pattern creates a higher habitat edge to woodland interior ratio than is found in the more continuous deciduous forests of eastern North America. In addition to the intrinsically high edge ratio, riparian habitats in the northern prairie region have been substantially reduced in extent from historical conditions. For example, riparian woodlands along the middle and lower Missouri River have been reduced by at least 40%–80% from 1892–1982 (Hesse et al. 1988), due mainly to conversion to agricultural fields. Additional woodland habitat, however, has been established within the last century in the form of isolated shelterbelts and woodlots associated with farmsteads. These isolated, human-planted fragments now account for a considerable amount of the woodland nesting habitat in the northern prairie region (Castonguay 1982). Avian density and species richness generally increase with woodlot area for both migrating and breeding birds (Martin 1980, Yahner 1983), but density and richness of Neotropical migrants in these isolated patches of habitat were similar to those found in continuous riparian habitat during migration (Carlisle 1998, Dean 1999, Swanson et al. 2003, in press). However, to our knowledge no studies have yet compared avian abundance and richness between these habitats during the breeding season.

Relative nesting success in these two habitats is also unstudied in the northern prairie region. Data from eastern deciduous forests suggest that nesting success should be higher in the comparatively larger riparian woodlands than in the much smaller woodlots, but this supposition is untested. Additionally, the much smaller extent of the landscape composed of woodland habitat compared to eastern forests and regional variation in the densities of nest predators and brood parasites might affect nesting success of local avian communities.

Some authors have hypothesized that farmstead woodlots and fragmented forest patches may serve as ecological traps (Gates and Gysel 1978, Robinson 1992, Dobkin 1994). They suggest that the fragmented habitat may attract birds to the forest patches for breeding, although the isolated woodlots may offer only limited nesting success. Such ecological traps could reduce overall nesting success for a species and therefore contribute to population declines.

The main goal of this study was to determine the success rate of open-cup and pendant nesting Neotropical and short-distance migrants breeding in natural and anthropogenic deciduous woodlands of southeastern South Dakota, to ascertain if anthropogenic habitats provide an adequate environment for successful nesting, and therefore if human-planted woodlots can substitute for lost native riparian woodlands for nesting forest birds in the northern prairie region (Dobkin 1994). We also examined whether relative avian abundance and species richness differed between habitat types. We addressed two specific hypotheses. First, we predicted that nesting success would be higher in river corridor habitats than in woodlots, because the larger and more contiguous woodlands of river corridors contain less edge habitat, which in turn should lower rates of predation and brood parasitism. Second, we hypothesized that relative abundance and species richness of the avian community would be greater in riparian corridors than in woodlots, because river corridor woodlands are larger and contain greater vegetation diversity and variation in habitat structure (Dean 1999, Swanson et al. 2003).

METHODS

STUDY SITES

In 2000 we used the six woodlots used by Swanson et al. (2003) and one additional woodlot, and the four riparian areas described by Dean (1999). In 2001 and 2002, we retained these study sites and added six woodlots and 4 riparian areas for a total of 13 woodlots and 8 riparian areas. The 13 woodlots were scattered along an approximately 40-kilometer route in Clay County, South Dakota (Fig. 1) and ranged from approximately 0.7 to 3.5 hectares in area. All woodlots were separated from each other by at least 1 km. The architecture of the woodlots

was roughly rectangular or arranged in an "L"-shape. Common tree species in woodlots surveyed by Swanson et al. (2003) included elms (*Ulmus* spp., 54% of all trees), white mulberry (*Morus alba*, 20%), boxelder (*Acer negundo*, 9%), hackberry (*Celtis occidentalis*, 8%) and green ash (*Fraxinus pennsylvanica*, 4%).

Four riparian study sites were located in the Big Sioux River (and Brule Creek) riparian corridor in Union and Lincoln counties, and four in the Missouri River corridor in Clay and Union counties. The Big Sioux River study sites included three riparian woodlands along the Big Sioux River and one site with both riparian and upland woodlands along Brule Creek (a tributary of the Big Sioux River). Big Sioux River corridor sites included River Sioux Park, where South Dakota Highway 50 crosses the river into Iowa (42°45′N, 96°37′W), Wilson Savanna Preserve (43°09′N, 96°30′W), and Oak Ridge Game Production Area (43°10′N, 96°30′W). Union Grove State Park (42°55′N, 96°46′W) contained the Brule Creek site. The Missouri River study sites were located in state-owned riparian habitats west, south, and southeast of Vermillion, South Dakota. These included Clay County Park (42°42′N, 97°00′W), Myron Grove River Access Area (42°46′N, 97°07′W), a game production area south of the Vermillion Airport (42°45′N, 96°58′W), and a river access area southeast of Burbank (42°42′N, 96°48′W). All river corridor woodlands were bordered by agricultural fields, and woodland width varied from 50 m to 300 m at all sites.

Habitat structure differed between the Big Sioux River and its tributaries and the Missouri River corridor (Dean 1999; Swanson et al., in press). Big Sioux River (and tributaries) sites were more frequently disturbed by flooding and contained a mixture of hardwood species, including boxelder, elm, silver maple (*Acer saccharinum*), green ash, and some cottonwood (*Populus deltoides*) and hackberry. The canopy was comparatively low but continuous, and the understory was relatively sparse and dominated by buckthorn (*Rhamnus cathartica*) and herbaceous vegetation. Three of the Big Sioux River sites also contained upland bur oak (*Quercus macrocarpa*) savanna habitats continuous with riparian woodlands, which were not found in the Missouri River corridor sites. Missouri
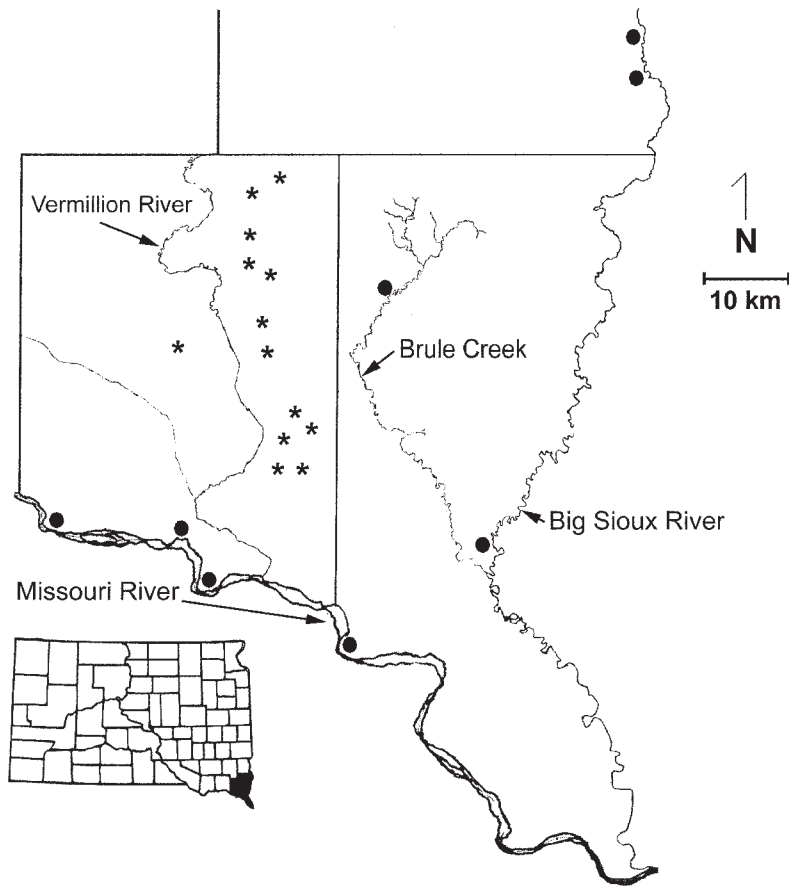
FIGURE 1. Location of study units in southeastern South Dakota, 2000–2002. Circles represent river corridor study sites and stars represent woodlot study sites. Inset map is of South Dakota, showing counties.

River riparian habitats were dominated by a cottonwood gallery forest with some box-elder, elm, hackberry, and white mulberry (*Morus alba*) also present. These sites generally had a dense mixed understory dominated by dogwood (*Cornus* spp.) and prickly ash (*Zanthoxylum americanum*). Two of the Missouri River study sites also contained areas of early successional vegetation, dominated by willows (*Salix* spp.) and young cottonwoods, which were not present at Big Sioux River sites. Because of the considerable differences in vegetation composition and habitat structure of the two riparian corridors sampled in this study, we treated the two river corridors separately for comparisons of avian community metrics. However, although we addressed the Missouri and Big Sioux River drainages individually for species richness and density, we

combined nest data from the two riparian corridors because woodland area was roughly similar (and much greater than in woodlots), and to maximize the sample size used for the nest success analysis.

BREEDING BIRD ABUNDANCE AND SPECIES RICHNESS

We used point counts for species density and richness determinations (Hutto et al. 1986, Rosenstock et al. 2002). Five or six points were established along roughly linear transects at riparian sites, spaced at 200 m intervals to avoid double counting of birds. We established 21 and 20 points at Big Sioux and Missouri River corridor sites, respectively. Each woodlot contained one point, with the exception of the two largest, which contained two points separated by more than 200 m, for a total of 15

points in woodlots. All points in both habitats were at least 30 m from the habitat edge. We conducted surveys four times during the breeding seasons of 2000–2002, including early (2–9) and late (27–30) June, mid (13–21) July, and early (3–12) August. Counts were performed in the early morning between 04:45 and 09:00 (CST) and were not performed on days with rain or high winds. Survey periods lasted 10 min at each point. We reversed the direction of survey routes on successive counts, and at least 10 days separated each count. This number of points and replicates has been shown to provide stable density estimates in habitats with heterogeneous vegetation (Morrison et al. 1981). Birds detected by sight or sound were identified and counted and their distance (or estimated distance for auditory detections) from the point center was measured with a Ranging Model 620 rangefinder. We only counted birds flying overhead if they were potential users of the habitat (e.g., a crow but not a shorebird). Birds detected while walking between points were counted and their distance, or estimated distance, from the nearest point documented. Relative abundance (birds per point) was computed from all detections (Rappole et al. 1979, Swanson et al. 2003), and density estimates (birds per km²) were calculated for all species that had at least 30 observations after data truncation at 90 m with program DISTANCE version 4.1, release 2 (Thomas et al. 2003).

NEST SUCCESS

We targeted Neotropical and short-distance migrants building open-cup or pendant nests in woodlots and riparian corridors. Cavity-nesting species were not monitored as these nests generally suffer lower predation rates. Birds meeting the criteria listed by DeGraaf and Rappole (1995) were considered Neotropical migrants. In particular, we focused on some of the more common species because roughly 15–20 nests per species in each habitat are required for adequate determination of nesting success (Hensler and Nichols 1981, Willson and Gende 2000). These species included Eastern Kingbird (*Tyrannus tyrannus*), American Robin (*Turdus migratorius*), Gray Catbird (*Dumetella carolinensis*), Brown Thrasher (*Toxostoma rufum*), Yellow Warbler (*Dendroica petechia*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*),

and Orchard (*Icterus spurius*) and Baltimore Orioles (*I. galbula*). Of these species, local, regional, or continent-wide declines in populations have been documented for Brown Thrashers, Rose-breasted Grosbeaks, and Orchard and Baltimore Orioles (DeGraaf and Rappole 1995, Peterson 1995, Rich et al. 2004).

We followed the techniques described by Martin and Geupel (1993) to find active nests. Nest searching started in late April or early May and continued through early August. These dates covered the majority of the nesting season for Neotropical and short-distance migrants in South Dakota (Peterson 1995, Tallman et al. 2002). We conducted a pilot study in the summer of 2000, with two nest searchers and an incomplete survey of available nesting habitat. During the breeding seasons of 2001 and 2002 we thoroughly searched four Missouri River and two Big Sioux River (and tributaries) sites, and five of the woodlots for nests. For each nest found, we recorded the date, time, presence and activity of adults, number of eggs, presence of cowbird eggs, and number and age of nestlings. Each nest was checked every three to four days with a mirror attached to an extendable pole (nest pole), to monitor activity, count eggs and nestlings, and determine success or failure. Nests that were too high to view with a nest pole were monitored through observations of adult behavior so that all data could be taken with the exception of egg and nestling numbers. The location of each nest was described on its nest data card and any nests that were difficult to relocate were marked with flagging at a distance of 5–20 m to avoid the potential for increased predation associated with nest marking (Martin and Geupel 1993). Each nest that fledged at least one chick was considered successful. Any nestlings observed at 80% or more of their mean fledging age that were absent at the final nest check and present at the previous nest check were considered to have fledged, unless the condition of the nest suggested predation. We used the midpoint method to calculate the number of exposure days for nests with certain fate (success or failure), and the last day active method to calculate exposure days for nests whose fate was uncertain (Manolis et al. 2000).

After the young fledged or the nest failed we measured vegetation surrounding the nest, to determine if vegetation characteristics influ-

enced nest success. Data collected included the plant species in which the nest was built, height and location of the nest (e.g., fork, branch, ground), vegetation category, and distance to edge. The three different categories of nest vegetation were ''shrub'' for habitats with dense, shrubby vegetation with most vegetation having a trunk diameter <5 cm at breast height (dbh), ''closed canopy woodlands'' for closed canopy habitats with most trees having trunks >5 cm dbh, and ''open woodland'' for habitats with an open canopy and a low density of trees with trunk diameter >5 cm dbh. Birds that nested high in the canopy in open woodland habitats with a shrubby understory were included in the ''open woodland'' category because of the potential exposure of their nests to avian predators.

STATISTICAL ANALYSIS

Comparisons of species richness among different sites and different studies are confounded by differences in sampling effort and numbers of observations because more species should be detected with an increased number of observations. The technique of rarefaction calculates an expected number of species ($E[S_n]$) for a given sample size from each site (James and Rathburn 1981) and thus may be used to compare species richness at sites with different numbers of observations. We calculated rarefaction curves for both riparian woodlands and farmstead woodlots to determine if species richness differed between the two habitats.

We used program DISTANCE version 4.1, release 2 (Thomas et al. 2003) to calculate the density of each species for which we had ≥30 observations. This minimum number of observations (30), although less than what is recommended, was chosen to increase the number of species compared. Based upon recommendations by Buckland et al. (2001), the data were grouped into seven distance intervals and all observations beyond 90 m (approximately 5% of observations) were excluded from the analysis. A uniform key function with a cosine series expansion best fit the data and was used for all density calculations. All results are presented as means ± SD. The significance level for all tests was set at α < 0.05.

We used Mayfield (1961, 1975) calculations of daily nest survival to estimate overall nesting success in each habitat. A Z-test (Johnson 1979) was used to compare Mayfield estimator results to determine if there was a difference in nesting success among habitats or vegetation variables. This test was conducted for the overall migrant population (all species pooled), for Neotropical and short-distance migrants, and for individual species for which we found sufficient numbers of nests (n ≥15 in each habitat). We ran additional comparisons for nest site variables such as height, distance to edge, and vegetation habitat category (e.g., shrub, closed canopy forest, open canopy forest) to determine whether nest site characteristics and breeding strategies affected nesting success. We divided the nesting season into three periods to examine possible temporal influences on nesting success. Periods were defined such that the early season contained approximately 25% of nests, mid season contained approximately 50% of nests, and late season contained approximately 25% of nests; thus, early season nests were initiated from late April to 25 May, mid season nests were initiated from 26 May through 14 June, and late season nests were initiated on or after 15 June, the majority in late June and early July.

RESULTS

BREEDING BIRD ABUNDANCE AND SPECIES RICHNESS

We detected a total of 73 species using point counts, 63 in the Big Sioux River (and tributaries) corridor, 55 in the Missouri River corridor, and 47 in the woodlots. Similarly, rarefaction curves generated from the point count data revealed a higher expected species richness ($E[S_n]$) in river corridors than in woodlots, with the two riparian corridors having similar $E[S_n]$ up to a sample size of about 200, after which the Big Sioux River corridor had higher expected species richness than the Missouri River corridor (Fig 2).

Relative abundance, calculated as birds per point, was 15.0 at Missouri River sites, 13.5 at Big Sioux River (and tributaries) sites, and 13.6 in woodlots. Overall densities for birds in each habitat were 3645 ± 265 birds per km² at Missouri River sites, 2754 ± 120 birds per km² at Big Sioux River (and tributaries) sites, and 4156 ± 176 birds per km² in woodlots. Several Neotropical migrants had higher densities in riparian corridor woodlands than in woodlots,
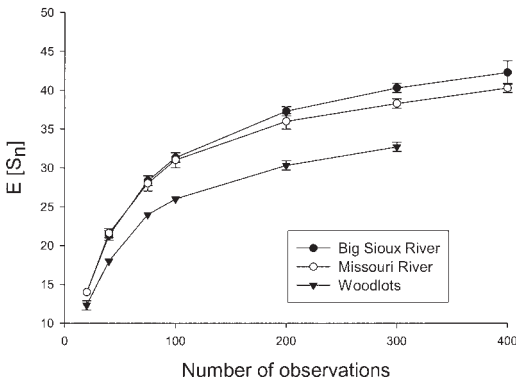
FIGURE 2.   Mean three-year rarefaction results for woodlots, the Missouri River corridor, and the Big Sioux River (and tributaries) corridor in southeastern South Dakota. The graph shows the expected number of species ($\pm$ SE) for any given number of observations.

whereas some short-distance migrants had higher densities in woodlots (Table 1). No Neotropical migrants had higher densities in the woodlot habitats.

NEST SUCCESS

We found 651 nests during the summers of 2000–2002, 320 nests of 15 species in woodlots and 331 nests of 25 species in river corridors (Table 2). Forty-four nests were found in 2000, 373 in 2001, and 234 in 2002. Of the nests in woodlots, 140 failed, 145 were successful, and 35 had uncertain outcomes. One hundred and fifty of the nests in riparian corridors failed and 136 were successful, and 45 had uncertain nest fates. Comparisons of daily survival rate revealed no significant differences among years for all nests combined (2002 vs. 2001: $Z = 0.8$, $P = 0.21$; 2001 vs. 2000: $Z = 0.8$, $P = 0.19$; 2002 vs. 2000: $Z = 0.4$, $P = 0.33$), for nests in each habitat (corridor 2002 vs. 2001: $Z = 0.5$, $P = 0.33$; insufficient nests in corridors in 2000 for statistical comparison; woodlots 2002 vs. 2001: $Z = 0.6$, $P = 0.27$; woodlots 2001 vs. 2000: $Z = 1.0$, $P = 0.16$; woodlots 2002 vs. 2000: $Z = 0.6$, $P = 0.28$), or for American Robins, the only species with adequate sample sizes in each year (2002 vs. 2001: $Z = 0.5$, $P = 0.29$; 2001 vs. 2000: $Z = 0.1$, $P = 0.50$; 2002 vs. 2000: $Z = 0.3$, $P = 0.37$). Therefore, we pooled data for all three years to increase sample sizes for comparisons between habitats. Daily survival rates for all species pooled did not differ between the two habitats (river corridors = 0.968, woodlots = 0.971: $Z = 0.6$, $P = 0.26$). Neotropical migrants exhibited higher daily nest survival than short-distance migrants in both woodlots (Neotropical migrants = 0.982, short-distance migrants = 0.962: $Z = 3.1$, $P < 0.001$) and river corridors (Neotropical migrants = 0.973, short-distance migrants = 0.952: $Z = 2.3$, $P = 0.01$). In addition, Neotropical migrants had higher daily nest survival in woodlots than in riparian corridors ($Z = 1.7$, $P = 0.05$). Daily nest survival rate for individual species with $\geq$15 nests was compared between habitats; results were not significant for any species (Eastern Kingbird: $Z = 0.4$, $P = 0.36$; American Robin: $Z = 0.5$, $P = 0.31$; Gray Catbird: $Z = 0.6$, $P = 0.27$; Orchard Oriole: $Z = 0.9$, $P = 0.17$; and Baltimore Oriole: $Z = 1.1$, $P = 0.14$; Fig. 3). Of 321 woodlot nests, 21% were too high to monitor with nest poles, and of 330 river corridor nests, 28% were too high to monitor. Parasitism rates of nests for which we could observe contents were 3.2% in woodlots and 3.8% in river corridors. Overall nesting success in both habitats pooled for species with $\geq$15 nests ranged from 12% for Chipping Sparrows to 72% for Baltimore Orioles (Table 3).

Mean nest height was 5.3 $\pm$ 3.4 m in woodlots and 5.9 $\pm$ 5.9 m in river corridors, and was not significantly different between habitats ($t_{646} = 1.6$, $P = 0.1$). Nests 5 m or higher were significantly more successful than nests below 5 m in both habitats (woodlots: 0–5 m = 0.961, 5+ m = 0.980: $Z = 2.8$, $P = 0.01$; river corridors: 0–5 m = 0.958, 5+ m = 0.980: $Z = 3.1$, $P < 0.001$). Mean distance-to-edge of nests in woodlots (7.1 $\pm$ 10.4 m) was significantly less ($t_{639} = 6.2$, $P < 0.001$) than those in river corridors (24.4 $\pm$ 48.7 m). Comparisons of nesting success between distance-to-edge categories within woodlots (0–5 m vs. 5–20 m: $Z = 0.1$, $P = 0.45$; 5–20 m vs. 20+ m: $Z = 1.2$, $P = 0.11$; 0–5 m vs. 20+ m: $Z = 1.3$, $P = 0.09$) and river corridors (0–5 m vs. 5–20 m: $Z = 0.9$, $P = 0.19$; 5–20 m vs. 20+ m: $Z = 0.5$, $P = 0.31$; 0–5 m vs. 20+ m: $Z = 0.3$, $P = 0.38$) yielded no significant differences (Fig. 4). Comparisons of nesting success in these same distance-to-edge categories between habitat types also yielded nonsignificant results (0–5 m: $Z = 0.2$, $P = 0.42$; 5–20 m: $Z = 1.0$, $P = 0.15$; 20+ m: $Z = 0.9$, $P = 0.18$).

TABLE 1.   Density (birds per km^2) and 95% confidence limits calculated with program DISTANCE for all species with at least 30 total observations in woodlots and Big Sioux and Missouri River corridors in southeastern South Dakota.

Species		Total observations	Woodlots		Big Sioux River		Missouri River	
			Density	95% CI	Density	95% CI	Density	95% CI
House Wren	*Troglodytes aedon*	1022	658	591–732	586	510–673	526	447–620
Blue Jay[a]	*Cyanocitta cristata*	440	168	133–213	107	91–127	76	62–96
Mourning Dove	*Zenaida macroura*	391	142	68–302	30	12–72	99	63–157
American Robin[a]	*Turdus migratorius*	361	595	499–709	92	69–124	68	44–107
Gray Catbird[b]	*Dumetella carolinensis*	312	128	84–196	247	196–312	255	199–328
Black-capped Chickadee	*Poecile atricapilla*	309	105	77–144	158	127–196	148	78–285
Eastern Kingbird	*Tyrannus tyrannus*	294	213	156–294	23	12–44	175	142–218
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	277	82	59–115	172	54–315	164	121–224
American Goldfinch	*Carduelis tristis*	265	103	60–178	70	56–87	160	126–205
Baltimore Oriole	*Icterus galbula*	264	189	135–266	31	22–46	208	161–271
Eastern Wood-Pewee[b]	*Contopus virens*	246	4	2–11	59	48–72	151	122–186
Red-headed Woodpecker[a]	*Melanerpes erythrocephalus*	222	224	163–310	13	9–21	70	49–101
Warbling Vireo	*Vireo gilvus*	219	44	18–109	35	21–57	113	96–133
Eastern Towhee[b]	*Pipilo erythrophthalmus*	189	0	–	95	60–149	71	52–96
Yellow Warbler[b]	*Dendroica petechia*	185	19	10–36	119	82–173	146	106–201
White-breasted Nuthatch[b]	*Sitta carolinensis*	180	17	8–35	87	63–120	69	48–98
Common Grackle	*Quiscalus quiscula*	156	189	133–269	9	2–40	185	93–364
Northern Cardinal[b]	*Cardinalis cardinalis*	156	6	2–12	55	45–67	64	44–93
Indigo Bunting	*Passerina cyanea*	147	51	34–78	58	37–91	50	34–74
Downy Woodpecker	*Picoides pubescens*	144	63	44–90	75	46–120	53	38–75
Wood Thrush[b]	*Hylocichla mustelina*	143	0	0–1	23	8–62	28	11–71
Brown-headed Cowbird	*Molothrus ater*	139	67	36–123	50	29–87	97	58–161
Common Yellowthroat	*Geothlypis trichas*	139	58	29–115	40	31–52	14	9–23
Northern Flicker[a]	*Colaptes auratus*	121	85	59–123	12	7–19	31	23–43
European Starling	*Sturnus vulgaris*	114	84	26–268	13	6–29	42	13–138
Cedar Waxwing	*Bombycilla cedrorum*	110	43	9–198	55	24–127	70	49–102
American Redstart[b]	*Setophaga ruticilla*	108	0	–	127	62–256	70	43–113
Field Sparrow	*Spizella pusilla*	101	7	3–15	36	21–64	4	2–10
American Crow	*Corvus brachyrhynchos*	87	5	3–9	6	4–8	7	5–11
Brown Thrasher	*Toxostoma rufum*	78	73	42–127	21	12–39	69	30–159
Song Sparrow	*Melospiza melodia*	75	42	21–86	9	5–17	12	6–25
Yellow-billed Cuckoo	*Coccyzus americanus*	75	15	7–35	14	9–22	39	25–61
House Sparrow[a]	*Passer domesticus*	71	119	73–194	0	–	0	–
Red-bellied Woodpecker	*Melanerpes carolinus*	71	4	1–10	12	3–44	26	14–50
Red-eyed Vireo[b]	*Vireo olivaceus*	70	0	–	29	18–49	57	40–81
Orchard Oriole	*Icterus spurious*	63	15	6–28	1	0–3	94	45–199
Ovenbird	*Seiurus aurocapillus*	37	0	–	44	21–90	1	0–5
Bell's Vireo	*Vireo bellii*	34	0	–	0	–	46	30–72

[a] Significantly higher density in woodlots than in both river corridors as determined by comparisons of 95% CI.
[b] Significantly lower density in woodlots than in both river corridors as determined by comparisons of 95% CI.

TABLE 2. Number of nests of each species found in river corridor and woodlot habitats during the breeding seasons of 2000–2002 in southeastern South Dakota. See Table 1 for Latin names.

Species	Corridor nests	Woodlot nests
Yellow-billed Cuckoo	1	2
Eastern Wood-Pewee	10	0
Eastern Phoebe	4	0
Eastern Kingbird	29	26
Bell's Vireo	7	0
Red-eyed Vireo	1	0
Warbling Vireo	7	1
Wood Thrush	8	0
American Robin	32	151
Gray Catbird	35	29
Brown Thrasher	33	7
Cedar Waxwing	3	7
Yellow Warbler	38	0
Common Yellowthroat	1	1
American Redstart	8	0
Eastern Towhee	4	0
Field Sparrow	6	0
Chipping Sparrow	5	15
Rose-breasted Grosbeak	36	8
Northern Cardinal	2	2
Blue Grosbeak	1	0
Indigo Bunting	1	0
Red-winged Blackbird	0	2
Common Grackle	9	20
Orchard Oriole	15	24
Baltimore Oriole	35	25
TOTALS	331	320

Daily survival rate of nests in riparian corridors initiated during the early, mid, and late breeding season periods did not differ significantly (early to mid: $Z = 1.0$, $P = 0.15$; mid to late: $Z = 0.3$, $P = 0.39$; early to late: $Z = 0.7$, $P = 0.25$). In woodlots, there was no significant difference in daily nest survival rate between nests initiated late in the breeding season and those initiated early ($Z = 0.9$, $P = 0.19$) and mid season ($Z = 1.3$, $P = 0.1$), but nests initiated mid season were more successful than those initiated early in the season ($Z = 2.2$, $P = 0.01$; Fig. 5).

DISCUSSION

BREEDING BIRD ABUNDANCE AND SPECIES RICHNESS

The absence of some Neotropical migrants from woodlots, that were present in higher numbers in river corridors, is the primary
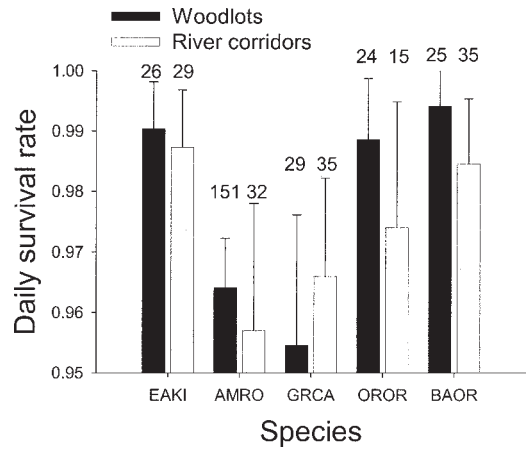

FIGURE 3. Differences in daily survival rate (± SE) between nests in anthropogenic woodlots and native river corridors for Eastern Kingbird (EAKI), American Robin (AMRO), Gray Catbird (GRCA), Orchard Oriole (OROR), and Baltimore Oriole (BAOR) in southeastern South Dakota. The number over each bar represents sample size.

distinction between the two habitats in this study. These species included Eastern Wood-Pewee (*Contopus virens*), Bell's Vireo (*Vireo bellii*), Red-eyed Vireo (*Vireo olivaceus*), Warbling Vireo (*Vireo gilvus*), Wood Thrush (*Hylocichla mustelina*), Yellow Warbler, Ovenbird (*Seiurus aurocapillus*), American Redstart (*Setophaga ruticilla*), and Eastern Towhee (*Pipilo erythrophthalmus*). Many of these are area-sensitive species (Van Horn and Donovan 1994, McCarty 1996, Roth et al. 1996, Sherry and Holmes 1997, Cimprich et al. 2000) and the small size of the woodlots we sampled may account for their absence from these sites, although other factors such as vegetation structure and distance from riparian corridors may also have contributed. No Neotropical migrants were significantly more abundant in woodlots than in river corridors, and birds that were more abundant in woodlots than in river corridors were not species of special conservation concern (regional or national), except for Red-headed Woodpeckers (*Melanerpes erythrocephalus*, South Dakota Natural Heritage Program 2002, Rich et al. 2004). The high density of Red-headed Woodpeckers in the woodlots we studied is worth noting. This species is thought to be in decline over much of its range (Rich et al. 2004) but woodlots in southeastern South Dakota appear to be providing valuable

TABLE 3.   Daily nest survival rate and overall Mayfield nesting success (%) for all species with ≥15 nests after pooling data from both river corridor and woodlot habitats in southeastern South Dakota. Such pooling provides an overall regional estimate of nest success for these species.

Species	n	Daily survival rate	Overall nesting success
Eastern Kingbird	55	0.989	66
American Robin	183	0.963	30
Gray Catbird	64	0.961	34
Brown Thrasher	40	0.942	19
Yellow Warbler	35	0.953	28
Chipping Sparrow	20	0.923	12
Rose-breasted Grosbeak	44	0.969	42
Common Grackle	29	0.974	39
Orchard Oriole	38	0.982	60
Baltimore Oriole	60	0.989	72

habitat for this species, probably because of the many standing dead snags typical of these habitats. Many species were common in every habitat including Mourning Doves (*Zenaida macroura*), American Robins, Song Sparrows (*Melospiza melodia*), and Brown-headed Cowbirds, which are all partial or short-distance migrants. Gray Catbirds and Indigo Buntings (*Passerina cyanea*), both edge-associated (De-Graaf and Rappole 1995) Neotropical migrants, were also common in all habitats.

NEST SUCCESS

Our data indicate that anthropogenic woodlots in southeastern South Dakota provide similar nesting success to natural riparian woodlands for migrant songbirds nesting in the region. Daily nest survival did not differ between river corridor woodlands and anthropogenic woodlots for any individual species examined or for all species combined. Additionally, most of the physical nest site variables measured (except for nest height) did not affect nest success. Most of the differences in daily nest survival were dependent upon nest initiation date and migrant category (Neotropical vs. short-distance).

The higher nest success of canopy nesters relative to understory and shrub or ground nesters may account for the higher nesting success of Neotropical migrants in woodlots than in river corridors. Of the 116 Neotropical migrant nests found in woodlots, 83 (72%) belonged to species whose average nest height was above 5 m, the cutoff we used to distinguish understory from canopy nesters. In
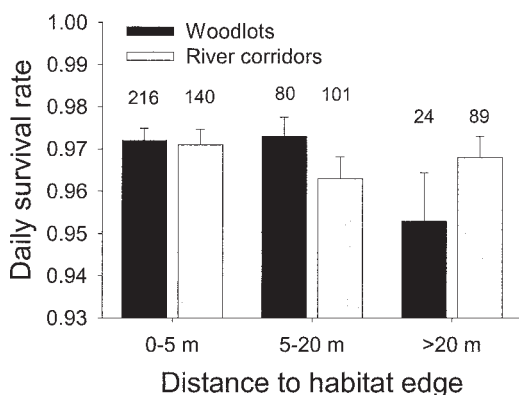

FIGURE 4.   Differences in daily survival rate (± SE) among nests located at varying distances from the habitat edge in anthropogenic woodlots and native riparian corridors in southeastern South Dakota. The number over each bar represents sample size.
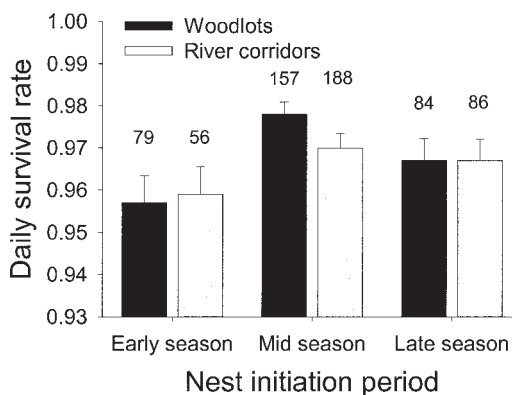

FIGURE 5.   Differences in daily survival rate (± SE) for nests initiated early (April–25 May), mid (26 May–14 June), and late (15 June–August) in the nesting season in woodland habitats of southeastern South Dakota. The number over each bar represents sample size.

contrast, only 40% (94 of 236) of river corridor Neotropical migrant nests were from species whose average nest height was above 5 m. Moreover, the population of Neotropical migrants nesting in woodlots was not as diverse as the nesting Neotropical migrant population in river corridors, so pooling all Neotropical migrants in the two habitats for comparison does not compare populations with similar species compositions. Thus, the generalization that nests of Neotropical migrants were more successful in woodlots than in riparian corridors is likely an artifact of differing nest height and species composition in the two habitats sampled. Such a result reinforces the conclusion of Faaborg (2002) that grouping bird species by migration strategy (e.g., Neotropical migrants) is not always informative in addressing population, ecology, or conservation questions.

There was no evidence of an edge effect on nesting success in this study, despite the greater mean distance-to-edge for nests in river corridors compared to woodlots. However, the mean distance-to-edge for nests in riparian corridors was much smaller than the distances used to separate nests into edge and forest interior habitats in previous studies documenting edge effects on nesting success. Gates and Gysel (1978) determined that nesting success increased for nests that were greater than 45 m from the habitat edge, and Robinson et al. (1995) suggested the forest interior began 250 m from the edge. Knutson et al. (2004) proposed that most of the remaining tracts of native riparian forests in the midwestern United States, including those sampled in this study, are too narrow to provide nonedge forest habitat according to these definitions. Thus, the absence of edge effects may be due to the lack of true woodland interior habitats in the northern prairie region. In addition, several recent studies have provided evidence that landscape-level effects on predator populations and nesting success may overwhelm patch-level effects, such that forests within agricultural landscapes exhibit little or no edge effects (Donovan et al. 1997, Hartley and Hunter 1998, Rodewald and Yahner 2001, Peak et al. 2004). Because landscapes of southeastern South Dakota are dominated by agricultural habitats, our results are consistent with these studies.

The lack of an edge effect might also be partly attributable to a comparatively low brood parasitism rate for the midwestern United States (Robinson et al. 1995), although Knutson et al. (2004) found similar parasitism rates to those in this study. The cause of the low parasitism rate is unclear, as cowbirds occurred regularly in all habitats. One possible explanation is that parasitism efforts of Brown-headed Cowbirds may be related to overall landscape patterns. Woodlands comprise less than 4% of available land in eastern South Dakota (Castonguay 1982). Consequently, local cowbirds may be focusing more on grasslands and agricultural habitats than on woodlands because they represent a much larger percentage of the local landscape, although avian densities are lower in agricultural habitats than in other habitat types (Best et al. 1995).

Most of our predictions concerning fragmented habitats and edge effects on nesting success were not supported. We suspect this is the result of a reduction in size and fragmentation of natural riparian habitats, which effectively decreases the amount of forest interior habitat and increases the amount of edge, and the landscape-level effects from the agriculturally dominated landscapes of the region. Despite the apparent lack of a difference in nest success, the absence of many Neotropical migrants from anthropogenic habitats implies that those habitats will not successfully replace riparian habitats for long-distance migrants. However, if this is simply because of the small area of woodlot habitats then increasing the area of woodlots may make them more attractive to long-distance migrants. In addition, planting understory shrubs might make woodlots more attractive by increasing the structural complexity of the habitat.

Predation is the most common cause of nest failures in open-cup nesters (Ricklefs 1969, Martin 1993a, 1993b), and because nest success rates were similar between woodlots and river corridors in this study, we suggest predator densities may also have been similar. This study was not designed to document differences in predator densities between habitats. Thus, the only predator data we have are from our point counts in which we documented densities of two common corvid nest predators, Blue Jays (Cyanocitta cristata) and American Crows (Corvus brachyrhynchos), as well as House Wrens, which are known to puncture eggs and kill recently hatched young of both conspecifics

and other species nesting in the same habitat (Belles-Isles and Picman 1988, Johnson 1998, Doherty and Grubb 2002). Although crows were commonly counted only at Missouri River sites, Blue Jay densities were high in every habitat, and more than twice as high as the highest crow densities. This suggests that Blue Jays may have been an important avian nest predator. House Wrens were the most common bird counted in every habitat sampled and potentially represent a serious threat to nesting success, although actual demonstration of House Wren depredation in this area will require further study.

Our hypothesis that nesting success of open-cup nesting songbirds would be higher in natural river corridor woodlands than in human-planted farmstead woodlots was not validated by the data in this study. The possibility remains, however, that these data describe current conditions and do not reflect historical habitats in the northern prairie region. The "natural" riparian habitats we sampled shared many characteristics with woodlots, including being surrounded by agricultural fields, having relatively high amounts of edge, and close proximity to farmhouses and other human habitation so that nest predators associated with humans (e.g., domestic cats) may have been present. Because unfragmented river corridor woodlands with natural bordering vegetation are now very rare in southeastern South Dakota, it is unknown what the historical nesting success in these habitats might have been. A recent study by Rodewald and Yahner (2001) suggested that habitats disturbed by agriculture contained fewer long-distance migrants and more nest predators and brood parasites than similar sites with nonagricultural disturbances or with a successional gradient instead of an abrupt habitat change at the border. Thus, the reduction in width and lack of a natural border around our riparian corridor study sites likely resulted in changes in woodland structure so that they functioned similarly to fragmented habitats. Such changes likely affect diversity, abundance, and nesting success of Neotropical migrants in river corridor woodlands relative to historical levels.

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