

# Riparian and Woodlot Landscape Patterns and Migration of neotropical Migrants in Riparian Forests of Eastern South Dakota<sup>1</sup>

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## Abstract

Woodland habitat types in the northern Great Plains compose only a very small fraction of the total land surface. These woodlands occur primarily as natural riparian forests or as scattered anthropogenic woodlots and shelterbelts. Natural riparian woodlands have been markedly reduced over the past century, but anthropogenic woodlands have increased during this same period. In this paper, we review and synthesize mist net and point count data from riparian corridor woodlands (Missouri and Big Sioux rivers) and farmstead woodlots in southeastern South Dakota to compare neotropical migrant abundance, species richness, diversity, and community similarity in these two habitats during spring and fall migrations. We hypothesized that the larger and more contiguous woodland area and greater vegetative diversity of riparian corridor woodlands relative to woodlots would attract higher numbers and more species of neotropical migrants. Point count abundances were higher in woodlots than in riparian corridors in both spring and fall, whereas capture rates were similar in spring, but higher in Missouri River woodlands than at other sites in fall. Species richness and diversity were similar in riparian corridors and woodlots at both seasons. Community overlap between riparian corridors and woodlots was high in spring, but was lower in fall. In general, these data suggest that overall abundance and diversity of neotropical migrant communities are similar between riparian corridors and farmstead woodlots, despite some differences for individual species. In addition, recaptured migrants were capable of gaining mass during stopover in woodlots. Farmstead woodlots appear to effectively supplement natural riparian corridor woodlands as stopover sites for neotropical migrants. Thus, conservation of even small woodland parcels may benefit neotropical woodland migrants during migration.

## Introduction

Woodland habitats in the northern Great Plains are scarce, making up less than 4 percent of the total land surface area in southeastern South Dakota (Castonguay 1982). Two principal types of woodland habitats currently exist in this area, natural riparian corridor woodlands and human-planted farmstead woodlots and shelterbelts. Historically, woodlands in eastern South Dakota existed almost exclusively along riparian corridors (Van Bruggen 1996). The extent of these natural woodlands has been markedly reduced by clearing for agriculture and inundation behind dams. For example, Hesse et al. (1988) documented reductions of at least 41 percent in riparian woodland area along the Missouri River from the mouth to Ponca, Nebraska, since the late 1800s. The section of river studied by Hesse et al. (1988) is downstream from the dams, so does not include woodland area lost by inundation under reservoirs. Natural woodland area in eastern South Dakota, however, has been supplemented since the time of European settlement by human-planted woodlands around agricultural fields and farmsteads. Such artificial woodlands occur in narrow linear strips (shelterbelts) or as larger, less linear, woodlots. The size and vegetative diversity of shelterbelts and woodlots are lower than those for natural riparian woodlands (Martin 1980, Dean 1999).

neotropical migrants occur in both natural and artificial woodlands during migration through eastern South Dakota (Martin 1980, Tallman et al. 2002). Populations of many of these species are declining (e.g., Robbins et al. 1989). Reductions in available stopover habitat along the migratory route potentially contribute to these population declines because migration is a period of the annual cycle where energy demands peak (Moore et al. 1995). Since marked reductions in available riparian corridor woodlands in the northern Great Plains have occurred concomitantly with increases in artificial woodland habitats, artificial woodlands might serve, at least partially, to substitute as stopover habitat for lost riparian corridor woodlands. No previous studies have compared neotropical migrant use of these two habitats during migration. We studied migrant use of these woodland habitats using both mist nets and point counts to determine if abundance, species richness, and diversity of neotropical migrants during migration differ between natural riparian corridor woodlands and farmstead woodlots in southeastern South Dakota. We reasoned that the greater woodland area, more contig-

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uous nature of woodland habitats, and higher vegetative diversity of riparian corridor woodlands should make them more favorable as stopover habitat for neotropical migrants than farmstead woodlots. Thus, we hypothesized that neotropical migrant abundance, species richness, and diversity should be higher in natural riparian corridor woodlands than in anthropogenic farmstead woodlots.

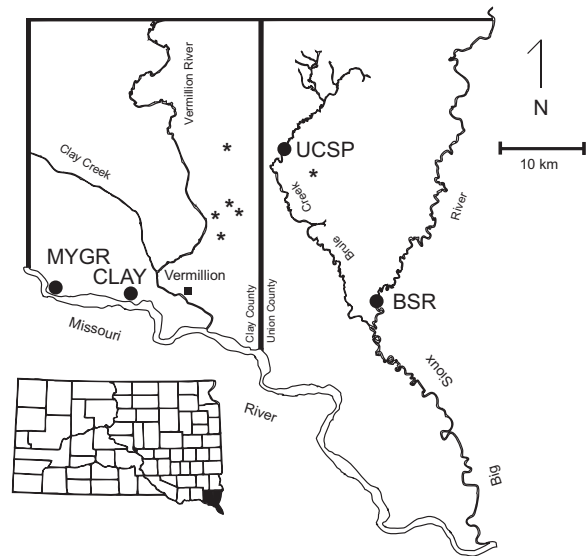
## Methods

### Mist Net and Point Count Sampling

We review here point count and mist net data for neotropical migrants from Dean (1999) for riparian corridors in southeastern South Dakota and from Carlisle (1998) and Swanson et al. (2003) for farmstead woodlots in the same area. Dean (1999) studied four riparian corridor woodland sites in Clay and Union counties, South Dakota, two in the Missouri River riparian corridor, one in the Big Sioux River riparian corridor, and one on a tributary (Brule Creek) of the Big Sioux River (fig. 1). Prominent neotropical migrants in southeastern South Dakota are flycatchers, vireos, thrushes, warblers, and tanagers (Tallman et al. 2002). Other neotropical migrant species, such as cuckoos, Gray Catbird (*Dumetella carolinensis*), grosbeaks, Indigo Buntings (*Passerina cyanea*), and orioles, migrate through and also nest in the area; and resident and migrant birds of these species are difficult to distinguish. For this study, we limited analyses to flycatchers, vireos, thrushes, warblers, and tanagers to reduce the confounding effects of residents in the analyses.

Dean (1999) conducted point counts and mist net sampling (5-7 9-m nets, 30-mm mesh) daily, weather permitting, during both spring (15 April-2 June) and fall (15 August-5 October) migration periods in 1993-1995. Sampling was rotated among the four study sites on a 4-d cycle. Spring and fall sampling periods covered the bulk of the neotropical migrant movement through eastern South Dakota (Tallman et al. 2002). Point counts and mist net sampling (7-10 9-m nets, 30-mm mesh) were conducted during the same dates in spring and fall in 1996 and 1997 in woodlots in Clay and Union counties, South Dakota (Carlisle 1998, Swanson et al. 2003). Farmstead woodlot mist netting was conducted in a single woodlot of about 3.5 hectares in area for at least six days per week, weather permitting, during the migration periods. In riparian corridor woodlands, nets were opened from sunrise until approximately 1100 CST. Mist nets were opened during the same time period in the farmstead woodlot, but nets were also often opened for 2-3 h prior to sunset. Capture rates did not differ substantially for morning and evening capture periods in woodlots, so data

were pooled. In neither riparian corridors nor the woodlot was sampling conducted on days with rain or with winds in excess of 35 km/h. For captured birds we measured mass to the nearest 0.1 g (Ohaus LS200 Model portable scale), wing chord, tarsus, and visible fat (on a scale of 0-5, Helms and Drury 1960). Birds were then banded with a standard U.S. Geological Survey aluminum leg band and released.



**Figure 1**— Map of the study area in southeastern South Dakota showing the locations of the four riparian corridor and the six woodlot (asterisks) study sites. MYGR and CLAY are study sites in the riparian corridor woodlands of the Missouri River. The BSR study site is in the riparian corridor of the Big Sioux River and the UCSP study site includes riparian woodland along Brule Creek (a tributary of the Big Sioux River) and adjacent (and contiguous) upland deciduous forest. Modified from Dean (1999).

Swanson et al. (2003) surveyed seven points in six different farmstead woodlots (fig. 1), which ranged from about 0.7 to 3.5 hectares in area. The largest woodlot had two points separated by over 200 m. All other woodlots had a single survey point. Woodlot points were surveyed three times per week during the migration periods. Each riparian corridor study site had 5-10 survey points established at 200-m intervals along roughly linear transects (Dean 1999). Fixed radius (25-m) point counts were used in both studies (Hutto et al. 1986). Surveys at each point lasted 10 min and all birds detected by sight or by sound, and their distances from the point center (inside or outside of 25 m), were recorded. Birds observed while walking between points were also identified and counted as beyond 25 m from the point center. Point counts in both studies were conducted between 0600 and 1000 CST and survey routes were traversed in opposite directions on successive counts to reduce possible temporal variation. Point count surveys were not undertaken on days with rain or

winds in excess of 35 km/h. From point count data, we calculated densities (birds • km<sup>-2</sup>) from detections ≤25 m from the point center and relative abundance (birds/point) from all detections, irrespective of their distance from the point center (Swanson 1999).

### Statistical Analyses

Spring and fall capture and point count data were pooled over the entire study periods for both riparian corridors (three years pooled) and farmstead woodlots (two years pooled) to reduce effects of year-to-year variation in migration traffic. Overall abundance (numbers of observations) and captures in riparian corridors and woodlots were compared by Chi-square goodness-of-fit tests, after correcting for differences in sampling effort (numbers of points surveyed or number of net hours) (Rappole et al. 1979). The correction for differences in sampling effort was accomplished by adding the total numbers of points surveyed or the total number of net hours for the two riparian corridors and the woodlots and dividing by three to produce an average effort for the three habitats. A correction factor was then generated by dividing the actual effort for each of the two riparian corridors and the woodlots by the average effort for the three habitats. The numbers of captures or observations in each habitat were then divided by the correction factor to provide values for point count observations or captures corrected to equal effort. Because sampling effort and sample sizes (numbers of birds observed and captured) differed among riparian corridors and woodlots (table 1), we calculated rarefaction curves (James and Rathbun 1981) for combined observation and capture data for each study area. Rarefaction curves were compared by ANCOVA after double-logarithmic transformation to produce straight lines. Diversity was calculated as the Shannon Diversity Index ( $H' = -\sum p_j \ln p_j$ , where  $p_j$  is the proportion of total individuals belonging to species  $j$ ) and diversities for the different study areas were compared by  $t$ -test (Zar 1996). In cases where multiple comparisons were made, we employed a sequential Bonferroni procedure for adjusting  $\alpha$ -levels to reduce the probability of type 1 errors (Rice 1989). Community overlap among the two riparian corridors and farmstead woodlots was determined as Morisita's Index, which ranges from 0.0 (no similar species) to 1.0 (identical communities).

Mass change for recaptured birds in woodlots was calculated as mass at recapture minus mass at initial capture. Mass was standardized to the same time of day (1200, Cherry 1982) for these calculations to avoid confounding effects of mass gains during the day (Carlisle 1998). This was accomplished by first regressing condition index (mass/wing chord, Winker 1995) on time of day for each species (10 captures per season minimum) and calculating an average change in condi-

tion index per h. Condition index for an individual bird was standardized to 1200 by multiplying the average change in condition index per h for that species by the time difference between capture and 1200, then adding or subtracting this value from the condition index at the time of capture. Mass at 1200 was then computed from the value for condition index at 1200. Carlisle (1998) grouped recaptured birds into 1-d (recaptured one day after initial capture) and 2+-d (recaptured two or more days after initial capture) categories for analyses of mass changes to determine whether low initial rates of mass gain occurred during stopover in farmstead woodlots. ANOVA was then used to test for differences in percent mass change (all neotropical migrants pooled) among stopover duration categories, years and seasons. Few recaptures were obtained in riparian corridors. To examine mass changes during stopover for migrants in riparian corridors, variation in condition index ( $[\text{mass} \cdot \text{wing chord}^3] \cdot 10,000$ ) at first capture with time after sunrise was analyzed by least squares regression for individual species with greater than 30 captures per season (Winker et al. 1992).

**Table 1**– Sampling effort for point counts (total points surveyed) and mist netting (net hours) in riparian corridors (1993-1995) and farmstead woodlots (1996-1997) in southeastern South Dakota during spring and fall migration periods. Data are from Carlisle (1998), Dean (1999) and Swanson et al. (2003).

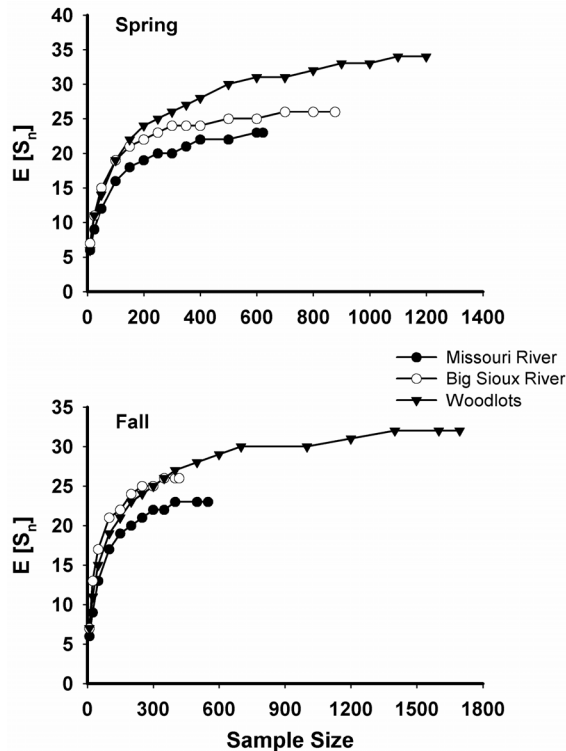
Site	Points surveyed		Net hours	
	Spring	Fall	Spring	Fall
Missouri River	336	377	1,013	1,073
Big Sioux River	495	513	1,173	1,037
Woodlots	232	284	4,342	5,107

## Results

### Point Counts

Densities (birds • km<sup>-2</sup>) and relative abundances (birds/point) over the entire migration period were higher in woodlots than in either riparian corridor in both spring and fall (table 2). We compared the overall numbers of observations among study areas by Chi-square, after correcting for unequal sampling effort (Rappole et al. 1979). The overall numbers of neotropical migrants observed in woodlots was significantly higher than that in both Missouri and Big Sioux River riparian corridors in both spring and fall. Test statistics for these comparisons ( $P < 0.001$  and  $df = 1$  in all cases) were: Woodlots vs. Missouri River (spring),  $\chi^2 = 241$ ; Woodlots vs. Big Sioux River (spring),  $\chi^2 = 307$ ; Woodlots vs. Missouri River (fall),  $\chi^2 = 441$ ; Woodlots vs. Big Sioux River (fall),  $\chi^2 = 570$ . Overall numbers of observations

did not differ significantly between the two riparian corridors at either season.



**Figure 2**— Rarefaction curves generated from pooled observation and capture data for riparian corridor and woodlot study sites in southeastern South Dakota. These curves provide a cumulative measure of the expected number of species for any given sample size. These curves indicate that species richness in woodlots and Big Sioux River sites was higher than at Missouri River sites at both seasons. In general, woodlot species richness during migration is similar to that at riparian corridor woodland sites.

**Mist Net Sampling**

Capture rates were higher at the Missouri River study sites than at other study sites during both spring and fall (table 2). Overall captures among sites were also compared with Chi-square tests corrected for different net hours (df = 1 in all cases). The overall number of

captures in spring (table 2) was significantly ( $P < 0.001$ ) greater at Missouri River sites than at other sites ( $\chi^2 = 46.2$  for Big Sioux River;  $\chi^2 = 204$  for the woodlot). Overall capture numbers were also significantly greater at Big Sioux sites than at the woodlot site in spring ( $\chi^2 = 13.9$ ,  $P < 0.001$ ). Missouri River sites also had significantly ( $P < 0.001$ ) higher overall capture numbers than other sites during fall migration ( $\chi^2 = 319$  for Big Sioux River;  $\chi^2 = 267$  for the woodlot). Capture numbers in the woodlot were significantly higher than those at Big Sioux River sites in fall ( $\chi^2 = 73.3$ ,  $P < 0.001$ ).

**Species Richness and Diversity**

The overall numbers of neotropical migrant species (flycatchers, vireos, thrushes, warblers, and tanagers) observed or captured in spring were 26 at Big Sioux River sites, 25 at Missouri River sites (29 for the two riparian corridors combined), and 35 for woodlots. In fall, comparable numbers were 27 at Big Sioux River sites, 25 at Missouri River sites (28 for the two riparian corridors combined), and 33 for woodlots. Because sampling effort varied among study sites, we calculated rarefaction curves (fig. 2) for expected species richness for a given sample size (James and Rathbun 1981). ANCOVA on double log10-transformed rarefaction curve data indicated that the expected number of species ( $E[S_n]$ ) for a given sample size differed significantly among sites in both spring ( $F_{3, 42} = 240$ ,  $P < 0.001$ ) and fall ( $F_{3, 37} = 177$ ,  $P < 0.001$ ). In spring,  $E[S_n]$  was greatest in woodlots and lowest at Missouri River sites, and all sites differed significantly from each other. In fall,  $E[S_n]$  was greatest at Big Sioux River sites and lowest at Missouri River sites, but the woodlot site  $E[S_n]$  did not differ significantly from either riparian corridor site after sequential Bonferroni adjustment of  $\alpha$ -levels. Significant P-values for individual-site comparisons were  $<0.001$  (woodlot vs. Missouri sites), 0.005 (Big Sioux vs. Missouri sites), and 0.048 (woodlot vs. Big Sioux sites) in spring, and  $<0.001$  (Big Sioux vs. Missouri sites) in fall. Shannon diversity indices ( $\pm$  SE) in spring were  $0.97 \pm 0.02$ ,  $1.14 \pm 0.01$ , and  $1.11 \pm 0.01$  for Missouri River, Big Sioux River,

**Table 2**— Overall densities, relative abundances (RA), total captures and capture rates (Rate) for neotropical migrants in riparian corridor woodlands and farmstead woodlots in southeastern South Dakota during spring and fall migration periods. The riparian corridor values are from Dean (1999) and represent three-year (1993-1995) mean values, except for total captures. The woodlot data are from Carlisle (1998) and Swanson et al. (2003) and represent overall captures and capture rates over a two-year period (1996-1997).

Site	Density (birds·km <sup>-2</sup> )		RA (birds·point <sup>-1</sup> )		Total captures		Rate (birds·[100 net h] <sup>-1</sup> )	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Missouri River	593	208	1.76	0.74	328	719	32.4	67.0
Big Sioux River	677	135	1.77	0.68	223	144	19.0	13.9
Woodlots	1,302	898	4.02	3.05	668	1,211	15.4	23.7

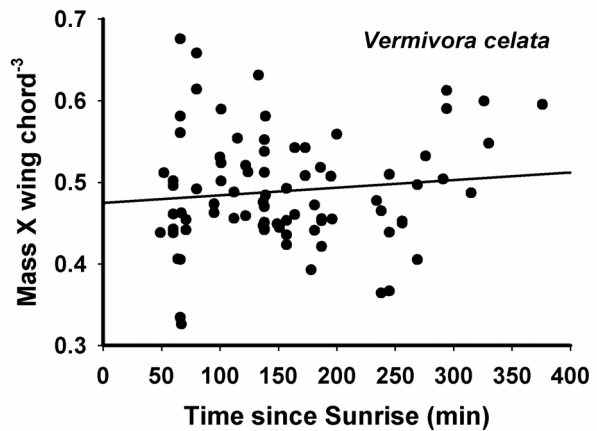
and woodlot sites, respectively. Fall diversities were  $0.94 \pm 0.02$  for Missouri River sites,  $1.22 \pm 0.01$  for Big Sioux River sites, and  $1.15 \pm 0.01$  for woodlot sites. Spring diversity was significantly higher at both woodlot ( $t_{1929} = 6.83, P < 0.001$ ) and Big Sioux River sites ( $t_{1835} = 8.29, P < 0.001$ ) than at Missouri River sites, but did not differ between woodlots and Big Sioux River sites. In the fall, diversity was highest at Big Sioux River sites ( $t_{1404} = 11.50, P < 0.001$  for Missouri River sites;  $t_{898} = 4.03, P < 0.001$  for woodlots), and woodlots also had significantly greater diversity than Missouri River sites ( $t_{1448} = 9.82, P < 0.001$ ).

Community overlap, measured by Morisita's index, was relatively high among all sites in spring. Morisita's Index values were 0.88 between Missouri and Big Sioux river sites, 0.87 between Missouri River and woodlot sites, and 0.89 between Big Sioux River and woodlot sites. Community overlap was lower and more variable in fall, as Morisita's Index values were 0.57 between Missouri and Big Sioux river sites, 0.43 between Missouri River and woodlot sites, and 0.73 between Big Sioux River and woodlot sites.

**Body Mass and Stopover**

Because of the 4-d sampling cycle among study sites in riparian corridors and the relatively large woodland area at these sites, there were very few recaptures of banded birds. Thus, we could not assess the efficacy of these woodlands for mass gains by recapture data. Winker et al. (1992) presented a method for assessing mass gains during stopover by regression of energetic condition ( $[\text{mass} \cdot \text{wing chord}^{-3}] \cdot 10,000$ ) on time since sunrise. A positive slope in these regressions suggests that migrants are gaining mass during the day. In this study, all regressions of condition index with time of day for neotropical migrants captured in riparian corridors were not significantly different from zero slope (fig. 3, table 3), which suggests that migrants did not gain mass during the morning sampling period. For

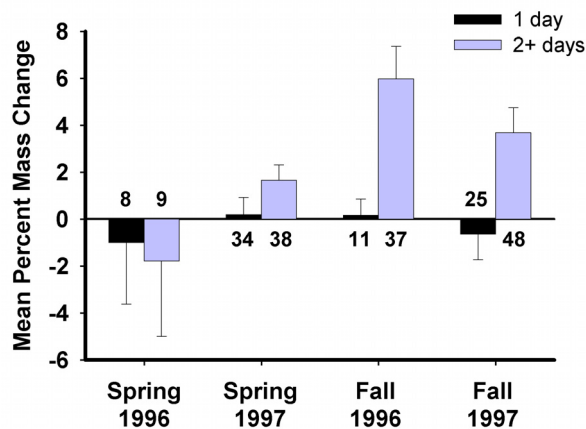
woodlots, where sampling was conducted at the same site on a daily basis, we recaptured 8-14 percent of all birds banded at least one day after their initial capture (Carlisle 1998), thus allowing calculation of mass gain for migrants from recapture data. For woodlots, migrants generally lost mass or maintained mass during the first day of stopover, but gained mass during subsequent days (fig. 4). Birds recaptured two or more days after initial capture gained significantly more mass than birds captured only one day after initial capture ( $F_{1, 207} = 9.34, P < 0.001$ , Carlisle 1998). In addition, fall birds gained significantly more mass than spring birds ( $F_{1, 207} = 4.89, P = 0.028$ , Carlisle 1998).



**Figure 3**— Condition Index ( $[\text{mass} \cdot \text{wing chord}^{-3}] \cdot 10,000$ ) as a function of time since sunrise for Orange-crowned Warblers (*Vermivora celata*) in spring in riparian corridors. The regression line was not significantly different from zero slope ( $P = 0.33$ ). Similar regressions for all other neotropical migrant species having > 30 captures per season were also not significant (table 3), suggesting that migrants did not gain appreciable mass at riparian corridor stopover sites in either spring or fall over the morning hours sampled in this study.

**Table 3**— Regression statistics for condition index ( $[\text{mass} \cdot \text{wing chord}^{-3}] \cdot 10,000$ ) vs. time since sunrise (h) for neotropical migrants with > 30 captures in riparian corridors in spring and fall.

Species	Season	n	Y-intercept	Slope	F	R <sup>2</sup>	P
Least Flycatcher ( <i>Empidonax minimus</i> )	Spring	90	0.45	0.005	2.066	0.02	0.15
Warbling Vireo ( <i>Vireo gilvus</i> )	Spring	51	0.46	-0.006	1.422	0.03	0.24
-----	Fall	261	0.45	0.002	0.550	0.002	0.46
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	Fall	41	0.40	0.006	0.924	0.02	0.34
Swainson's Thrush ( <i>Catharus ustulatus</i> )	Spring	44	0.40	-0.0002	0.002	<0.001	0.97
Orange-crowned Warbler ( <i>Vermivora celata</i> )	Spring	83	0.47	0.006	0.965	0.01	0.33
-----	Fall	143	0.44	0.004	1.076	0.01	0.30
Nashville Warbler ( <i>Vermivora ruficapilla</i> )	Fall	72	0.45	0.001	0.199	0.003	0.66
Yellow Warbler ( <i>Dendroica petechia</i> )	Spring	54	0.47	-0.0005	0.009	0.001	0.93
Yellow-rumped Warbler ( <i>D. coronata</i> )	Spring	56	0.40	-0.003	0.985	0.02	0.33
Common Yellowthroat ( <i>Geothlypis trichas</i> )	Spring	31	0.68	-0.006	0.728	0.02	0.40



**Figure 4**— Mean ( $\pm$  SE) percent mass change for neotropical migrants (all species pooled) captured one day and  $\geq 2$  days after initial capture at the farmstead woodlot stopover site. Values under the bars are sample sizes. Mass values have been standardized to the same time of day (1200), as described in the text, to account for daily mass gains for migrants captured and recaptured at different times. Migrants were generally able to gain mass during multiple-day stopovers at this site, except during the wet spring of 1996. From Carlisle (1998).

## Discussion

During the nesting season, abundance and species richness of woodland birds, particularly neotropical migrants, often are positively related to woodland area (see Askins 2000 for review). Much of the work documenting this positive relationship of abundance and richness of neotropical birds with woodland area in North America was conducted in eastern deciduous forest. Several studies, however, have documented a similar relationship (increasing species richness with increasing area) in the midwestern United States (Blake and Karr 1984, 1987; Cable et al. 1992), including eastern South Dakota (Martin 1981, Bakker 2000). Riparian woodlands in eastern South Dakota, with their greater woodland area, also support higher avian species richness than shelterbelts and farmstead woodlots, and some birds occur as nesting species only in the larger woodland areas of riparian corridors (Emmerich and Vohs 1982, D. Gentry and D. Swanson, unpubl. data). However, avian abundance may be equal or greater in shelterbelts and woodlots than in riparian corridor woodlands (Emmerich and Vohs 1982, D. Gentry and D. Swanson, unpubl. data). Connor and McCoy (1979) and Johnson (2001) caution that passive sampling effects (sampling larger areas in larger habitat patches) could also account for a positive species-area relationship. Most of the studies cited above have not accounted for passive sampling effects, so the contribution of passive sampling effects to the general

species-area relationship detected in these studies is unknown.

A few studies have also examined species-area relationships during migration in the midwestern United States, with somewhat variable results (Martin 1980, Yahner 1983, Blake 1986). Martin (1980), in a study of shelterbelts in eastern South Dakota, found that abundance and species richness of spring migrants were as strongly and positively related to area as in breeding birds (Martin 1981). The shelterbelts studied by Martin (1980) were generally small, and were grouped into three size categories, with mean areas of 0.25 ha, 0.53 ha, and 1.46 ha, so those results apply only to smaller-sized shelterbelts. The number of transient birds during migration periods was positively correlated with woodlot area for woodlots in east-central Illinois that ranged in size from 1.8 to 600 ha (Blake 1986). Yahner (1983), however, found no relationship between avian species richness and woodland area during summer or during spring and fall migration periods for small shelterbelts (0.2-0.8 ha) in southern Minnesota. Again, these studies have not accounted for passive sampling effects, so the precise nature of the relationship between species numbers and woodland area during migration is not certain.

Our results documented similar abundance, diversity, and species richness in riparian corridors and woodlots during both spring and fall, despite the total woodland area being much greater in riparian corridors than in woodlots. Several factors may contribute to this result. The areas of the woodlots in this study fall mostly within the largest of the three size classes of Martin (1980), so species-area relationships of migrant birds may approach an asymptote at woodland areas approximating those for woodlots in this study. Martin (1980), however, suggested that the species-area data for shelterbelts in eastern South Dakota fit a curvilinear relationship better than an asymptotic relationship. Another possible explanation for the similar abundance, diversity, and species richness between woodlots and riparian corridors in this study is that riparian corridor woodlands in this region are more linear and narrow than the more extensive eastern deciduous forest habitats (Van Bruggen 1996). As a result, the full benefits of large areas of unfragmented forest to species richness and abundance are probably not realized, even in riparian corridor woodlands, in southeastern South Dakota. Finally, if passive sampling effects prominently influence the nature of the species-area relationship in woodland habitats, then the degree of association between species numbers and woodland area detected in studies not accounting for passive sampling may be overestimated. However, passive sampling effects are unlikely to account for the similarity in species richness among riparian corridors and woodlots in this study because we sampled more points in the larger

woodland areas of riparian corridors, although net hours were greater in the woodlot than in either riparian corridor (*table 1*). If passive sampling effects were pervasive in this study, then higher numbers of species would likely be expected at riparian corridor sites because of the higher numbers of points surveyed, but this is not what we found.

Some differences in abundance of individual species between riparian corridor woodlands and woodlots did occur in this study. For example, Warbling Vireos (*Vireo gilvus*) composed 41.5 percent of all captures and observations during fall migration in the Missouri River riparian corridor (Dean 1999). Comparable values for the Big Sioux River riparian corridor and for woodlots were only 8.5 percent and 3.3 percent, respectively. Such individual species differences were more prominent in fall than in spring, resulting in lower species overlap between riparian corridors and woodlots in fall than in spring. Nevertheless, most neotropical migrant species could be found in both riparian corridors and woodlots during spring and fall migration. Of species with at least nine total captures or observations, only Yellow-throated Vireo (*Vireo flavifrons*; riparian corridors in spring and fall) and Gray-cheeked Thrush (*Catharus minimus*; woodlots in spring) were restricted to either riparian corridors or woodlots. These species do occur in small numbers in both habitats during migration through southeastern South Dakota (pers. obs.), but they were not detected in both habitats during this study. Thus, both woodland types provided stopover habitat for most neotropical migrant species passing through this region.

These data suggest that neotropical migrants show generally similar patterns of occurrence in both riparian corridor woodlands and farmstead woodlots during migration periods, but they do not allow discrimination of the relative suitability of the two woodland types for stopover. This latter question requires assessment of whether or not migrants are able to gain mass at these sites during stopover periods. For woodlots, Carlisle (1998) reported recapture rates (individuals recaptured at least one day after their initial capture) of 8-14 percent for woodlots. Recaptured individuals tended to exhibit low initial refueling rates during the first day after initial capture, but, in three of four seasons, migrants gained substantial mass if recaptured two or more days after their initial capture (*fig. 4*). The lone exception was the spring of 1996, which was an unusually rainy season. Carlisle (1998) speculated that arthropod numbers might have been reduced relative to other years by this wet weather, thereby decreasing relative mass gain during that season. A similar pattern of low initial refueling rates at stopover sites, followed by mass gains during longer stopover periods, has been documented at a number of additional stopover sites (see Schilch and Jenni 2001 for review). Such a

pattern may relate to competition, to a lack of familiarity with the stopover site, or to a rebuilding of the gut following a period of migratory flight (Hume and Biebach 1996; Yong and Moore 1997; Karasov and Pinshow 1998, 2000). Alternatively, Schilch and Jenni (2001) suggest that a low initial rate of mass gain may be an artifact of handling effects and that detection of such a pattern may be confounded by not knowing when a captured migrant actually arrived at a stopover site. These authors argue that low initial refueling rates are not a common phenomenon in migrating birds. In any event, the data of Carlisle (1998) indicate that migrants are capable of gaining mass during stopover in farmstead woodlots, so woodlots generally appear to serve as suitable stopover habitat for these birds.

Because of the 4-day sampling interval among sites in the riparian corridor study of Dean (1999), recapture rates of migrants were too low (<1 percent) to perform a similar analysis of mass changes during stopover. Regressions of energetic condition ( $[\text{mass} \cdot \text{wing chord}^{-3}] \cdot 10,000$ ) on time since sunrise were not significantly different from zero slope for any species during either spring or fall migration at riparian corridor stopover sites. This result may occur because sampling in riparian corridor woodlands occurred only during the morning and not over the entire day, so regressions generally covered only about a 5-hour period.

These data suggest, therefore, that riparian corridor woodlands and farmstead woodlots provide similar potential for stopover habitat for neotropical migrants, at least in this region, and possibly over a broad geographic range. This finding has some potentially major implications for the conservation of neotropical migrants, suggesting that conservation of even small woodland areas (1-4 ha) can provide benefits for migrants as stopover sites. Because much of the available woodland in eastern and central North America consists of relatively small parcels, and because restoration of small woodland parcels is more feasible than restoration of large, contiguous woodlands, increasing the number of small woodlots could enhance available stopover habitat for neotropical migrants. This could prove beneficial to neotropical migrant populations, as loss of stopover habitat is one potential factor contributing to population declines for some species (Moore et al. 1995). However, conservation of small woodland parcels in this area is of less benefit to breeding neotropical migrants because smaller parcels have lower species richness and lower percentages of neotropical migrants (D. Gentry and D. Swanson, unpubl. data). This reduced species richness of breeding birds in smaller woodlands is also apparently true elsewhere in eastern and central North America (Blake and Karr 1984, 1987; Cable et al. 1992; Bakker 2000). In addition, Bakker (2000) showed that small woodlands adjacent to grassland areas depressed occurrence of

grassland bird species in those grasslands. This is important because many species of grassland nesting species are also experiencing marked population declines (see Askins 2000 for review). Thus, overall conservation programs for birds must prioritize which species and which seasons are most important to conservation efforts in particular areas. Nevertheless, these results suggest that for migratory periods, conservation of small woodland parcels can offer important benefits to neotropical migrants.

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## Literature Cited

- Askins, R. A. 2000. **Restoring North America's birds: Lessons from landscape ecology**. New Haven, CN: Yale University Press.
- Bakker, K. K. 2000. **Avian occurrence in woodlands and grasslands on public areas throughout eastern South Dakota**. Brookings, SD: South Dakota State University. Ph.D. dissertation.
- Blake, J. G. 1986. **Species-area relationship of migrants in isolated woodlots in east-central Illinois**. *Wilson Bulletin* 98: 291-296.
- Blake, J. G. and J. R. Karr. 1984. **Species composition of bird communities and the conservation benefit of large versus small forests**. *Biological Conservation* 30: 173-187.
- Blake, J. G. and J. R. Karr. 1987. **Breeding birds of isolated woodlots: Area and habitat relationships**. *Ecology* 68: 1724-1734.
- Cable, T. T., R. L. Schroeder, V. Brack, Jr., and P. S. Cook. 1992. **Summer bird use of Kansas windbreaks**. *Prairie Naturalist* 24: 175-184.
- Carlisle, H. A. 1998. **Abundance, diversity, and energetic condition of neotropical woodland migrants during stopover in a geographically isolated farmstead woodlot in southeastern South Dakota**. Vermillion, SD: University of South Dakota. M.A. thesis.
- Castonguay, M. 1982. **Forest area in eastern South Dakota, 1980**. Research Note NC-291. St. Paul, MN: North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture.
- Cherry, J. D. 1982. **Fat deposition and length of stopover of migrant White-crowned Sparrows**. *Auk* 99: 721-732.
- Connor, E. F. and E. D. McCoy. 1979. **The statistics and biology of the species-area relationship**. *American Naturalist* 113: 791-833.
- Dean, K. L. 1999. **Stopover ecology of neotropical migrant songbirds in riparian corridors in the northern Great Plains**. Vermillion, SD: University of South Dakota. Ph.D. dissertation.
- Emmerich, J. M. and P. A. Vohs. 1982. **Comparative use of four woodland habitats by birds**. *Journal of Wildlife Management* 46: 43-49.
- Helms, C. W. and W. H. Drury, Jr. 1960. **Winter and migratory weight and fat field studies on some North American buntings**. *Bird-Banding* 31: 1-40.
- Hesse, L. W., C. W. Wolfe, and N. K. Cole. 1988. **Some aspects of energy flow in the Missouri River ecosystem and a rationale for recovery**. In: N. G. Benson, editor. *The Missouri River: The resources, their uses and values*. Omaha, NE: North Central Division Species Publication 8; 13-29.
- Hume, I. D. and H. Biebach. 1996. **Digestive tract function in the long-distance migratory Garden Warbler, *Sylvia borin***. *Journal of Comparative Physiology B* 166: 388-395.
- Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. **A fixed-radius point count method for nonbreeding and breeding season use**. *Auk* 103: 593-602.
- James, F. C. and S. Rathbun. 1981. **Rarefaction, relative abundance, and diversity of avian communities**. *Auk* 98: 785-800.
- Johnson, D. G. 2001. **Habitat fragmentation effects on birds in grasslands and wetlands: A critique of our knowledge**. *Great Plains Research* 11: 211-231.
- Karasov, W. H. and B. Pinshow. 1998. **Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site**. *Physiological Zoology* 71: 435-448.
- Karasov, W. H., and B. Pinshow. 2000. **Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site**. *Physiological and Biochemical Zoology* 73: 335-343.
- Martin, T. E. 1980. **Diversity and abundance of spring migratory birds using habitat islands on the Great Plains**. *Condor* 82: 430-439.
- Martin, T. E. 1981. **Limitation in small habitat islands: Chance or competition**. *Auk* 98: 715-734.
- Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1995. **Habitat requirements during migration: Important link in conservation**. In: T. E. Martin and D. M. Finch, editors. *Ecology and management of neotropical*

- migratory birds. New York, NY: Oxford University Press; 121-144.
- Rappole, J. H., M. A. Ramos, R. J. Oehlenschlager, D. W. Warner, and C. P. Barkan. 1979. **Timing of migration and route selection in North American songbirds.** Proceedings of Welder Wildlife Symposium 1: 199-214.
- Rice, W. R. 1989. **Analyzing tables of statistical tests.** Evolution 43: 223-225.
- Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. **Population declines in North American birds that migrate to the neotropics.** Proceedings of the National Academy of Science, USA 86: 7658-7662.
- Schwilch, R. and L. Jenni. 2001. **Low initial fueling rate at stopover sites: A methodological effect?** Auk 118: 698-708.
- Swanson, D. L. 1999. **Avifauna of an early successional habitat along the middle Missouri River.** Prairie Naturalist 31: 145-164.
- Swanson, D. L., H. A. Carlisle, and E. T. Liknes. 2003. **Abundance and richness of neotropical migrants during stopover at farmstead woodlots and associated habitats in southeastern South Dakota.** American Midland Naturalist 149:176-191.
- Tallman, D. T., D. L. Swanson, and J. S. Palmer. 2002. **Birds of South Dakota. Third edition.** Aberdeen, SD: South Dakota Ornithologists' Union.
- Van Bruggen, T. 1996. **The vascular plants of South Dakota.** Third edition. Vermillion, SD: T. Van Bruggen.
- Winker, K., D. W. Warner, and A. R. Weisbrod. 1992. **Daily mass gains among woodland migrants at an inland stopover site.** Auk 109: 853-862.
- Yahner, R. H. 1983. **Seasonal dynamics, habitat relationships, and management of avifauna in farmstead shelterbelts.** Journal of Wildlife Management 47: 85-104.
- Yong, W. and F. R. Moore. 1997. **Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico.** Auk 114: 263-278.
- Zar, J. H. 1996. **Biostatistical analysis. Third edition.** Upper Saddle River, NJ: Prentice Hall.