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The importance of local and regional factors in predicting effective conservation
Planning strategies for wetland bird communities in agricultural and urban landscapes

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Abstract

Wetland assessment techniques have generally focused on rapid evaluations of local and site impacts; however, wetland biodiversity is often influenced both by adjacent and regional land use. Forty wetlands were studied in the Red River Valley (RRV), Southwest Prairie (SWP), and the Northern Hardwood Forest (NHF) ecoregions of Minnesota, USA, to assess the strength of association between local and landscape condition and avian community composition. We examined the relationship between bird assemblages and local and landscape factors (connectedness, isolation, road density, and site impacts). Landscape variables were calculated for three spatial scales at 500 m (79 ha), 1000 m (314 ha), and 2500 m (1963 ha). Connectedness and road density are important measures for predicting bird assemblages in both agricultural ecoregions (SWP and RRV). Connectedness and its relationship with wetland bird assemblages were most pronounced at the larger scale (2500 m), where the largest remnant patches can be discerned. In contrast, road effects on bird assemblages were most pronounced at the smallest scale (500 m). Wetland isolation corresponded to bird community patterns as well, but only in one ecoregion (SWP). In the urbanizing ecoregion (NHF), species richness was considerably lower than elsewhere but community patterns did not correspond to landscape variables. The focus of wetland conservation planning needs to shift from the site scale to the landscape scale to ensure that connection with the regional wetland pattern is accounted for, therefore, affording the best opportunity to successfully maintain wetland avian diversity. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Wetland conservation; Land use; Birds

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1. Introduction

Wetlands pose unique challenges to predicting the influence of landscape pattern on wetland biodiversity that is essential for conservation planning. Wetlands are often heterogeneously distributed in many landscapes, particularly in glaciated regions. These wetlands generally appear as small isolated patches that are strongly influenced by their surrounding matrix. The patchy nature of wetlands may resemble 'biogeographical islands' at a local scale, but a shift in scale may reveal that individual wetland patches may cluster to form a large wetland complex. The reverse is also true; a wetland that appears to be extensive at the local scale may actually be an isolated patch when evaluated at a regional scale. The impact of surrounding land use stressors on these isolated patches likely diminishes with increasing distance, making it difficult to select an effective evaluation area.

Wetland planning for biodiversity is problematic because characterizing landscapes to adequately predict suitability for many organismal groups is uncertain. Selecting features, landscape metrics, and scale for wetland assessment and planning has not been thoroughly examined, although wetland patch size, isolation, and condition of surrounding landscape have been shown to affect animal biodiversity. Findlay and Houlahan (1997) found that increases in paved road density within 2 km of a wetland significantly decreased plant, bird, and herptile species richness. Also, Richter and Azous (1995) detected significant decreases in amphibian richness in wetlands when more than 40% of the watershed was urbanized. Likewise, amphibian assemblages were lower when wetland isolation, road density, and proportion of urban land were higher (Lehtinen et al., 1999). Mensing et al. (1998) found that fish species richness and diversity in riparian wetlands were lower as cultivated land was higher in the surrounding landscape.

In a multi-organismal study (plants, birds, fish, amphibians, and invertebrates) Galatowitsch et al. (1999) suggest that bird assemblages more often reflect land use conditions than other organismal groups. Similarly, other studies have clearly shown the relationship between landscape pattern and birds. Brown and Dinsmore (1986) found that clusters of small marshes contained more avian species than did larger isolated marshes. Mensing et al. (1998) suggest that bird diversity decreases as the percentage of cultivated land increases (within a 1000 m radius) of riparian wetlands. Baines (1988) suggests that agricultural improvements (drainage, inorganic fertilizing, and reseeding) of grasslands in northern England have resulted in the disappearance of snipe (*Gallinago gallinago*) and a marked reduction in the density of other waders. Likewise, in The Netherlands, grassland waders (e.g. lapwing (*Vanellus vanellus* (L.), black-tailed godwit (*Limosa limosa* (L.), and snipe) experienced increases in egg loss and brood mortality with intensification of agricultural land (Bientema et al., 1997). Reduced hatching was attributed to early mowing and increased stocking of cattle, while reduced brood survival was linked with increased fertilization rates.

As landscape use intensifies, the approach to conservation planning approach typically relies on preserving and managing reserves dedicated for wildlife use. The surrounding matrix receives relatively little conservation attention despite its importance (Harris, 1984; Hobbs, 1993). For example, wetland reserve planning in the US relies heavily on incentive programs (e.g. RIM, WRP) to attract individual landowners to set aside a tract of land for wetland restoration (Galatowitsch et al., 1999). Although these approaches are amiable, generally little upland is included when establishing wetland reserves (Preston and Bedford, 1988). In addition, project planning often does not consider regional wetland patterns when developing protection priorities (Galatowitsch et al., 1998). If a landscape approach was available to identify the critical aspects of regional wetland pattern, it should be more feasible to shift the focus of conservation planning from single reserves to larger areas that encompass landscape-level processes (Brussard et al., 1992; Naveh, 1994; Wiens, 1997). Through the use of geographic information systems (GIS), characterization of the landscape at a broad regional scale can be used to measure several landscape features (e.g. patch isolation, patch contiguity, patch size and shape etc.) that are influential on plant and animal populations (Turner and Gardner, 1990; Robbins and Bell, 1994).

The glaciated landscapes of the prairie and forest regions of southwestern, northwestern, and central Minnesota are ideal locations for investigating the influence of landscape variables at different scales on avian wetland biodiversity. These landscapes were once composed of tallgrass prairies and woodlands interspersed with several wetland complexes. Currently, these regions include both wetlands that are isolated and those that remain in large complexes. The landscapes of western Minnesota are predominately agricultural (with some large tracts of grasslands found throughout this region) and have been tiled, drained, and ditched to increase the area of tillable and developable land. In central Minnesota, an urban/woodland matrix exists that has been greatly impacted by both agriculture and urban development. Consequently, the quality of the remaining wetlands varies greatly. In northwestern Minnesota, several large wetland complexes still exist. In contrast, a majority of the wetlands in southwestern and central Minnesota occur in either small wetland complexes or individual wetland patches. The diversity of wetland quality and the diversity of land use impacts within this region provide an opportunity to investigate the influence of land use on avian wetland biodiversity.

By assessing impacts both at the local and the landscape level, wetland managers will be able to maintain diversity in regional wetland ecosystems and in turn strengthen and preserve wetland biodiversity. In this study, we compare the biological composition of 40 wetlands that vary in land use context from a relatively unimpacted environment to an agricultural or urban setting. The objectives of this study were to determine (1) what land use metrics best reflect changes in avian biodiversity, and (2) the scale(s) at which biodiversity corresponds to land use impacts.

2. Methods

2.1. Study area

Forty wetlands were studied in central, northwestern, and southwestern Minnesota, USA (48°50′N, 96°27′W; 43°40′N, 95°06′W; 45°10′N, 92°52′W; Fig. 1). The wetlands are distributed across three ecoregions, Southwest Prairie (SWP) (North Central Glaciated Plains/Western Corn Belt Plains) (15 sites), the Red River Valley (RRV) (11 sites), and the Northern Hardwood Forest (NHF) (Hardwood Hills, Highland Woods) (14 sites) (Omernik, 1997; MN DNR, 1996). Within each ecoregion, sites were chosen to represent a land use gradient from least impacted to most impacted, based on preliminary field assessments of local and landscape conditions (Tables 1–3). The sites considered to be most impacted have both on-site degradation (e.g., draining, cultivation) and landscape alteration (high percentage of surrounding urban or agricultural land). Least impacted wetlands have minimal site and landscape alteration. The pool of sites available for this study was restricted by land ownership and uncertain land use history; therefore,

Table 1
Local and landscape variables for each wetland site within the Southwest Prairie[a]

Local and landscape variables	Site codes														
	BS	CP	DO	KS	LT	LY	ML	PM	PP	SN	SO	SP	TO	VM	WL
Size (ha)	1.5	0.8	10.9	12.8	0	10.5	4.6	1.2	11.9	8.9	8.9	6.5	0	3.2	10.6
Percent vegetation	30	30	10	10	100	10	70	10	70	70	70	70	90	30	30
Ditched	N	N	Y	N	N	Y	N	N	N	N	N	N	N	N	Y
Storm water impacts	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Cultivated	N	N	N	N	Y	N	N	N	N	N	N	N	Y	N	N
Connectedness 500 m (%)	22	40	56	0	0	21	47	84	100	72	16	84	1	96	64
Connectedness 1000 m (%)	9	26	45	0	0	5	13	53	89	55	10	37	1	84	40
Connectedness 2500 m (%)	20	4	25	0	0	1	2	20	69	37	10	21	1	60	13
Road density 500 m (km km^{-2})	1.58	2.50	0.73	0.00	0.94	2.09	1.80	0.00	2.23	0.00	0.25	0.76	2.52	0.00	2.01
Road density 1000 m (km km^{-2})	1.17	1.26	0.58	1.22	1.13	1.22	1.19	0.11	1.18	0.73	0.94	1.13	1.27	0.81	1.44
Road density 2500 m (km km^{-2})	1.04	1.28	1.22	1.17	1.20	1.24	1.01	0.88	1.13	0.95	0.80	1.25	1.23	0.95	1.04
Wetland isolation (km)	1.45	0.20	0.29	0.48	0.64	0.51	0.31	0.17	0.08	0.11	0.69	0.21	1.51	0.15	0.98

[a] Wetland sites are identified as two-letter codes for each site following Galatowitsch et al. (1997). Percent vegetation is described as density of canopy cover within the wetland. Connectedness is described as percent connected at a given scale. Wetland isolation is defined as the average distance to the five nearest wetlands (0.2 ha minimum).

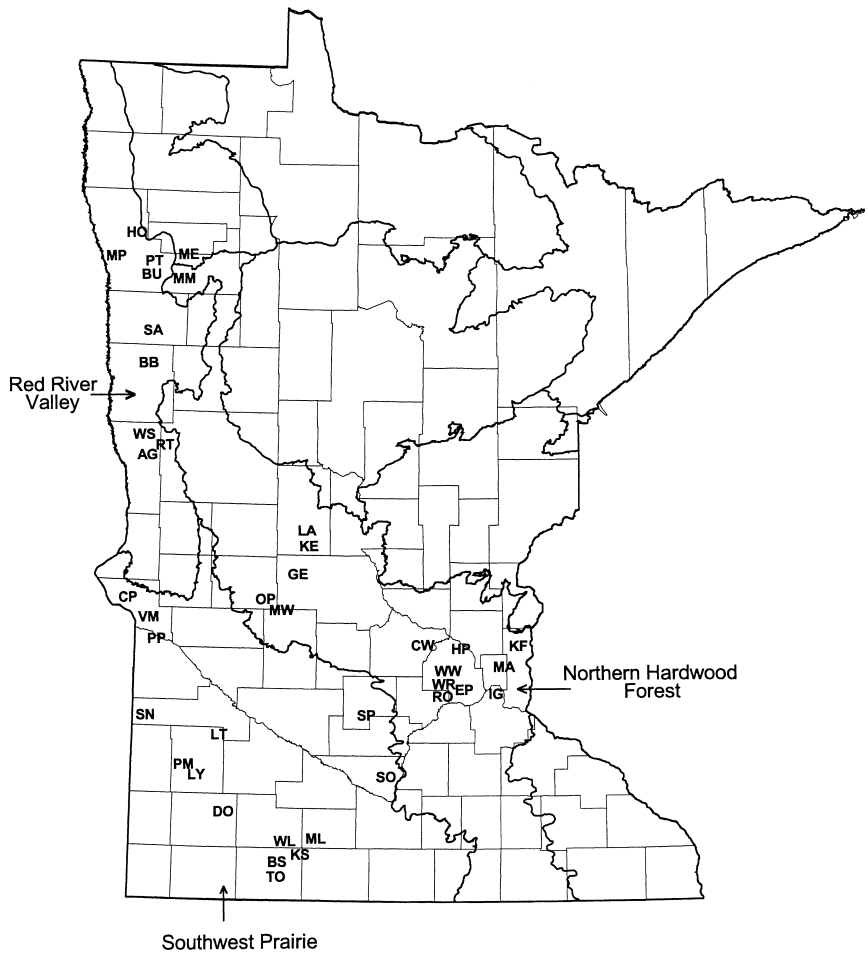

Fig. 1. Location of 40 depressional wetland study sites and ecoregion boundaries in Minnesota. Wetland sites are identified by a two-letter acronym for each site.

randomly selecting study sites was not feasible. Galatowitsch et al. (1997) provide a detailed description of site selection. In the present study, the prevalent non-riverine wetland type was selected for each ecoregion (based on ponding duration): temporary to seasonally flooded wetlands in the RRV, and seasonally to semi-permanently flooded wetlands in the SWP and NHF (State of Minnesota, 1997). Environmental characteristics (conductivity and pH of water, soil profile features, and size) were described for each wetland during site visits in 1995 and 1996. Characterization of each ecoregion is provided below.

Wetlands of the SWP ecoregion occur in upland depressions set in late Quaternary till lacking a connected network of surface drainage (Richardson et al., 1994). Extensive drainage (tile and ditch) and cultivation (primarily corn (*Zea mays* (L.)), soy beans (*Glycine max* (L.) Merr.)) have resulted in wetland losses exceeding 95% in this region (State of Minnesota, 1997). Prior to agricultural conversion, this landscape was a matrix of tallgrass prairie (e.g, switchgrass (*Panicum virgatum* (L.)), Indian grass (*Sorghastrum nutans* (L.) Nash.), big bluestem (*Andropogon geradii* (Vitman)) on upland ridges and knolls, with wetlands interspersed in low-lying areas. A mosaic of ephemerally to permanently flooded wetlands occupied as much as 40% of this landscape (Galotwitsch and van der Valk, 1994). Prairie wetlands included in this study

Table 2
Local and landscape variables for each wetland site within the Red River Valley[a]

Local and landscape variables	Site codes										
	AG	BB	BU	HO	ME	MM	MP	PT	RT	SA	WS
Size (ha)	509	343	83	0	0	294	0.1	43.5	54.8	28	11.8
Percent vegetation	100	90	100	100	100	100	100	100	90	100	90
Ditched	N	N	Y	Y	Y	Y	Y	N	N	N	Y
Storm water impacts	N	N	N	N	N	N	N	N	N	N	N
Cultivated	N	N	N	Y	Y	N	N	N	N	N	N
Connectedness 500 m (%)	98	66	56	0	0	100	32	100	97	88	98
Connectedness 1000 m (%)	74	71	42	0	0	87	9	93	78	71	50
Connectedness 2500 m (%)	39	44	24	0	0	39	2	43	55	28	12
Road density 500 m (km km^{-2})	0.00	1.80	0.96	0.00	0.00	0.00	1.58	0.00	0.60	0.00	0.65
Road density 1000 m (km km^{-2})	0.25	1.60	0.90	0.33	0.00	0.15	1.21	0.24	0.56	0.07	0.86
Road density 2500 m (km km^{-2})	0.64	1.00	0.94	1.08	0.54	0.93	1.26	0.28	0.42	0.61	0.83
Wetland isolation (km)	0.05	0.32	0.04	0.18	0.72	0.03	0.34	0.03	0.08	0.13	0.26

[a] Wetland sites are identified as two-letter codes for each site following Galatowitsch et al. (1997). Percent vegetation is described as density of canopy cover within the wetland. Connectedness is described as percent connected at a given scale. Wetland isolation is defined as the average distance to the five nearest wetlands (0.2 ha minimum).

ranged in size from 0 (drained) to 12.8 ha (Table 1), had conductivities of 389–1595 uS cm^{-1}, and a pH of 6.9–8.8. Two sites (SN, VM) are located in very large tracts of native grassland that include intact wetland complexes; four others have minimal site impacts but are within small grassland remnants (CP, KS, PM, PP). Seven sites have little grassland buffer from agriculture (DO, TF, BS, LY SO, SP, WL). Two sites (LT, TO) have recently been cultivated.

The RRV ecoregion is located in the Glacial Lake Agassiz basin, a nearly level landscape (elevation changes of only 0.2 m km^{-1}) with silty, sandy and clayey lacustrine deposits. Wetlands occur in swales between ancient beach ridges, and in slight depressions with perched water tables (State of Minnesota, 1997). Land use in northwestern Minnesota is predominately agriculture (e.g., wheat (*Triticum aesitivum* (L.)), sugar beets (*Beta vulgaris*)). Extensive

Table 3
Local and landscape variables for each wetland site within the Northern Hardwood Forest[a]

Local and landscape variables	Site codes													
	CW	EP	GE	HP	IG	KE	KF	LA	MA	MW	OP	RO	WR	WW
Size (ha)	0.9	0.8	3.1	6.1	0.2	0.5	1.1	1.5	1.5	4.2	15.6	0.6	2.4	1.4
Percent vegetation	100	10	70	70	70	30	70	70	10	70	70	70	70	90
Ditched	N	N	N	N	N	N	N	N	N	Y	N	N	N	N
Storm water impacts	N	N	N	Y	Y	N	N	N	Y	N	N	Y	Y	N
Cultivated	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Connectedness 500 m (%)	65	2	84	64	2	46	100	54	2	100	100	1	42	76
Connectedness 1000 m (%)	56	1	91	63	1	33	99	43	1	92	85	1	36	70
Connectedness 2500 m (%)	38	1	67	52	1	6	72	36	1	79	85	1	30	63
Road density 500 m (km km^{-2})	1.34	7.16	0.00	4.51	5.82	2.39	0.00	1.55	5.67	0.00	0.69	5.25	4.78	2.10
Road density 1000 m (km km^{-2})	1.19	6.69	0.00	3.59	5.26	1.25	0.74	1.76	6.98	0.34	0.58	5.55	5.61	2.10
Road density 2500 m (km km^{-2})	1.09	6.80	0.70	4.05	5.06	1.01	0.91	1.34	6.43	0.76	0.84	4.13	4.71	3.06
Wetland isolation (km)	0.18	0.10	0.21	0.09	0.12	0.45	0.09	0.23	0.22	0.25	0.10	0.19	0.10	0.28

[a] Wetland sites are identified as two-letter codes for each site following Galatowitsch et al. (1997). Percent vegetation is described as density of canopy cover within the wetland. Connectedness is described as percent connected at a given scale. Wetland isolation is defined as the average distance to the five nearest wetlands (0.2 ha minimum).

ditch systems have drained over 80% of the wetlands (State of Minnesota, 1997). Prior to agricultural conversion, this landscape was extensive wet prairie (e.g., prairie cord-grass (*Spartina pectinata* (Link)), switchgrass (*P. virgatum* (L.)), sedges (*Carex* spp.), rushes (*Juncus* spp.)). RRV wetlands included in this study ranged in size from drained to 509 ha (Table 2), with conductivities of 613–1423 uS cm^{-1}, and a pH of 7.1–7.9. Two sites are within agricultural fields and have recently been cultivated (HO, ME); five sites have been heavily grazed and/or periodically hayed (MP, MM, RO, SP, WS), four others are relatively unimpacted and are surrounded by native grassland (AG, BB, BU, PT).

The NHF ecoregion includes the rapidly urbanizing Minneapolis/St. Paul metropolitan area, agricultural and rural lands on the exurban fringe, and remnant forested landscapes (e.g., sugar maple (*Acer saccharum* Marsh), basswood (*Tilia americana* (L.)), oaks (*Quercus* spp.)) in public lands, preserves, and regional parks. Soils are primarily loams to clay loams on Wisconsin till with some sandier soils on outwash plains. Wetlands occur in morainal depressions. NHF wetlands included in the study ranged in size from 0.2 to 16 ha (Table 3), had conductivities of 47–740 uS cm^{-1}, and a pH of 5.9 to 8.2. Three sites receive high stormwater inputs (EP, RO, MA); three others are within a residential landscape (HP, IG, WR). The remaining sites have less urbanized use in their immediate vicinity. Three sites are adjacent to agriculture (KF, KE, LA); two others are surrounded by prairie and second growth forest (OP, GE). The least impacted sites (MW, CW, WW) have little past use and the surrounding land has not been historically converted.

2.2. Land use/land cover characterizations

A GIS land use/cover database was developed using Arc/INFO 7.1.2 (ESRI, 1996) at a 100 m resolution to characterize landscape condition. Existing digital land use data were obtained from the Land Management Information Center (late 1980s) and the Twin Cities Metropolitan Council (1991). Land use was classified into 18 categories including urban (industrial/urban, rural residential complex, rural residential other, and farmsteads), forest (deciduous, coniferous, and mixed), grassland (grassland, grassland-forest), agriculture (cultivated, and tree farms and nurseries), water bodies, wetlands, gravel pits and open mines, bare rock, exposed soil and sand, and others. The Twin Cities Metropolitan Council data were updated with 1994 color infrared aerial photography (1:15840) to delineate new urban development and to distinguish differences in forest and grassland cover type. Changes were identified on plots and digitized into the GIS database. National Wetland Inventory (USFWS 1981–1994, 1:24,000) data was united with the land use data to improve the accuracy of wetland classification within the land use database. A statewide Conservation Reserve Program (CRP) coverage was obtained from the Minnesota Department of Agriculture to define newly established grassland areas that were previously cultivated. Additional infrastructure data (roads, railroads, utility lines etc.) were obtained from the Minnesota Department of Transportation and managed as separate coverages.

Three land use variables from the GIS database were used to describe landscape pattern for each site: road density, connectedness, and wetland isolation. These variables were selected based on preliminary analysis to minimize autocorrelation among variables while including a broad range of landscape variables. Road density was calculated as the ratio of the length of road to the total area within a study site. Connectedness was defined as a contiguous polygon of relatively unimpacted land cover (i.e. wetland, water bodies, grassland, and forest cover) surrounding the wetland site (following Baudry and Merriam, 1988) (Table 4). Essentially, connectedness is a measure of the remnant patch size that surrounds each individual wetland site. Once all wetland/water, grassland, and forest polygons connected to each site were identified, the proportion of area of the connected polygon to the entire sampled area was calculated (i.e. 50% of the total area was calculated as connectedness). Wetland isolation was estimated as the average distance from the edge of each wetland site to the edges of the five nearest wetland polygons (0.2 ha minimum). Two of the land use variables (connectedness and road density) were assessed at three different scales around each site using radii of 500 m (79 ha), 1000 m (314 ha), and 2500 m (1963 ha) (Fig. 2). The minimum radius was defined by data resolution and the maximum by data availability. A total of seven land use measures were used; they include road density

Table 4
Composition of connectedness polygons for the three ecoregions[a]

Connectedness composition	Southwest Prairie		Red River Valley		Northern Hardwood Forest	
	Mean	Range	Mean	Range	Mean	Range
500 m						
Grassland cover (%)	47.1	0–88	40.5	0–93	27.4	0–81
Forest cover (%)	2.9	0–15	2.3	0–16	32.8	0–84
Water bodies (%)	13.5	0–57	0.1	0–1	3.6	0–10
Wetlands (%)	23.1	0–65	39.0	0–93	22.0	0–60
1000 m						
Grassland cover (%)	45.5	0–86	44.5	0–91	25.7	0–65
Forest cover (%)	3.3	0–13	3.9	0–19	28.4	0–67
Water bodies (%)	11.0	0–67	0.1	0–1	6.4	0–21
Wetlands (%)	26.9	0–76	33.5	0–67	25.3	0–60
2500 m						
Grassland cover (%)	44.5	0–85	43.4	0–93	23.3	0–54
Forest cover (%)	7.4	0–31	6.5	0–24	27.2	0–67
Water bodies (%)	12.9	0–67	0.2	0–1	6.4	0–20
Wetlands (%)	21.9	0–71	31.8	0–72	21.7	0–44

[a] For each scale, the range and the mean of each cover type are shown for each ecoregion and described as percentages of the connectedness polygons.

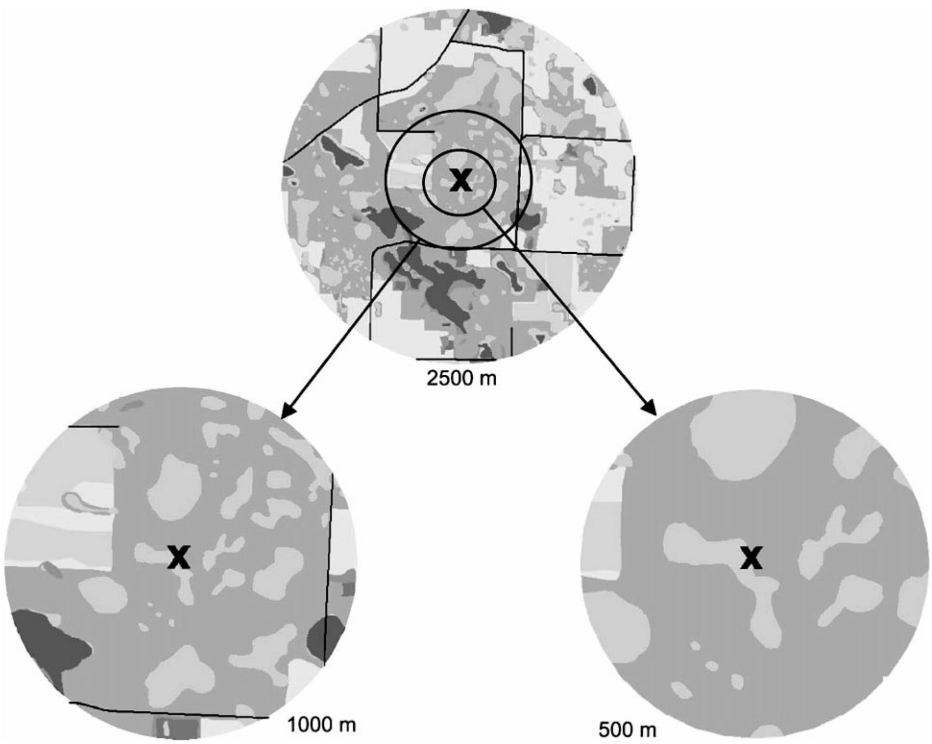

Fig. 2. Example of GIS land use data. Spatial scales depicted: 500, 1000, and 2500 m.

(RD500, RD1000, RD2500), connectedness (CON500, CON1000, CON2500), and wetland isolation (WETI).

Pertinent site impacts were mapped and documented in the field including type, number, size, and impacts associated with roads, bridges, buildings, culverts, drain tile, ditches, feedlots etc. One site land use variable (SITE) was developed from these field evaluations. The SITE variable included presence or absence of ditching, storm water, and cultivation impacts. All sites with ditches had artificially constructed channels with inlets and outlets. Wetlands classified as stormwater-impacted had urban runoff directed to the basin through culverts. In addition, two other variables were used to define local wetland conditions: wetland size (SIZE) and percent vegetation (VEG). Vegetated cover at a wetland was classified as percent vegetation as opposed to open water.

2.3. Biological surveys

Animals were surveyed twice from mid-May to mid-July 1996. The number of survey points for breeding birds varied with wetland size, as follows: sites less than 1.6 ha contained two points; three points were used for sites between 1.7 and 2.8 ha; sites between 2.9 and 5.0 ha contained four points; and five points were used at sites greater than 4.0 ha. Survey points were separated by 220 m in the RRV and by 120 m in the SWP and in the NHF, and they were located at least 20 m from the wetland–upland edge following Bibby et al. (1992) and Ralph et al. (1993). Breeding birds were surveyed within 100 m (RRV) or 50 m (SWP and NHF) of the survey points. Observers spent 10 min at each survey point, recording all birds seen or heard and any evidence of breeding. Tapes were also played (total of 3 min over two separate surveying periods) to elicit responses from secretive species (e.g. pied-billed grebe (*Podilymbus podiceps* (L.)), sora (*Porzana carolina* (L.)), Virginia rail (*Rallus limicola* (Vieillot)), common moorhen (*Gallinula chloropus* (L.))) (Delphey and Dinsmore, 1993). Low flyovers (height less than 25 m) were counted in the survey (recorded separately from other occurrences), whereas high flyovers were not. Surveys were conducted between dawn and 9:00 a.m. Bird surveys were not done when it was raining or when wind speeds exceeded 13 km h^{-1}. All birds observed (both visits) were used in the analysis. Bird species were grouped into guilds based on wetland dependency (Brooks and Croonquist, 1990). Taxonomy follows Sibley and Monroe (1990).

2.4. Statistical analysis

Mantel tests, (Manley, 1991; NTSYS, 1993), a non-parametric method for comparing two distance matrices, were used to test the ability of local and landscape condition to account for bird community differences among wetlands in each ecoregion. The Mantel test measures the association between the elements in two matrices and gauges the significance of this association by comparison with the distribution of values found randomly reallocating the elements of the second matrix (Manley, 1991). A dissimilarity matrix was calculated for the avian community using 1-Jaccard's coefficient (Legendre and Legendre, 1983). Dissimilarity matrices were calculated for all landscape variables, wetland size, and percent vegetation using Euclidean distances. Euclidean distances are useful measures of differences in physical, chemical, and geological properties between sites (Legendre and Legendre, 1983). All dissimilarity matrices were standardized (mean=0 and standard deviation=1) before distance matrices were calculated to eliminate inconsistencies among the measures. The SITE variable was represented as presence/absence data; therefore, the site dissimilarity matrix was calculated using the simple matching coefficient (Sokal and Michener, 1958). The simple matching coefficient was chosen because it accepts double zeros and assumes there is no difference between double zero and double one (Legendre and Legendre, 1983). Within each ecoregion, 11 Mantel tests were run: landscape variables (connectedness and road density) at three spatial scales, wetland isolation, site impacts, wetland size, and percent vegetation. Relationships were considered to be significant at the random *P*-value of 0.05. Tests of the null hypothesis were made by randomizing the second (land use) matrix 2000 times and recalculating the '*G*' statistic (the index of matrix similarity) (Manley, 1991). The 2000 '*G*' values comprise the statistical distribution used to determine the significance of observed similarity.

Table 5
Pearson correlation coefficients for each variable within each ecoregion[a]

	CON500	CON1000	C0N2500	RD500	RD1000	RD2500	WETI
Southwest Prairie							
CON500	–						
CON1000	0.93**	–					
CON2500	0.80**	0.92**	–				
RD500	−0.18	−0.21	−0.21	–			
RD1000	−0.41	−0.41	−0.30	0.67**	–		
RD2500	−0.28	−0.28	−0.29	0.53*	0.49*	–	
WETI	−0.62*	−0.59*	−0.43	0.39	0.44	0.08	–
Red River Valley							
CON500	–						
CON1000	0.93**	–					
CON2500	0.78**	0.92**	–				
RD500	−0.11	−0.13	0.01	–			
RD1000	−0.05	−0.08	0.03	0.97**	–		
RD2500	−0.43	−0.50	−0.49	0.56	0.58*	–	
WETI	−0.67*	−0.67*	−0.61*	0.18	0.09	0.12	–
Northern Hardwood Forest							
CON500	–						
CON1000	0.99**	–					
CON2500	0.96**	0.97**	–				
RD500	−0.91**	−0.89**	−0.82**	–			
RD1000	−0.89**	−0.87**	−0.78**	0.96**	–		
RD2500	−0.83**	−0.79**	−0.69**	0.95**	0.97**	–	
WETI	0.03	−0.02	−0.15	−0.26	−0.31	−0.34	–

[a] Land use variables are described in the text. A single asterisk indicates significance at the 0.05 level. Two asterisks indicate significance at the 0.01 level.

Based on the Mantel tests, results were examined by either principal components analysis (PCA) or by plotting. First, plots of species richness/distribution were interpreted with landscape pattern (i.e. site impacts, connectedness, isolation). If the plots did not reveal a biological interpretable result, PCA was used to show species distribution patterns and to suggest ways to efficiently simplify the data set.

Pearson correlations were calculated for all pairs of landscape variables (Table 5). Of 63 combinations, 32 were not significant, and 17 pairs of the same measure (different scales) were significant. Fourteen combinations of different measures were correlated. Connectedness was correlated with wetland isolation in two of the three ecoregions (RRV and SWP) and road density in the NHF ecoregion. Although some correlations existed, all variables were kept due to the lack of correlation consistency across variables and the desire to show how variables responded across ecoregions.

3. Results

Avian community patterns corresponded to landscape pattern for 10 of the 33 tested relationships. Two relationships were found at the local scale: site impacts and percent vegetation. Eight landscape level relationships corresponded to bird assemblages: wetland isolation in the SWP, road density in the RRV and in the SWP, and connectedness in RRV and SWP. Connectedness showed concordance across three scales in the RRV and two scales in the SWP, while road density relationships were only recorded at the 500 m scale.

3.1. Southwest Prairie

Wetland isolation was correlated with connectedness but not road density in the SWP (Table 5). Compared to the other two ecoregions, wetland isolation was relatively high; from 0.08 to 1.5 km (mean=0.5 km). Road densities ranged from RD500 (mean=1.16 km km^{-2}), RD1000 (mean=1.02 km km^{-2}), to RD2500 (mean=1.09 km km^{-2}). Connectedness was low across all spatial scales: CON500 (mean=49%), CON1000 (mean=32%), and CON2500 (mean=19%).

A total of 68 species of birds were observed at the sites; richness ranged from 7 to 24 species, with a mean of 16 species per site. Red-winged blackbirds (*Agelaius phoeniceus* (L.)), were observed at all of the 15 sites. Other birds common to the sites include killdeer (*Charadrius vociferus* (L.)), common yellowthroat (*Geothlypis trichas* (L)), yellow-headed blackbird (*Xanthocephalus xanthocephalus* (Bonaparte)), and barn swallow (*Hirundo rustica* (L.)). Twenty-five species were observed only at one site (36% of the total).

Three landscape matrices explained significant differences in bird assemblages: connectedness, wetland isolation, and road density (Table 6). Bird species richness was greatest (max=24) at an intermediate level of isolation (0.6 km, Fig. 3). Only at the 500 m scale did road density correspond to bird ($P<0.003$) assemblages (Table 6). At all spatial scales, differences in connectedness corresponded to differences in bird assemblages (500 m, $P<0.003$; 1000 m, $P<0.002$; 2500 m, $P<0.05$). A maximum of 24 species were observed at the wetland (LY) with maximum connectedness at 500 m (21%), 1000 m (5%), and 2500 m (1%).

Two local matrices accounted for significant differences in bird assemblages: site impacts (cultivation, ditching) and percent vegetation (Table 6). Ditched and cultivated wetlands generally were typified by having high road densities (>2 km km^{-2}) at the 500 m scale. The PCA of bird assemblages resulted in sites grouped by ditching, cultivation, and vegetative cover along the first PCA axis that explains 22% of the data variation (Fig. 4). Ditched wetlands with low vegetative cover (<30%) and cultivated wetlands have high axis 1 values and were typified by red-winged blackbird, yellow-headed blackbird, barn swallow, and killdeer. Wetlands with bird assemblages including ruddy duck (*Oxyura jamaicensis* (Gmelin)), wood duck (*Aix sponsa* (L.)), and sedge wren (*Cistothorus platensis* (Latham)), are positioned low on axis 1. These sites generally have few site impacts, have a high percentage of hydrophytic vegetation (>70%), and have low road densities (<2 km km^{-2}) at the 500 m scale. A meaningful interpretation of axis 2 could not be formulated. Vegetative cover of non-cultivated sites comprised herbaceous hydrophytic plants such as cattail (*Typhax glauca* (Godr.)), softstem bulrush (*Scirpus validus* (Vahl.)), and lake sedge (*Carex lacustris* (Wild.)). The two cultivated sites (both with 100% cover), however, are dominated by cultivated crops and annual plants typical of agricultural fields (Pennsylvania smartweed (*Polygonum pensylvanicum* (L.) and barnyard grass (*Echinochloa muricata* (P. Beauv.) Fern)).

When species richness of sites is grouped by connectedness and site impacts across scales, habitat preferences of wetland taxa are apparent (Fig. 5a and b). At the 500 m scale, nine wetlands with more than 35% connectedness had a higher ratio of wetland taxa (mean=2.4) than six wetlands with less than 35% connectedness (mean ratio of wetland taxa=0.8). At the 2500 m scale, three wetland sites (SN, VM, PP) with more than 35% connectedness had the highest ratio of wetland taxa (mean=4.0), while 12 wetland sites with less than 35% connectedness had a mean ratio of wetland taxa of 1.2. Wetland taxa that preferred sites with high connectedness include (proportion of occurrences at sites >35% connectedness at the 2500 m scale): ruddy duck (1.00), mallard (*Anas platyrhynchos* (L.)) (0.88), sedge wren, Canada goose (*Branta canadensis* (L.)) (0.77), canvasback (*Aythya valisineria* (Wilson)) (1.00), gadwall (*Anas strepera* (L.)) (1.00), and redhead (*Aythya americana* (L.)) (1.00). At both 500 and 2500 m, sites with low connectedness can be grouped into distinct groups by site impacts and isolation. At 500 m, two sites that were recently cultivated (TO, LT) and the most isolated wetland (BS) formed a group with lower species richness. These three sites also form a group with low species richness at 2500 m along with another site (PM).

3.2. Red River Valley

Wetland isolation was correlated with connectedness but not road density in the RRV (Table 5). Wetland isolation ranged from 0.03 to 0.72 km (mean=2.0 km). Connectedness was different across spatial scales: CON500 (mean=70%), CON1000

Table 6
Results of matrix comparisons of bird assemblages to land use using Mantel tests are shown for each ecoregion[a]

	SWP		RRV		NHF	
	r	P	r	P	r	P
Road density 500 m	0.250	0.0030	0.240	0.0030	0.150	0.0990
Connectedness 500 m	0.320	0.0020	0.430	0.0050	0.130	0.1230
Road density 1000 m	−0.050	0.4220	0.200	0.0850	0.170	0.0830
Connectedness 1000 m	0.350	0.0165	0.490	0.0040	0.140	0.0910
Road density 2500 m	−0.090	0.2270	0.180	0.1000	0.080	0.2200
Connectedness 2500 m	0.320	0.0430	0.240	0.0490	0.140	0.0800
Wetland isolation	0.270	0.0500	−0.010	0.4900	−0.140	0.2050
Site impacts	0.330	0.0266	0.200	0.0830	0.080	0.2890
Size	−0.110	0.1190	−0.050	0.3360	0.030	0.5850
Vegetation	0.270	0.0065	−0.166	0.1070	−0.110	0.2510

[a] All land use dissimilarity matrices are Euclidean distances. Species composition matrices were constructed from Jacard (1-J). Land use variables are described in the text. The value P is the probability that random Z is greater than or equal to observed Z, where Z is the measure of matrix concordance. P-values less than 0.05 were considered to be significant.

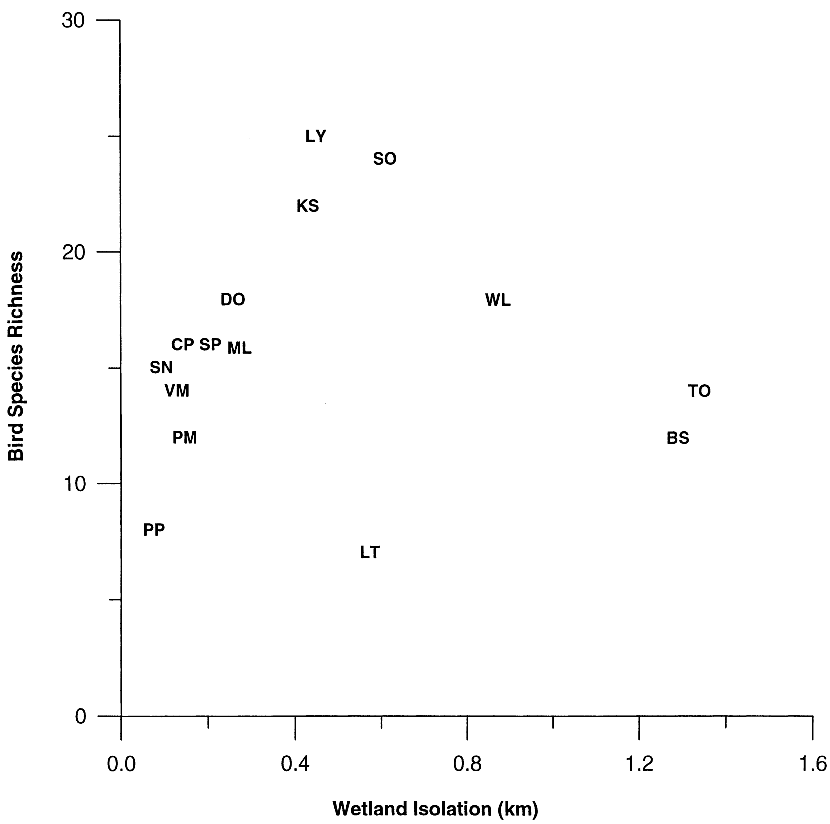

Fig. 3. Relationship between wetland isolation and bird species richness in the SWP. Wetland sites are identified by a two-letter acronym for each site.

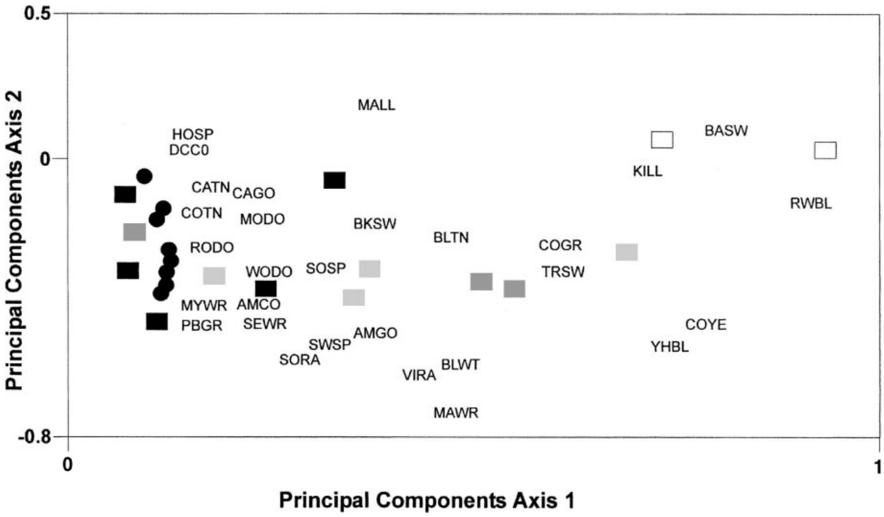

Fig. 4. Principal components biplot of bird species presence, absence and study sites, based on Euclidean distance dissimilarity matrices. The first two axes explain 39% of the variation of the bird assemblages. Bird species occurring at only one site are indicated by (●) symbol. All other species are identified by a four-character acronym. The square symbols indicate percent hydrophytic vegetation at a site: (■) 70% cover, (▩) 30% cover, (▩) 10% cover, and (□) no hydrophytic cover. Acronyms are as follows HOSP (*Passer domesticus*), DCCO (*Phlacrocorax auritus*), CATN (*Sterna caspia*), CAGO (*Branta candensis*), COTN (*Sterna hirundo*), MODO (*Zenaida macroura*), RODO (*Columba liva*), WODO (*Aix sponsa*), MYWR (*Dendroica coronata*), PBGR (*Podilymbus podiceps*), AMCO (*Fulica americana*), SEWR (*Cistothorus platensis*), SORA (*Porlana carolina*), SWSP (*Melospiza georgiana*), AMGO (*Carduelis tristis*), SOSP (*Melospiza melodia*), BKSW (*Riparia riparia*), MALL (*Anas platyrhynchos*), BLTN (*Chilidonias niger*), BLWT (*Anas discors*), VIRA (*Rallus limicola*), MAWR (*Cistothorus palustris*), COGR (*Quiscalus quiscula*), TRSW (*Tachycineta bicolor*), KILL (*Charadrius cristata*), YHBL (*Xanthocephalus xanthocephalus*), COYE (*Geothypis trichas*), BASW (*Hirundo rustica*), and RWBL (*Agelaius pheniceus*). Species occuring at only one site include *Anas acuta*, *Anas strepera*, *Aytha valisineria*, *Aythya americana*, *Oxyura jamaicensis*, *Ardea herodias*, *Botaurus lentiginosus*, *Nycticorax nyticorax*, *Cyanicitta cristata*, *Ammodramus bairdii*, *Ammodramus henslowii*, *Ammodramus lectonteii*, *Euphagus cyanocephalus*, *Spizella pusilla*, *Spizella passerina*, *Progue subis*, *Stelgidopteryx serripennis*, *Dumetella carolinesis*, *Colaptes auratus*, *Melanerpes erythtocephalus*, *Sturnus vulgaris*, and *Tyrannus tyrannus*.

(mean=54%), and CON2500 (mean=28%) (Table 2). In contrast, road densities were similar across scales: RD500 (mean=2.03 km km^{-2}), RD1000 (mean=1.76 km km^{-2}), and RD2500 (mean=2.44 km km^{-2}).

A total of 33 bird species were recorded from the 11 sites sampled: from 9 to 20 at each site (mean=14 species). Common species included bobolink (*Dolichonyx oryzivorus* (L.)), clay-colored sparrow (*Spizella pallida* Swainson), common yellowthroat, savannah sparrow (*Passerculus sandwichensis* Gmelin), swamp sparrow (*Melospiza georgiana* Latham), song sparrow (*Melospiza melodia* Wilson), and marsh wren (*Cistothorus platensis* Wilson).

Two landscape variables accounted for significant differences in bird assemblages: connectedness and road density (Table 6). At the 500 m scale, both road density ($P<0.003$) and connectedness ($P<0.005$) were concordant with bird assemblages (Table 6). Moderate to high bird species richness (mean=15, median=18) were found at sites with no roads present, while low species richness (mean=12, median=12) typified sites with roads present. As connectedness increases, bird species richness increases at all scales. Bird assemblages did not have preferential affinity to a particular landscape configuration. Connectedness at the 1000 m scale ($P<0.004$) and at the 2500 m scale ($P<0.049$) continued to show a strong relationship with richness, but road densities did not. Species richness relationships were also similar at these scales. No species show affinity to a particular landscape configuration.

3.3. Northern Hardwood Forest

Road density was correlated with connectedness but not wetland isolation in the NHF (Table 5). Road

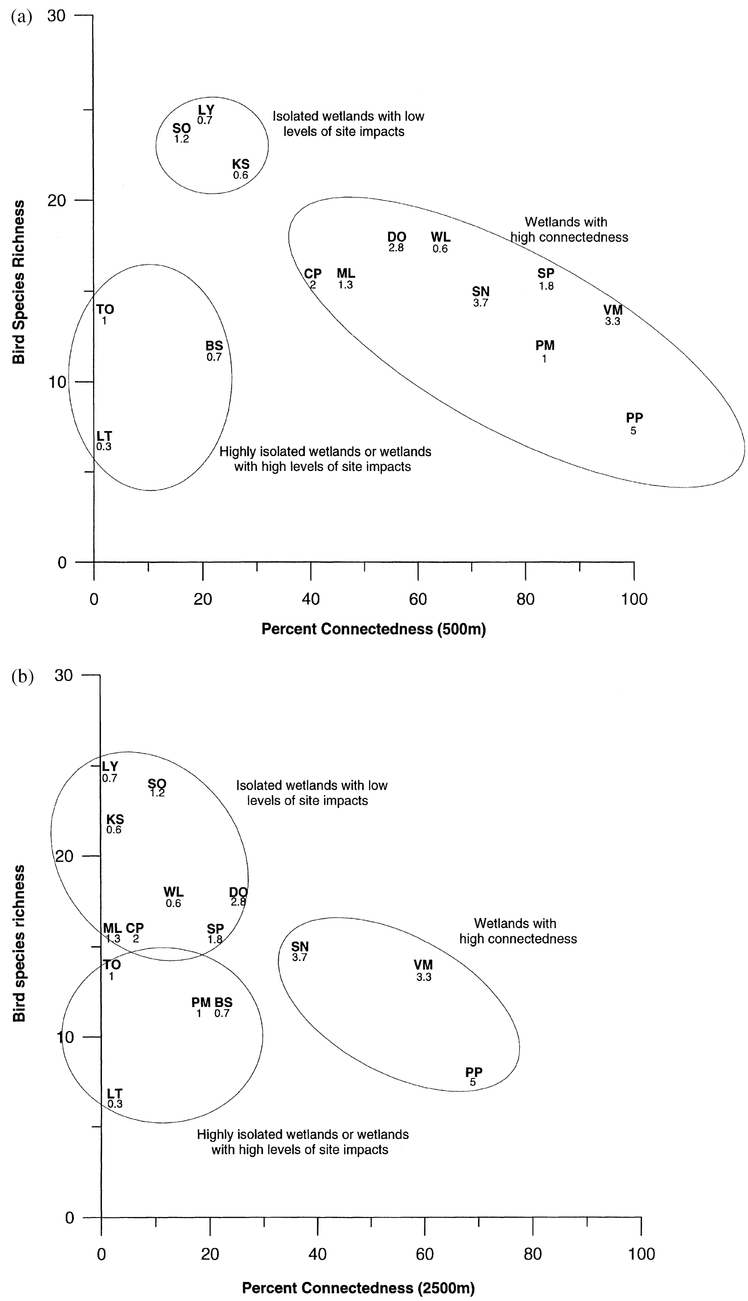

Fig. 5. (a) Relationship between bird species richness and percent connectedness within 500 m of the sites in the SWP. Wetland sites are identified by a two-letter acronym for each site. The number represents the ratio of wetland to non-wetland taxa found at each site. The ellipses group the sites into three distinct wetland patterns: wetlands with high connectedness, isolated wetlands with low levels of site impacts, and highly isolated wetlands or wetlands with high levels of site impacts. (b) Relationship between bird species richness and percent connectedness within 2500 m of the sites in the SWP. Wetland sites are identified by a two-letter acronym for each site. The number represents the ratio of wetland to non-wetland taxa found at each site. The ellipses group the sites into three distinct wetland patterns: wetlands with high connectedness, isolated wetlands with low levels of site impacts, and highly isolated wetlands or wetlands with high levels of site impacts. Site PM is an exception to these groupings; see text for explanation.

density was high across all scales: RD500 (mean= 2.94 km km^{-2}), RD1000 (mean=2.97 km km^{-2}), and RD2500 (mean=2.92 km km^{-2}). Connectedness ranged from CON500 (mean=53%), CON1000 (mean= 48%), and CON2500 (mean=38%). Wetland isolation ranged from 0.09 to 0.45 km (mean=0.19 km).

A total of 56 species of birds were recorded from the 14 sites sampled; from 6 to 18 species, with a mean of 12 species per site. Common species included red-winged black birds, American gold finch (*Carduelis tristis* (L.)), and tree swallow (*Tachycineta bicolor* (Vieillot)). No significant relationships were found in this ecoregion.

4. Discussion

Our results provide evidence that landscape characteristics correspond to patterns of avian biodiversity within depressional wetlands. Connectedness and road density are important measures for predicting bird assemblages in both agricultural ecoregions (SWP, RRV). Connectedness and its relationship with wetland bird assemblages were most pronounced at the larger scale (2500 m), where the largest remnant patches can be discerned. In contrast, road effects on bird assemblages were most pronounced at the smallest scale (500 m). Wetland isolation corresponded to bird community patterns as well, but only in one ecoregion (SWP). In the urbanizing ecoregion (NHF), species richness was considerably lower than elsewhere but community patterns did not correspond to landscape variables. Based on these results, wetland landscape assessment approaches that will be most effective are those devised for specific ecoregions.

Our results show that connectedness was the most consistent and strongest predictor for bird species richness in the SWP and in the RRV even though landscape pattern varies substantially between these ecoregions. Wetlands surrounded by large tracts of natural landscape are (1) less likely to be affected by land use stresses (e.g., pesticide drift, invasive species) that could diminish resource quality, (2) more likely to contain adequate patch diversity to sustain resident populations, and (3) more likely to provide unimpeded movement for organisms from uplands to nearby wetlands (Henein and Merrian, 1990; Taylor et al., 1993). In our study, remnant natural areas primarily comprise grasslands and wetlands within an agricultural matrix in both SWP and RRV. These large remnants have low road densities in the vicinity of the wetlands (500 m) and so road density was an important predictor as well. There were differences in connectedness between the two regions, however. Mean connectedness and maximum connectedness are lower in the SWP than in the RRV because of landform-generated wetland pattern rather than differences in agricultural extent. Since the RRV is glacial lake plain, wetlands are often expansive; in contrast, the morainal landscape of the SWP has resulted in more discreet basins (Table 1, MN DNR, 1996). In spite of these landform differences, agricultural land (crop production) comprises 78% of the counties of the SWP and 71% of the RRV (USDOC, 1994). In the RRV, even remnant wetland systems are typically large wetland complexes dominated by grassland with large shallow wetland depressions (Prince, 1997). In the RRV, where connectedness was the highest among all ecoregions, bird species richness increased with connectedness. Grassland dependent species such as the greater prairie-chicken (*Tympanuchus cupido* (L.)) and the short-eared owl (*Asio flammeus* (Pontoppidan)) were only recorded in this ecoregion. Also, species known to be area-dependent (see Galotwitsch and van der Valk, 1994), including the northern harrier (*Circus cyaneus* (L.)) and the sandhill crane (*Grus canadensis* (L.)), were observed only in the RRV.

In contrast to the RRV, bird species richness in the SWP peaks at relatively low levels of connectedness. Although wetlands in the SWP ecoregion with high levels of connectedness had low levels of bird species richness, these wetlands have the highest proportions of wetland taxa. Waterfowl comprised the greatest proportion of wetland bird richness in the SWP. Wetlands within this region are often not individually extensive but occur as complexes including ephemeral wetlands to permanent open water basins (Stewart and Kantrud, 1971). Open water is an important element of connectedness in the SWP that is minimal in the RRV (Table 4). High levels of connectedness in the SWP appear to correspond to wetland complexes that include sufficient landscape diversity to adequately satisfy waterfowl requirements for food and shelter during different lifestages: migration, courtship, brood rearing, and molting (e.g. Swanson and Duebbert, 1989). In Iowa wetlands within the SWP ecoregion, Brown and Dinsmore (1986) observed significantly more bird species in complex marshes (x=11) despite being only about half as large (x=14 ha) as isolated marshes (x=30 ha), which averaged nine species. Brown and Dinsmore (1986) found Canada goose, redhead, American coot (*Fulica americana* (Gmelin)), black tern (*Chlidonias niger* (L.)), and swamp sparrow to be sensitive to wetland complexes.

The influence of scale on connectedness (remnant patch size) and bird assemblages is most evident in the SWP. Although the relationship between bird assemblages and landscape pattern is predictable at both 500 and 2500 m scale analyses (Mantel tests), the 2500 m scale permitted interpretation of bird assemblage patterns not evident from the more restricted analysis. At the 2500 m scale (Fig. 5b), the three sites with the highest proportions of wetland taxa (SN, VM, PP) had connectedness values greater than 35%. At the 500 m scale (Fig. 5a), these three sites and six others with lower proportions of wetland taxa all appeared to high connectedness (>35%). At the 500 m scale, these additional six sites would be considered ideal for wetland taxa, but without the inclusion of a larger landscape context, those sites that are most attractive to wetland taxa (SN, VM, PP) could not be distinguished from those with a lower proportion of wetland taxa.

It is important to note that the proportion of wetland taxa was sensitive to connectedness, whereas species richness was concordant with site impacts and wetland size. At the 2500 m scale, the highly isolated or wetlands with high levels of site impacts (BS, LT, TO) (Fig. 5b) are generally the smallest in size and have low species richness. Even though site PM is not isolated or impacted, it is small (1.2 ha) and also has low species richness. Sites with the highest species richness (isolated wetlands with low levels of site impacts) (Fig. 5b) were not generally those with the highest connectedness but those that are larger in size and include some upland buffer to attract a variety of birds. Although site impacts and wetland size are good predictors of overall species richness, they do not predict where wetland taxa will be most prevalent. Wetland connectedness is a better predictor of proportion of wetland taxa. Consequently, adequate wetland reserve planning needs to include all three factors (connectedness, size, extent of site impacts) to adequately conserve avian diversity with a high proportion of wetland taxa.

Since wetland isolation is lower in complexes than in individual patches, similar bird community relationships were found with wetland isolation that were also detected with connectedness in the SWP. At less isolated sites, the bird communities consisted primarily of wetland taxa, while the bird communities at more isolated sites were dominated by generalist species (red-winged blackbirds, killdeer, and swallows). Generalist species prefer impacted areas and areas dominated by edge (Brooks and Croonquist, 1990). The bird community at intermediate levels of isolation reflected both generalist and wetland taxa communities, thus elevating the number found at these sites. Using bird guilds related to habitat specificity, Schik (1998) showed that the proportion of generalist bird species increased while the proportion of landscape-dependent bird species decreased with increasing landscape impacts surrounding prairie wetlands.

The results of this study also demonstrate that land use–biota relationships are detectable only when sufficient variability exists in the landscape. Although land use diversity exists in the NHF ecoregion, the matrix of each site was either impacted (urban) or was a relatively unimpacted environment (forest). Consequently, no land use–biota relationships were detected likely due to the lack of land use variability within this ecoregion. Similarly, Miller et al. (1997) suggest that land–use biota relationships may be more likely to be detected in landscapes with contrasting patterns (high level of diversity). When the landscape exhibited sufficient diversity (e.g. SWP), land use–biota relationships were evident. This study also suggests that criteria for wetland assessments based on observed land use–biota relationships need to be specific to ecoregions. For example, connectedness is an effective measure for predicting wetland bird assemblages in the SWP, but not in the other two ecoregions.

The results of this study demonstrate the influence of landscape characteristics and scale on patterns of avian biodiversity in depressional wetlands. Connectedness was an optimal landscape measure for predicting bird species assemblages in wetland communities. The use of connectedness appears to be an effective surrogate measure for other landscape measures, such as road density and wetland isolation. High levels of connectedness were typified by large remnant patches of wetland and grassland with low levels of wetland isolation and minimal impacts from roads. In addition, it is important to note that connectedness was a better predictor of bird assemblages in agricultural ecoregions than was wetland size. Therefore, many of the existing wetland conservation strategies that focus solely on wetland protection without regard to upland context may be limited in their potential to sustain vertebrate biodiversity. Prioritizing which remnant wetlands are most important for avian species conservation requires measuring connectedness over large areas to ensure sensitive species are accommodated.

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