Scale-dependent habitat use in three species of prairie wetland birds

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Abstract

We evaluated the influence of scale on habitat use for three wetland-obligate bird species with divergent life history characteristics and possible scale-dependent criteria for nesting and foraging in South Dakota, USA. A stratified, two-stage cluster sample was used to randomly select survey wetlands within strata defined by region, wetland density, and wetland surface area. We used 18-m (0.1 ha) fixed radius circular-plots to survey birds in 412 semipermanent wetlands during the summers of 1995 and 1996. Variation in habitat use by pied-billed grebes (*Podilymbus podiceps*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), two sedentary species that rarely exploit resources outside the vicinity of nest wetlands, was explained solely by within-patch variation. Yellow-headed blackbirds were a cosmopolitan species that commonly nested in small wetlands, whereas pied-billed grebes were an area-sensitive species that used larger wetlands regardless of landscape pattern. Area requirements for black terns (*Chlidonias niger*), a vagile species that typically forages up to 4 km away from the nest wetland, fluctuated in response to landscape structure. Black tern area requirements were small (6.5 ha) in heterogeneous landscapes compared to those in homogeneous landscapes (15.4–32.6 ha). Low wetland density landscapes composed of small wetlands, where few nesting wetlands occurred and potential food sources were spread over large distances, were not widely used by black terns. Landscape-level measurements related to black tern occurrence extended past relationships between wetlands into the surrounding matrix. Black terns were more likely to occur in landscapes where grasslands had not been tilled for agricultural production. Our findings represent empirical evidence that characteristics of entire landscapes, rather than individual patches, must be quantified to assess habitat suitability for wide-ranging species that use resources over large areas.

Introduction

Local measures of vegetative structure have long been known to affect habitat use by prairie wetland birds (e.g., Weller and Spatcher 1965; Kaminski and Prince 1981, 1984; Murkin et al. 1997) whereas more recent research has indicated that landscape-level attributes also may influence local species abundance and diversity (e.g., Pearson 1993; Koopowitz et al. 1994; Vos and Stumpel 1995). Recent advances in geographic information systems, remote sensing technologies,

and quantitative methods have enabled researchers to incorporate landscape-level measures into ecological research (Turner 1989; Turner and Gardner 1991; Forman 1995). For example, Robbins et al. (1989) found that relative abundances of breeding birds in the Middle Atlantic states were related to forest area and patch isolation. Similarly, Pearson (1993) found that species richness and diversity of birds wintering in the Georgia Piedmont, USA, was explained solely by landscape-level habitat measures. Landscape-scale studies that complement what has been learned at local scales are
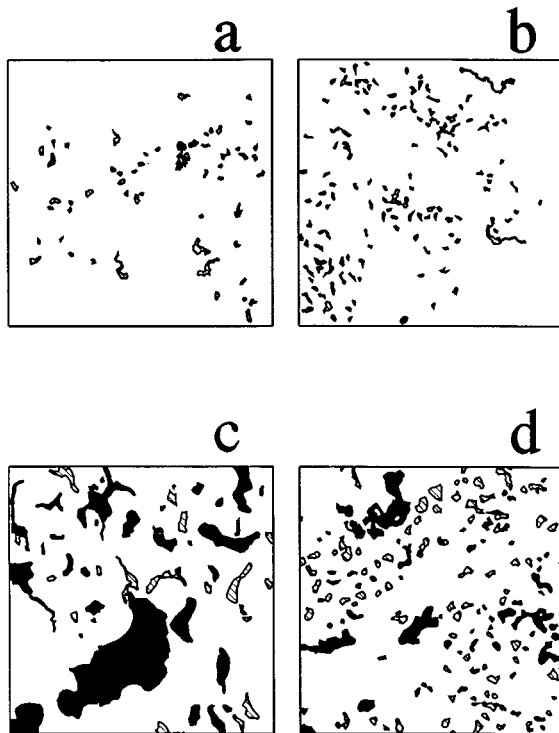
Figure 1. Examples of the four Landscape Types that were defined in this study to characterize the structure of the wetland community surrounding surveyed wetlands. Solid polygons depict semipermanent wetlands while hatched polygons are seasonal wetlands. Each of four squares are 25.9-km^2 (10-mi^2) in area.

being used to direct conservation efforts and design nature reserve systems over large geographic areas (Hansson and Angelstam 1991; Flather and Sauer 1996). For these reasons, additional research is needed to identify how species with differing life histories relate to habitat variability across local and landscape scales.

The purpose of this study was to investigate the influence of scale in the use of nesting and foraging habitat by prairie wetland birds. We selected for study, three wetland-obligate bird species with divergent life history characteristics and possible scale-dependent criteria for nesting and foraging (Pearson et al. 1996). We hypothesized that our species-specific approach to evaluating habitat suitability would reveal diverse perceptions of landscape structure among wetland bird species.

Methods

Sample design

Our sampling frame was a grid of ∼3800 25.9-km^2 (10-mi^2) cells overlayed on a geographic information system (GIS) that was constructed from National Wetland Inventory (NWI) data (1979–1986 photography) containing semipermanent and seasonal wetlands in eastern South Dakota (Johnson and Higgins 1997). Cell area (25.9 km^2) was selected to maximize between-cell variability (Wiens 1989; Stoms 1992). Wetland centers, calculated using the GIS, were used to assign wetlands to a particular cell. Median values of the frequency distributions of seasonal and semipermanent wetland densities (110 wetlands) and areas (124 ha) within cells were used to define four distinct landscape types (Figure 1). Semipermanent and seasonal wetland densities and areas were used to define landscape types because these two wetland types support the highest densities of breeding prairie wetland birds (Kantrud and Stewart 1984). Landscape Type *a* (Figure 1) was low in density and area of semipermanent and seasonal wetlands, Landscape *b* was high density and low area, Landscape *c* was low density and high area, and Landscape *d* cells were high density and area. Strata were defined by landscape types and three regions, the Prairie Coteau, James River Lowlands, and Missouri Coteau regions of eastern South Dakota (Johnson et al. 1995) (Figure 2). Sample sizes were allocated proportionally across regions, and cells (*n* = 216) were selected randomly across landscape types within each region. Once cells had been selected, semipermanent wetlands within cells were sorted by area, and target wetlands were systematically selected using a random starting point. Wetlands that were dry, farmed, burned, mowed, or hayed were not sampled. Bird surveys were conducted in two wetlands in each cell after ∼750 landowners had been contacted to obtain access to wetlands.

Bird survey methodology and preliminary accuracy assessments

We initially surveyed 412 semipermanent wetlands from 5 May–10 July 1995–1996 to obtain habitat use information for black terns (*Chlidonias niger*), pied-billed grebes (*Podilymbus podiceps*), and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) over an extensive geographic region (Figure 2). We also revisited wetlands that were classified as used during the first visit to confirm nesting by black terns,
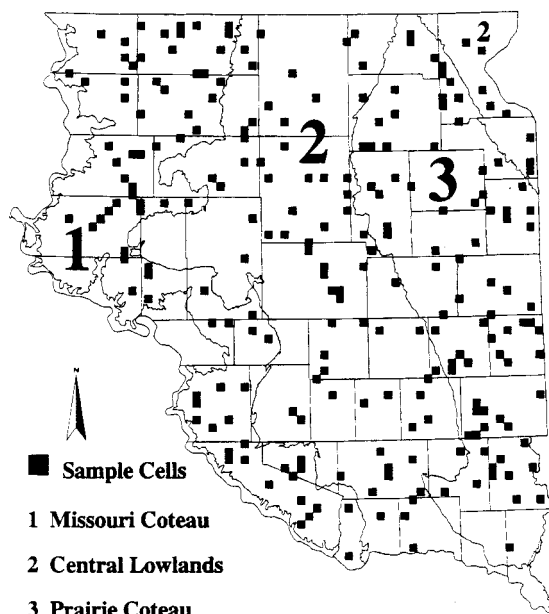
Figure 2. Distribution of 25.9-km^2 (10-mi^2) cells that were used to evaluate prairie wetland bird use of semipermanent wetlands in the Missouri Coteau, Central Lowlands, and Prairie Coteau regions of eastern South Dakota, 1995 and 1996.

a highly mobile species that forages extensively in wetlands other than its nest wetland and typically initiates nesting in early June (Dunn and Agro 1995). We recorded the presence of black terns, pied-billed grebes, and yellow-headed blackbirds that were seen or heard during 8-minute surveys (Scott and Ramsey 1981; Fuller and Langslow 1984) within 18-m (0.1 ha) fixed radius circular-plots (Reynolds et al. 1980; Edwards et al. 1981; Brown and Dinsmore 1986). We waited two minutes within circular-plots before beginning surveys to allow birds to return to their normal behavior (Bollinger et al. 1988). Number of circular-plots used in surveys increased with increasing wetland area and complexity of wetland vegetation (Brown and Dinsmore 1986). A maximum of four circular-plots was used to survey birds in each wetland. Plots were dispersed throughout the wetland to facilitate sampling within multiple types of vegetation. Coverage of the total wetland area varied from nearly 100% in small wetlands to <1% in large wetlands. When no vegetation was present, circular-plots were placed near the wetland edge and birds were surveyed before approaching the wetland. Target species that were detected outside of circular-plots during surveys or while moving between plots were recorded (Brown and Dinsmore 1986; Hemesath and Dinsmore

1993). We also traversed wetland perimeters to ensure that each species present was recorded. Wetlands were classified as used by a particular species if we observed adults, active nests, or young. Surveys were conducted when birds were most active (sunrise to 1000 h and 1800 h to sunset [Verner and Ritter 1986]). Surveys were not conducted during rainy or windy (≥24 km/h) days.

Survey methodology followed an established sampling protocol that has been used extensively to survey wetland birds (Brown and Dinsmore 1986; Hemesath and Dinsmore 1993; VanRees-Siewert and Dinsmore 1996). Despite widespread use of methods in this study, some investigators believe that use of a variable number of circular-plots may bias survey results because observers spend more time surveying larger wetlands. Therefore, we conducted preliminary accuracy assessments of our methods in 1995 by surveying a random sub-set of 10 wetlands twice within the same sampling season to determine how effectively a single survey characterized wetland occupancy rates of target species and to determine whether the length of time observers spent within wetlands influenced species detection. Each second survey was conducted by an observer who did not have prior knowledge of the species that were recorded during the first survey. Observers who surveyed wetlands a second time recorded birds for 32 min (the length of time required to complete four circular-plots in large wetlands) in smaller wetlands in which <4 circular-plots were used. We found that we detected 89% (16 of 18) of the wetland bird species that were recorded during two surveys in the first survey. No additional wetland bird species were detected when observers remained at smaller wetlands for a time equal to that spent at larger wetlands. Positive results regarding our accuracy assessments enabled us to survey wetlands once in 1995 or 1996 to obtain a large sample ($n = 412$) over an extensive geographic region rather than surveying a small number of localized wetlands multiple times (Meentemeyer 1989). The modification in survey sampling intensity resulted in an increased number of wetlands surveyed, which provided adequate sample sizes for logistic regression analyses (Hosmer and Lemeshow 1989).

Landscape-level measures

Wetland area (ha) and shoreline length (m) of surveyed wetlands were estimated using the GIS. Densities and total areas of temporary, seasonal, semiperma-

nent and permanent wetlands (Stewart and Kantrud 1971) within cells were calculated to characterize the ecological neighborhood surrounding surveyed wetlands. Wetland densities and areas within cells, and wetland area and shoreline length measures were log transformed to provide a more symmetric distribution.

Digital land cover map

Landsat Thematic Mapper (TM) imagery from eight scenes covering eastern South Dakota were used to classify uplands into tilled and untilled vegetation classes to determine whether grassland abundance (i.e., perennial vegetation) within 25.9-km^2 cells was related to bird use of wetlands. Grain crops (e.g., corn [*Zea mays*], soybeans [*Glycine max*]), small grains (e.g., wheat [*Triticum aestivum*]), and annually fallowed areas were considered tilled lands. Untilled lands were permanent pastures, Conservation Reserve Program fields, and alfalfa. Trees, which were usually within isolated shelterbelt plantings that constituted <1% of area in eastern South Dakota, were not distinguished from untilled herbaceous grassland cover types.

We used spring imagery (i.e., leaf-off scenes in April and May of 1991 and 1992) that was acquired before row crops had emerged to enhance our ability to differentiate between tilled and untilled vegetation types. Spectral bands used were visible red (Band 3, 0.63–0.69 μm), near infrared (Band 4, 0.76–0.90 μm), shortwave infrared (Band 5, 1.55–1.75 μm), and thermal infrared (Band 7, 10.4–12.5μFm) at a spatial resolution of 30 m. Initial image processing of the four spectral bands into one image was completed using ERDAS image processing software on a SUN SPARC 10 workstation. An unsupervised classification (i.e., cluster analysis) was conducted on the four-band image using the Land Analysis System software (United States Geological Survey, EROS Data Center, Sioux Falls, SD). Unsupervised classification involves clustering (i.e., shading) individual pixels into 100 spectral classes by measured reflectance values from the TM four-band image. Spectral classes were then visually interpreted as tilled or untilled land cover units.

A digital coverage depicting land use for a 250-km^2 area of northeastern South Dakota during 1992 (Naugle et al. 1997), the period when TM data for this study were acquired, was used as a reference during land use interpretation. Black and white aerial photographs (1:8000 scale) depicting certified annual cropping history in 84 randomly selected 1.6-km^2 reference areas were obtained from the Farm Service Agency (U.S. Department of Agriculture) to enhance the visual land cover interpretation. Half the photographs were used during land use classification; the other half of the photographs, which were not viewed until land use classification had been completed, were used to evaluate the accuracy of tilled and untilled classifications. Overall, per-pixel classification accuracy for our map was 97% (Stoms 1994).

Classified imagery was converted from ERDAS to ARC/INFO software format. The NWI data in raster format were used to mask out wetland area. Untilled (i.e., grassland) area estimates were calculated from the classified imagery within 25.9-km^2 (10-mi^2) cells. The proportion of untilled area was defined as the sum of the untilled area divided by the sum of non-wetland area within cells. Percentage data were square-root transformed to provide a more symmetric distribution.

Local measures

Percent of the wetland area containing emergent cover was estimated visually using the Daubenmire (1959) scale in which the entire wetland was treated as a single quadrat (Bailey and Poulton 1968). Class intervals describing the percentage of vegetated area within wetlands were defined as: (1) <1%; (2) 1–5%; (3) 6–25%; (4) 26–50%; (5) 51–75%; (6) 76–95%; and (7) >95%. Distribution of emergent vegetation was classified using the four wetland cover type classifications of Stewart and Kantrud (1971).

Grazing intensity within wetlands was visually estimated as light, moderate, or heavy. Wetlands were lightly grazed when there was little or no evidence that cattle had been present within the wetland whereas emergent vegetation in moderately grazed wetlands showed signs of trampling or consumption. Emergent vegetation in heavily grazed wetlands was severely impacted by the presence of cattle. We also estimated grazing intensity on natural shorelines by visual inspection of residual vegetation and the current year's growth. Shorelines that ranged from idled (i.e., <1%) to heavily grazed (i.e., >95%) were recorded using the same seven class intervals that were used to estimate percent emergent cover.

Proportion of the wetland perimeter occupied by woody plants (i.e., willow [*Salix* spp.] and cottonwood [*Populus deltoides*]) also was estimated visually into one of the seven class intervals defined above. Class

interval mid-points were used to analyze categorical data.

We recorded the number of emergent hydrophytic species comprising ≥10% of the vegetated wetland area as an index to wetland vegetation heterogeneity. Emergent cover also was used to categorize wetlands into two classes of nesting substrates for wetland birds. Class 1 substrates contained primarily thick-stemmed emergent vegetation types (e.g., cattail [*Typha* spp.], river bulrush [*Scirpus fluviatilis*]) that were capable of supporting the weight of a bird nest. Class 2 substrates had only thin-stemmed emergent vegetation types (e.g., softstem bulrush [*Scirpus tabernaemontani*], burreed [*Sparganium eurycarpum*]) with weaker stems that were less capable of supporting a nest.

Logistic regression habitat analyses

Forward stepwise logistic regression (Hosmer and Lemeshow 1989) was used to evaluate relationships between local and landscape-level habitat variables and the probability of a wetland bird species occurrence. Single regression equations were constructed for pied-billed grebes and yellow-headed blackbirds that breed and forage within the nesting wetland and immediate upland habitat. Because black terns commonly forage up to 4 km away from their nest wetland (Dunn and Agro 1995), we constructed separate equations to evaluate habitat use where terns were recorded as present only when nesting was confirmed, when terns were observed foraging on a wetland with no apparent nesting activity and with nesting and foraging records combined. Eleven variables were used in analyses (Table 1) after eliminating wetland perimeter, density of wetlands within cells for each water regime, grazing intensity within wetlands and cover type classifications from the data set to reduce problems associated with multicollinearity ($r > 0.5$). To evaluate whether the probability of occurrence of individual species was influenced by habitat variables ($x_{1i...}x_{ii}$), we used the model

$$P(y_i = 1) = \frac{\exp(\beta_0 + \beta_1 x_{1_i} + \beta_2 x_{2_i})}{1 + \exp(\beta_0 + \beta_1 x_{1_i} + \beta_2 x_{2_i})}$$

where $P(y_i = 1)$ is the probability of the particular species being present in wetland i, β_0, β_1, and β_2 are model parameters to be estimated. Significance of regressions was tested using the Wald chi-square statistic (maximum likelihood estimate). McFadden's rho-squared statistic, which was used to evaluate model fit, is a transformation of the likelihood ratio statistic intended to mimic R^2 values in logistic regression. Low rho-squared values do not necessarily imply poor fit because rho-squared values are lower than R^2 values. We considered rho-squared values between 0.20 and 0.30 as satisfactory (Hensher and Johnson 1981). Explained variation was partitioned among significant predictors following initial stepwise procedures to evaluate the explanatory power of individual variables. Correct classification rates in used and unused wetlands also were evaluated as a means of cross-validating our ability to predict wetland bird habitat suitability.

Predicted probabilities of occurrence generated by logistic analyses were plotted against wetland area within landscape types. The 50% probability of occurrence was used as a conservative estimate of the minimum area required by a species (Robbins et al. 1989; Herkert 1994).

Results

Habitat regression models

Pied-billed grebe and yellow-headed blackbird occurrence was related solely to wetland area and local measures of habitat suitability whereas the presence of black terns was dependent upon wetland area and landscape-level measures (Tables 1–3). Each species was more likely to occur in larger wetlands (AREA) (Tables 2 and 3). Yellow-headed blackbirds were more likely to occur in wetlands with high proportions of emergent vegetation (COVER) that was predominantly comprised of thick-stemmed plant species (STEM) (Tables 2 and 3). Landscape-level measures of habitat suitability positively related to black tern occurrence were proportion of the matrix in untilled grassland cover (GRASS) and total semipermanent wetland area surrounding surveyed wetlands (SEMIA) (Tables 1–3).

Wetland area accounted for the most explained variation in habitat suitability equations for each species (Table 2). Significant predictors of black tern occurrence (AREA, GRASS and SEMIA) and their order in regression equations were identical regardless of whether nesting, foraging or a combination of records was used to define wetland use (Table 2). Habitat models correctly classified 81–93% and 78% of wetlands that were unused by black terns and pied-billed grebes, respectively. The yellow-headed blackbird model correctly classified 70% of used wetlands.

Table 1. Description of variables that were measured to evaluate wetland bird use of semipermanent wetland habitats in eastern South Dakota, 1995–1996.

Variable name	Description
AREA[a]	Natural logarithm of the area (ha) of the wetland
PERIM	Natural logarithm of the perimeter (m) of the wetland
TEMPA[a]	Natural logarithm of the total temporary wetland areas within cells
SEASA[a]	Natural logarithm of the total seasonal wetland areas within cells
SEMIA[a]	Natural logarithm of the total semipermanent wetland areas within cells
PERMA[a]	Natural logarithm of the total permanent wetland areas within cells
TEMPN	Natural logarithm of temporary wetland numbers within cells
SEASN	Natural logarithm of seasonal wetland numbers within cells
SEMIN	Natural logarithm of semipermanent wetland numbers within cells
PERMN	Natural logarithm of permanent wetland numbers within cells
COVER[a]	Percent vegetated wetland area
COVTYPE	Cover type classification [b]
WETGRAZ	Index to grazing intensity within wetlands
SHORGRAZ[a]	Index to grazing intensity on shorelines adjacent to wetlands
GRASS[a]	Proportion of untilled upland habitat within cells
TREES[a]	Proportion of the wetland perimeter encompassed by woody hydrophytes
STEM[a]	Variable indicating whether herbaceous hydrophytes within wetlands were predominately thick- or thin-stemmed
VEGNUM[a]	Number of emergent hydrophytes species composing ≥10% of the vegetated wetland area

[a] Variable was included in forward stepwise logistic regression analyses.
[b] Cover type classifications that follow Stewart and Kantrud (1971) describe the distribution of emergent vegetation within wetlands.

Minimum wetland area requirements varied between landscape types for black terns, a species that related to landscape-level measures (Figures 1 and 3). Predicted probabilities of occurrence were plotted against wetland area using nesting and foraging records combined to define black tern presence. Minimum wetland area for black terns was 32.6 ha in Landscape Type *b*, 15.4 ha in Landscape Type *c*, and 6.5 ha in Landscape Type *d* (Figures 1 and 3). Wetlands in Landscape Type *a* never reached the 50% probability of occurrence (Figures 1 and 3). Minimum wetland area requirements did not vary between landscape types for yellow-headed blackbirds or pied-billed grebes (Figures 1 and 3). Therefore, all records were combined to estimate minimum habitat area requirements for these species. Average minimum wetland areas (50% probability) were 5.7 ha for pied-billed grebes and 0.8 ha for yellow-headed blackbirds.

Discussion

Species responses to habitat variation at the patch scale

Wetland birds selected for inclusion in this study have divergent natural histories that influence the way each species interacts with the landscape (Pearson et al. 1996). The occurrence of pied-billed grebes and yellow-headed blackbirds was explained solely by wetland area and within-patch vegetation measures. Yellow-headed blackbirds and pied-billed grebes are sedentary species that rarely exploit resources outside the vicinity of the nest wetland during breeding season (Twedt and Crawford 1995). Natural history attributes reflected in our regression models for individual species indicated that pied-billed grebes are an area-sensitive species that use large wetlands (5.7 ha at 50% probability) regardless of the surrounding landscape pattern. In contrast, yellow-headed blackbirds are a cosmopolitan species that commonly nest in small wetlands (0.8 ha at 50% probability). Positive associations between yellow-headed blackbird occurrence and COVER and STEM relate to their need

Table 2. Habitat models that were generated using forward stepwise multiple logistic regression for three species of prairie wetland birds. All habitat variables included in models have $P \leq 0.01$ (see Table 3 for exact P values of individual variables). Variables are listed in the order that they entered into equations. McFadden's rho-squared is an index to explained variation for the entire equation. Proportion of explained variance attributed to individual variables is in parentheses. Variable definitions are in Table 1.

Species	Habitat model	Number of occurrences	McFadden's rho-squared[a]	Classification rate (% correct)	
				Used	Unused
Black Tern					
All occurrences	AREA + GRASS + SEMIA	106	0.24	0.46	0.81
	(0.11) (0.08) (0.05)				
Confirmed nest wetlands	AREA + GRASS + SEMIA	32	0.21	0.23	0.93
	(0.10) (0.08) (0.03)				
Foraging locations	AREA + GRASS + SEMIA	74	0.12	0.27	0.84
	(0.05) (0.04) (0.03)				
Pied-billed Grebe	AREA	120	0.20	0.45	0.78
Yellow-headed Blackbird	AREA + COVER + STEM[b]	250	0.17	0.70	0.52
	(0.09) (0.05) (0.03)				

[a]McFadden's rho-squared is a transformation of the likelihood ratio statistic intended to mimic R-squared values in logistic regression. Low rho-squared values do not imply poor model fit because rho-squared are usually much lower than R-squared values. Rho-squared values between 0.20 and 0.40 are considered very satisfactory (Hensher and Johnson 1981).
[b]STEM was a dummy-coded categorical variable which indicated whether a particular bird species presence was related to the type of emergent hydrophytes in the wetland. A positive sign preceding STEM indicates that the occurrence of yellow-headed blackbirds was positively associated with wetlands dominated by thick-stemmed emergent vegetation types (e.g., cattail [*Typha* spp.], river bulrush [*Scirpus fluviatilis*]) that were capable of supporting the weight of a bird nest.

Table 3. Estimated constants and coefficients (SE) for regression analyses describing habitat models for three prairie wetland bird species (see Table 2 for complete models). Predictor variables (Table 1) that did not enter habitat models for any of the bird species were excluded from table. Univariate tests for variables that stepped into equations and overall Wald chi-square statistics for complete models were each $P < 0.001$.

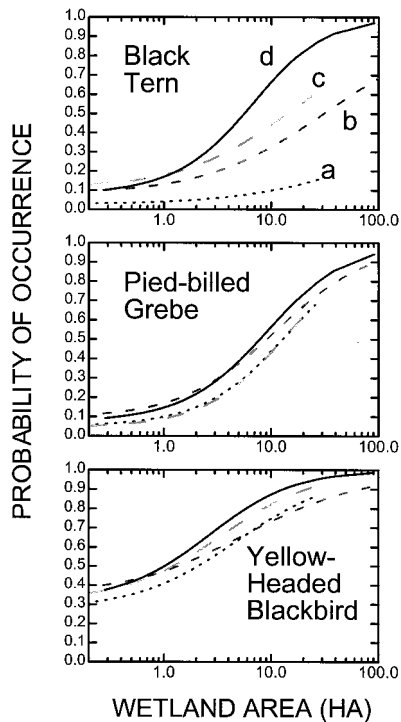|	Wetland bird species				
	Black tern				
	All occurrences	Confirmed nest wetlands	Foraging locations	Pied-billed Grebe	Yellow-headed Blackbird
Variable					
Constant	−8.27 (0.98)	−9.66 (1.42)	−5.89 (0.89)	−2.74 (0.26)	−1.64 (0.35)
AREA	0.93 (0.13)	0.87 (0.17)	0.53 (0.12)	1.14 (0.14)	1.05 (0.16)
GRASS	6.25 (1.10)	7.12 (1.63)	3.41 (1.05)		
SEMIA	0.32 (0.09)	0.16 (0.04)	0.29 (0.09)		
COVER				0.02 (0.01)	
STEM				1.15 (0.31)	

Figure 3. Probabilities of detecting three prairie wetland bird species within the four Landscape Types depicted in Figure 1.

for an abundance of thick-stemmed emergent plants to support the weight of over-water nests (Twedt and Crawford 1995).

Black tern response to landscape-level habitat variation

The prevalence of landscape-level features in the black tern habitat model indicated that the ecological neighborhood of black terns may be larger than a single wetland (Addicott et al. 1987). Logistic regression analyses indicated that the occurrence of black terns, a vagile species that regularly travels up to 4 km away from its nesting wetland to forage (Dunn and Agro 1995), are an area-dependent species whose wetland area requirements may fluctuate in response to structural attributes of the wetland landscape. Wetlands in Landscape Type *a*, a low wetland density landscape composed of primarily small wetlands, where few semipermanent nest wetlands occurred and potential food sources were spread over large distances, were not widely used by black terns. In contrast, black tern area requirements in Landscape Type *d*, a high wetland density landscape containing a mixture of large and small wetlands, were small (6.5 ha) compared to those

in more homogeneous landscapes composed of predominately large (Landscape Type *c*; 15.4 ha) or small wetlands (Landscape Type *b*; 32.6 ha). It is unlikely that black tern use of larger wetlands in Landscape Types *a*, *b*, and *c* was an artifact of wetland availability because pied-billed grebes, whose minimum area requirements were essentially identical to those of black terns in Landscape Type *d*, occurred on semipermanent wetlands of similar area regardless of landscape type (Figure 3).

Landscape-level measures associated with the occurrence of black terns extended past relationships between wetlands into the surrounding upland matrix. Each of three habitat models in this study indicated that nesting and foraging black terns were more likely to inhabit wetlands within landscapes where <50% of upland grasslands had been tilled for agricultural production. Relationships between grassland abundance and wetland use by over-water nesting species such as black terns may at first seem more difficult to interpret than those of upland nesting waterfowl (*Anas* spp.) because indirect impacts of agricultural practices on wetland habitats are poorly understood (Grue et al. 1986; van der Valk 1989). Attributes of the matrix were purposely included into the design of this study, knowing that the ability of the matrix to influence within-patch dynamics is the most important role the matrix plays in determining future landscape function (Forman 1995; pp. 277–278). Grassland abundance in this study was a surrogate measure depicting how pesticide and fertilizer runoff and siltation from agricultural lands negatively affects wetland habitats by altering vegetation composition (Kantrud 1986; Hands et al. 1989) and reducing favored invertebrate forage (Novak 1992; Dunn and Agro 1995). Findings from this study that link upland land use with wetland bird use warrant additional research to enhance our understanding of how human-induced modifications to the upland matrix are related to patch dynamics within wetlands (Forman 1995).

In the prairie pothole region, an ecosystem with an inherently unpredictable hydrologic cycle, wetland bird settling patterns are largely dictated by local vegetative wetland conditions and the number of ponded wetlands. Wetland bird surveys in this study (1995–1996) coincided with a series of wet years when habitat conditions were the most favorable since those of the 1950's (Caithamer and Dubovsky 1997). Rather than annually estimate change in wetland areas that may increase during wet years, we used NWI digital data that was delineated during average hydrologic

conditions to quantify area of surveyed wetlands and total wetland areas within cells. Our approach to identifying wetland suitability was conservative because we underestimated actual wetland area by using NWI areas. Consequently, classification of suitable wetland habitat may include wetlands that are unsuitable in drier years, but which provide suitable habitat during wet periods in the hydrologic cycle.

High classification rates of wetlands that were unused by black terns (81–93%) and pied-billed grebes (78%) indicated that unsuitable habitat can be reliably discriminated using wetland area and landscape-level attributes. Classification rates for suitable wetlands that were low (23–46%) compared to those of unsuitable wetlands indicated that more detailed and time-consuming measures of local vegetative conditions (e.g., Hickey and Malecki 1997) important to nesting black terns and pied-billed grebes were not quantified in this study. Classification rates that were low for suitable compared to unsuitable wetlands were not surprising because the development of models designed to assess broad-scale patterns for species such as black terns that relate to landscape-level variability often result in decreased predictive accuracy within a specific patch (Meentemeyer 1989). The coarse assessment of local vegetative conditions that adequately describe suitable habitat for yellow-headed blackbirds, a habitat generalist species that nested in small wetlands regardless of the surrounding landscape structure, was reflected in a high correct classification rate for used wetlands (70%).

Habitat suitability models for the three species that we studied exemplify the diverse perceptions of landscape structure exhibited by prairie wetland birds. Although local measures within wetlands characterized habitat suitability for pied-billed grebes and yellow-headed blackbirds, the selection of a broader scale at which habitat variables were measured (25.9-km^2 cells) enabled us to identify landscape-level measures influencing habitat suitability for black terns. These findings represent additional empirical evidence that characteristics of entire landscapes, rather than individual patches, must be quantified to assess habitat conditions for wide-ranging species (e.g., black terns) that exploit resources over broader spatial scales.

Acknowledgments

References

Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S., and Soluk, D. A. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340–346.

Bailey, A. W. and Poulton, C. E. 1968. Plant communities and environmental relationships in a portion of the Tillamook burn, Northwestern Oregon. Ecology 49: 1–13.

Bollinger, E. K., Gavin, T. A., and McIntyre, D. C. 1988. Comparison of transects and circular-plots for estimating bobolink densities. J. Wildl. Manage. 52: 777–786.

Brown, M. and Dinsmore, J. J. 1986. Implications of marsh size and isolation for marsh bird management. J. Wildl. Manage. 50: 392–397.

Caithamer, D. F. and Dubovsky, J. A. 1997. Waterfowl population status, 1997. U.S. Fish and Wildlife Service, Laurel, Maryland.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33: 43–64.

Dunn, E. H., and Agro, D. J. 1995. Black tern (*Chlidonias niger*). *In* The Birds of North America, No. 147. Pp. 1–24. Edited by Poole, A. and Gill, F. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Edwards, D. K., Dorsey, G. L., and Crawford, J. A. 1981. A comparison of three avian census methods. *In* Estimating numbers of terrestrial birds. Pp. 170–176. Edited by Ralph, C. J. and Scott, J. M. Stud. Avian Biol. No. 6.

Flather, C. H., and Sauer, J. R. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77: 28–35.

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge.

Fuller, R. J. and Langslow, D. R. 1984. Estimating numbers of birds by point counts: how long should counts last? Bird Study 31: 195–202.

Grue, C. E., DeWeese, L. R., Mineau, P., Swanson, G. A., Foster, J. R., Arnold, P. M., Huckins, J. N., Sheehan, P. J., Marshall, W. K., and Ludden, A. P. 1986. Potential impacts of agricultural chemicals on waterfowl and other wildlife inhabiting prairie wetlands: an evaluation of research needs and approaches. Trans. North Am. Wildl. Nat. Resour. Conf. 51: 357–383.

Hands, H. M., Drobney, R. D., and Ryan, M. R. 1989. Status of the black tern in the northcentral United States. Unpublished report, U.S. Department Interior, Fish and Wildlife Service, Minneapolis, Minnesota.

Hansson, L. and Angelstam, P. 1991. Landscape ecology as a theoretical basis for nature conservation. Landsc. Ecol. 5: 191–201.

Hemesath, L. M. and Dinsmore, J. J. 1993. Factors affecting bird colonization of restored wetlands. Prairie Nat. 25: 1–11.

Hensher, D. and Johnson, L. W. 1981. Applied Discrete Choice Modelling. Croom Helm, London.

Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecol. Appl. 4: 461–471.

Hickey, J. M. and Malecki, R. A. 1997. Nest site selection of the black tern in western New York. Colonial Waterbirds 20: 582–595.

Hosmer, D. W. Jr. and Lemeshow, S. 1989. Applied Logistic Regression. Wiley, New York.

Johnson, R. R. and Higgins, K. F. 1997. Wetland resources of eastern South Dakota. South Dakota State Univ., Brookings.

Johnson, R. R., Higgins, K. F., and Hubbard, D. E. 1995. Using soils to delineate South Dakota physiographic regions. Great Plains Res. 5: 309–322.

Kaminski, R. M. and Prince, H. H. 1981. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. J. Wildl. Manage. 45: 1–15.

Kaminski, R. M. and Prince, H. H. 1984. Dabbling duck-habitat associations during spring in Delta Marsh, Manitoba. J. Wildl. Manage. 48: 37–50.

Kantrud, H. A. 1986. Effects of vegetation manipulation on breeding waterfowl in prairie wetlands-a literature review. Technical Report No. 3. U.S. Fish and Wildlife Service, Washington, D.C.

Kantrud, H. A. and Stewart, R. E. 1984. Ecological distribution and crude density of breeding birds on prairie wetlands. J. Wildl. Manage. 48: 426–437.

Koopowitz, H., Thornhill, A. D., and Andersen, M. 1994. A general stochastic model for the prediction of biodiversity losses based on habitat conversion. Conserv. Biol. 8: 425–438.

Meentemeyer, V. 1989. Geographical perspectives of space, time, and scale. Landsc. Ecol. 3: 163–173.

Murkin, H. R., Murkin, E. J., and Ball, J. P. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. Ecol. Appl. 7: 1144–1159.

Naugle, D. E., Jenks, J. A., Kernohan, B. J., and Johnson, R. R. 1997. Effects of hunting and loss of escape cover on movements and activity of female white-tailed deer. Can. Field-Nat. 111: 595–600.

Novak, P. G. 1992. Black tern (*Chlidonias niger*). *In* Migratory Nongame Birds of Management Concern in the Northeast. Pp. 149–169. Edited by Schneider, K. J. and Pence, D. M. Department of the Interior, U.S. Fish and Wildlife Service, Newton Corner, Massachusetts.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landsc. Ecol. 8: 3–18.

Pearson, S. M., Turner, M. G., Gardner, R. H., and O'Neill, R. V. 1996. An organism-based perspective of habitat fragmentation. *In* Biodiversity in Managed Landscapes: theory and practice. Pp. 77–95. Edited by Szaro, R. C. and Johnston, D. W. Oxford University Press, New York, New York.

Reynolds, R. T., Scott, J. M., and Nussbaum, R. A. 1980. A variable circular-plot method for estimating bird numbers. Condor 82: 309–313.

Robbins, C. S., Dawson, D. K., and Dowell, B. A. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildl. Monogr. 103.

Scott, J. M. and Ramsey, F. L. 1981. Length of count period as a possible source of bias in estimating bird densities. *In* Estimating numbers of terrestrial birds. Pp. 409–413. Edited by Ralph, C. J. and Scott, J. M. Stud. Avian Biol. No. 6.

Stewart, R. E. and Kantrud, H. A. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish Wildl. Serv. Resour. Publ. 92.

Stoms, D. M. 1992. Effects of habitat map generalization in biodiversity assessment. Photogrammatic Eng. Remote Sensing 58: 1587–1591.

Stoms, D. M. 1994. Actual vegetation layer. *In* A handbook for Gap Analysis. Edited by Scott, J. M. and Jennings, M. D. Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20: 171–197.

Turner, M. G. and Gardner, R. H. (eds). 1991. Quantitative methods in landscape ecology. Springer, New York, NY.

Twedt, D. J. and Crawford, R. D. 1995. Yellow-headed blackbird (*Xanthocephalus xanthocephalus*). *In* The Birds of North America, No. 192. Pp. 1–27. Edited by Poole, A. and Gill, F. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

van der Valk, A. (ed.). 1989. Northern Prairie Wetlands. Iowa State University Press, Ames, Iowa.

VanRees-Siewart, K. L. and Dinsmore, J. J. 1996. Influence of wetland age on bird use of restored wetlands in Iowa. Wetlands 16: 577–582.

Verner, J. and Ritter, L. V. 1986. Hourly variation in morning point counts of birds. Auk 103: 117–124.

Vos, C. C. and Stumpel, A. H. P. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landsc. Ecol. 203–214.

Weller, M. W. and Spatcher, C. E. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa Agricultural Home Econ Exp. Stn. Spec. Rep. 43.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecol. 3: 385–397.