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Abstract

Wetlands throughout eastern South Dakota were surveyed (1995-97) for foraging and nesting black terns (Chlidonias niger) to evaluate local and landscape factors influencing habitat suitability. We surveyed 834 randomly selected, semipermanent, and seasonal wetlands that were stratified by physiographic domain, wetland density, and wetland surface area. A discriminant function model was used in a geographic information system (GIS) to classify habitat suitability of all semipermanent wetlands in eastern South Dakota. We calculated number of suitable, protected wetlands by combining wetlands with easement and fee-title tracts in the GIS. Black terns nested in 7.8% and foraged in an additional 17.9% of semipermanent wetlands. Significant variables in the discriminant function were wetland area, total semipermanent wetland area within the wetland complex, and grassland area in the upland matrix. Black terns were an area-dependent species that occupied large ($\bar{x} = 18.9$ ha) wetlands located within high-density wetland complexes. Black terns typically occurred in wetlands within landscapes where

Keywords

Black tern, discriminant function, easements, landscapes, prairie potholes, South Dakota wetlands, wetland protection programs

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LOCAL AND LANDSCAPE-LEVEL FACTORS INFLUENCING BLACK TERN HABITAT SUITABILITY

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Abstract: Wetlands throughout eastern South Dakota were surveyed (1995–97) for foraging and nesting black terns (*Chlidonias niger*) to evaluate local and landscape factors influencing habitat suitability. We surveyed 834 randomly selected, semipermanent, and seasonal wetlands that were stratified by physiographic domain, wetland density, and wetland surface area. A discriminant function model was used in a geographic information system (GIS) to classify habitat suitability of all semipermanent wetlands in eastern South Dakota. We calculated number of suitable, protected wetlands by combining wetlands with easement and fee-title tracts in the GIS. Black terns nested in 7.8% and foraged in an additional 17.9% of semipermanent wetlands. Significant variables in the discriminant function were wetland area, total semipermanent wetland area within the wetland complex, and grassland area in the upland matrix. Black terns were an area-dependent species that occupied large ($\bar{x} = 18.9$ ha) wetlands located within high-density wetland complexes. Black terns typically occurred in wetlands within landscapes where <50% of upland grasslands were tilled. Classification rates were high (76–100%), indicating that the model identified unsuitable wetlands using wetland area and landscape-level attributes. Characteristics of entire landscapes must be considered in habitat assessments because wetlands that do not correspond to landscape-scale habitat requirements may not be suitable despite favorable local conditions. Lower correct classification rates (22–78%) for occupied ponds indicated that suitability also is dependent on local conditions for wetlands which correspond to habitat requirements from a landscape perspective. Suitable black tern nest sites occurred within regenerating or degenerating wetlands where vegetation structure rather than species of vegetation dictated suitability of nest substrates. Wetland acquisition programs have protected 44% of wetlands suitable for black terns. Future wetland acquisitions should maintain the integrity of entire prairie landscapes in additional to attributes of individual wetlands.

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Key words: Black terns, discriminant function, easements, landscapes, prairie potholes, South Dakota, wetlands, wetland protection programs.

In a little over a century, the prairie pothole region (PPR) of the northern Great Plains has been transformed from a contiguous expanse of wetlands and grasslands into a highly fragmented agricultural landscape. Although vegetative attributes within wetlands have long been known to influence wetland use by black terns (Weller and Spatcher 1965, Bergman et al. 1970, Dunn 1979, Hickey and Malecki 1997), research has not been conducted to assess the role of landscape factors in evaluations of habitat suitability. As a result, resource managers confronted with preserving ecosystems extrapolate local recommendations to regional levels because landscape-scale studies are lacking (Flather and Sauer 1996, Haig et al. 1998). Recent advances in GIS and remote sensing technologies have enabled wildlife researchers to use sampling strategies that result in inferences over larger landscapes. Landscape-level research, which is currently being used in forested ecosystems to direct conservation efforts and design nature reserve systems (Askins et al. 1987, Robbins et al. 1989, Hansson and Angelstam 1991, Pearson 1993, Flather and Sauer

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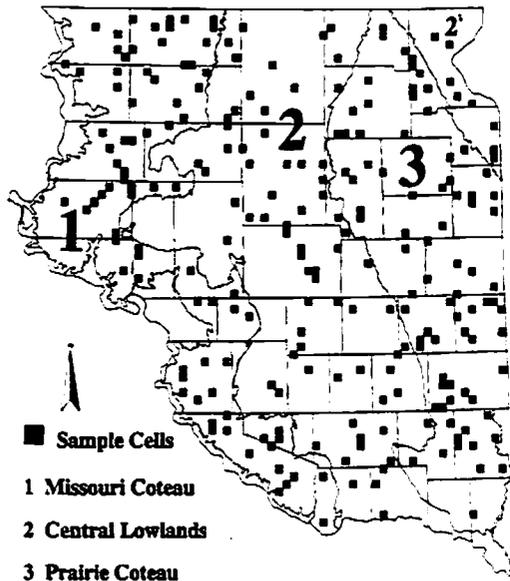
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Fig. 1.   Distribution of 25.9-km² cells that were used to evaluate habitat suitability of wetlands for black terns in the Missouri Coteau, Central Lowlands, and Prairie Coteau domains of eastern South Dakota. Mean with SE bar.

1996), could be used to enhance conservation planning for wetland ecosystems.

Federal and state agencies have been acquiring easement and fee-title tracts for >30 years to protect wetland habitats. Although much research has focused on benefits to waterfowl, less is known about habitat requirements or potential benefits of wetland protection programs for other species. In this study, we identify local and landscape factors influencing wetland suitability for black terns, a little-studied species that nests and forages in prairie wetlands. We also use discriminant functions to delineate suitable habitat across the PPR region of eastern South Dakota and assess the effectiveness of wetland acquisition programs in protecting black tern habitat.

STUDY AREA

The study area encompassed eastern South Dakota from the Minnesota border west to the Missouri River. We divided the region into 3 domains, Prairie Coteau (28.7%), Central Lowlands (44.3%), and Missouri Coteau (27.0%) based on similarity of wetland characteristics (Fig. 1). The Prairie Coteau is characterized by an abundance of semipermanent and permanent wetlands. The Central Lowlands, a low relief landscape, has an abundance of seasonal and temporary wetlands. The Missouri Coteau has numerous seasonal wetlands in the northeast and fluviatile wetlands throughout the south and west.

METHODS

Creation of GIS Data Layers

Wetland Coverages.—We used National Wetlands Inventory (NWI) maps based on 1975–86 color infrared photography and converted wetlands to wetland basins using techniques described by Cowardin et al. (1995) and Johnson and Higgins (1997). Polygons defining adjacent wetlands were combined to delineate contiguous wetland basins. Basins were classified as temporary, seasonal, semipermanent, or permanent by the water regime of the most permanent wetland they contained (Cowardin et al. 1995, Johnson and Higgins 1997). Approximately 1% of basins were manually compared to wetland coverages to assure accuracy in the basin creation process. Polygons labeled as excavated semipermanent wetlands were reclassified according to the most permanent water regime of the surrounding natural wetland to ensure that our findings would reflect wetland bird habitat use of natural depressions. Isolated excavated and impounded semipermanent wetlands were excluded from analyses. Linear wetlands (e.g., road and drainage ditches) were eliminated to minimize bias in estimated wetland density (Johnson et al. 1999).

Easement and Fee-title Tracts.—We manually transferred map boundaries for waterfowl production areas, perpetual wetland easements, and national wildlife refuges acquired by the U.S. Fish and Wildlife Service (USFWS; 1: 21,120 scale), and game production areas acquired by South Dakota Department of Game, Fish and Parks (1:63,360 scale) before 30 September 1994 to copies of NWI maps (1:24,000 scale). We then digitized tract boundaries to create wetland protection coverages encompassing eastern South Dakota.

Land Cover Data.—Landsat Thematic Mapper imagery from 8 scenes covering eastern South Dakota were used to classify uplands into tilled and untilled vegetation classes. Untilled lands were permanent pastures, Conservation Reserve Program (CRP) grasslands, and alfalfa. We used imagery newer than 1990 (April and May 1991 and 1992 scenes) to ensure that changes in CRP enrollment were incorporated

into our landuse classifications. Trees, which constituted <1% of area in eastern South Dakota, were not distinguished from untilled herbaceous grassland cover types. Crops (e.g., corn, soybeans, wheat) and annually fallowed areas were considered tilled lands. Naugle et al. (1999) provides descriptions of methods used to process imagery and assess accuracy of classifications. Overall, per-pixel classification accuracy for the map was 97%. Estimates of untilled area were calculated within 25.9 km² cells. Proportion of untilled area was defined as the sum of untilled area divided by the sum of non-wetland area. Percentage data were square-root transformed to approximate normality.

Sampling Methods

A grid comprised of approximately 3,800 25.9-km² cells was combined with the wetland GIS (Johnson and Higgins 1997). The center of wetlands was used to assign them to a single cell. Median values of the frequency distributions for wetland densities (110 wetlands) and areas (124 ha) were used to classify cells within domains into 4 landscape types: landscape type a cells were low in wetland density and area, type b cells were high in density and low in area, type c cells were low in density and high in area, and type d cells were high in density and area. We randomly selected 216 cells allocated equally across landscape types within domains in 1995 and 1996 (Fig. 1). In 1996, an additional 7 cells of landscape type a were randomly selected from each domain to ensure an adequate sample of semipermanent wetlands. Two seasonal and 2 semipermanent wetlands were randomly selected within each cell. Alternate wetlands replaced wetlands that were dry, farmed, burned, or mowed.

Field Methods

We surveyed 416 semipermanent and 418 seasonal wetlands from 5 May to 10 July 1995–96 (Fig. 1). We walked the perimeter of each wetland after walking a zig-zag pattern within wetlands to ensure that all black terns present were detected. Wetlands were classified as used if we observed adults, active nests, or young. In 1995 and 1996, we revisited wetlands that were classified as used during the first visit to confirm nesting. Nesting colonies were easily detected because black terns vigorously defend nesting areas by mobbing intruders (Dunn and Agro 1995). We returned in 1996 to wetlands that

had been occupied in 1995 to assess changes in vegetation condition and to determine number of wetlands used by black terns in consecutive years. Vegetative marsh stage (e.g., degenerating versus open marsh; van der Valk and Davis 1978) was recorded to assess wetland conditions.

Percent vegetated wetland area was estimated visually using a modification of the Daubenmire scale (Bailey and Poulton 1968). Percent of wetland area that was vegetated was recorded into the following class intervals: (1) <1%, (2) 1–5%, (3) 6–25%, (4) 26–50%, (5) 51–75%, (6) 76–95%, and (7) >95%. Pattern of emergent vegetation was recorded using the 4 cover-type classifications (e.g., open marsh, concentric rings of vegetation, highly dispersed vegetation pattern, closed marsh) of Stewart and Kantrud (1971). Land use surrounding wetlands was classified as cropland, grassland, or mixed. Grazing intensity on wetland shorelines was estimated by visual inspection of residual vegetation and current year's growth (Kirsch 1969). Shorelines that ranged from idled (i.e., <1%) to heavily grazed (i.e., >95%) were recorded using the modified Daubenmire scale. Grazing intensity within wetlands was visually estimated as light, moderate, or heavy.

Height and density of emergent vegetation were quantified in 10 randomly selected nesting wetlands to assess the role of vegetation structure in habitat suitability. Mobbing behavior and alarm calls (Dunn and Agro 1995) from black terns were used to locate nests. Colony boundaries were defined by the outer most nest locations. Within each wetland, structural attributes and dominate types of vegetation were obtained from 2 randomly selected black tern nests, 2 random points between nests within the colony, and at 2 locations outside the colony. Number of paces and direction to points were selected in the field using a random numbers table. Random points falling within unvegetated, open water areas or in dry portions of wetlands were excluded. We used a 2.4-m vegetation profile board (Nudds 1977, Haukos et al. 1998) marked with alternating black and white at 0.2-m height intervals (0.4-m wide) to quantify vegetative density. Proportion of each 0.2-m interval covered by emergent vegetation was recorded as a single digit density score, which corresponded to the mean value of a range of quintiles (e.g., 1 corresponded to the range 0–20%, 2 to 21–40%; Nudds 1977). Den-

Table 1. Description of local and landscape attributes quantified to evaluate wetland habitat suitability for black terns in eastern South Dakota.

Attributes
Local variables quantified within or immediately adjacent to the wetland
[a] Wetland area
[a] Percent vegetated wetland area
[a] Index to grazing intensity on shorelines adjacent to wetlands
[a] Proportion of wetland perimeter encompassed by trees
[a] Variable indicating whether herbaceous hydrophytes were thick- or thin-stemmed
[a] Number of emergent hydrophyte species comprising ≥10% of vegetated wetland area
Wetland perimeter
Cover type classification[b]
Index to grazing intensity within wetlands
Landscape attributes quantified within 25.9-km² cells surrounding surveyed wetlands
[a] Total temporary wetland area
[a] Total seasonal wetland area
[a] Total semipermanent wetland area
[a] Total permanent wetland area
[a] Grassland area
Number of temporary wetlands
Number of seasonal wetlands
Number of semipermanent wetlands
Number of permanent wetlands

[a] Variable was included in discriminant function analyses.
[b] Cover type classifications (Stewart and Kantrud 1971) described the distribution of emergent vegetation within wetlands.

sity scores were recorded in each cardinal direction at a standard distance of 5 m. We averaged density scores within height intervals and summed across sites within wetlands to avoid pseudoreplication (Hurlbert 1984, Haukos et al. 1998).

Analytical Methods

Forward stepwise discriminant function analysis (Wilkinson 1997) was used to produce a linear combination of variables that best classified wetland habitat suitability for black terns. The binary dependent variable was coded as presence–absence of black terns. Predictor variables calculated using the GIS were wetland area (ha) and shoreline length (m), and total area and density of wetlands for each of 4 water regimes (temporary, seasonal, semipermanent, permanent; Stewart and Kantrud 1971; Table 1). Data were log transformed to approximate normality. Class interval midpoints were used to analyze categorical data. Eleven variables were used in analyses after others were eliminated to reduce

collinearity among the independent variables (Table 1).

Wetlands were classified as suitable or unsuitable habitat according to the largest value of the classification function (Wilkinson 1997). The discriminant function was used in the GIS to classify all semipermanent wetlands throughout eastern South Dakota as suitable or unsuitable habitat for black terns. Apparent and jackknife classification rates were used to cross validate our ability to predict suitable habitat. We also cross validated our predictive capability using survey information collected in 1997 from 75 semipermanent wetlands on the Prairie Coteau domain that were not used in model construction. Number of protected suitable wetlands was calculated by combining easement and fee-title tracts with semipermanent wetlands in the GIS. Wetlands were considered protected when their borders were ≥90% encompassed by an easement or fee-title tract. Analysis of variance was used to evaluate relationships between structural characteristics of emergent vegetation and habitat suitability; significance was $P < 0.05$ for all hypothesis tests.

RESULTS

Wetland Use by Nesting and Foraging Black Terns

Black terns were recorded on 106 (25.7%) of 412 semipermanent wetlands. Nesting was confirmed on 32 (7.8%) wetlands during revisits and 74 (17.9%) semipermanent wetlands were used for foraging. Although black terns foraged on 29 (6.9%) of 418 of seasonal wetlands, nesting was confirmed in only 2 (<1%). Black terns nested in 36.4% (8 of 22) of semipermanent wetlands in both 1995 and 1996. Eleven of the 22 semipermanent wetlands containing black terns in 1995 reverted from a degenerating marsh stage to an open marsh phase. When these wetlands were excluded, wetland use by nesting black terns in consecutive years was 72.7% (8 of 11).

Landscape Factors Influencing Black Tern Habitat Suitability

The discriminant function was only used to classify suitability of semipermanent wetlands because black terns nested and foraged on few seasonal wetlands. Low occupancy rates of nesting black terns should not diminish the potential importance of seasonal wetlands to foraging black terns because intermittent occupancy of

Table 2. Coefficients of wetland area and landscape attributes that were used in a discriminant function to classify suitability of semipermanent wetlands for black terns in eastern South Dakota. Apparent, jack-knife, and true classification rates indicate the proportion of unsuitable and suitable wetlands that were correctly classified by the discriminant function.

Attributes	Wetland classification	
	Unsuitable	Suitable
Constant	−16.490	−23.403
Wetland area	1.862	2.888
Semipermanent area	0.854	1.127
Grassland area	39.670	45.528
% *Correctly classified*		
Apparent	76	78
Jack-knife	76	78
True[a]	100	22

[a] Black terns occurred on 9 of 75 wetlands that were used to calculate true classification rates.

Suitable Wetlands

— Zero
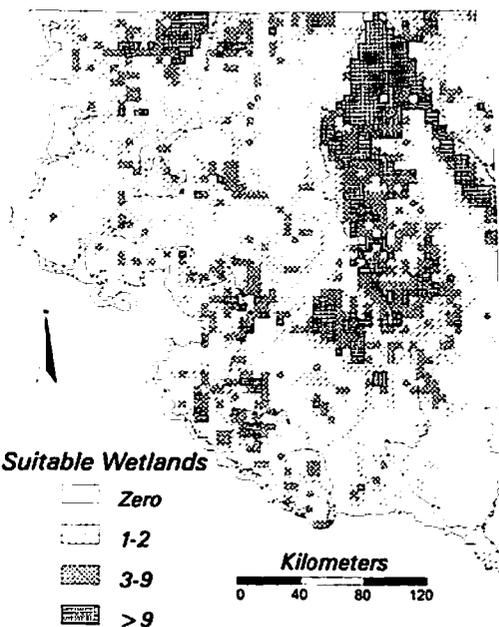⸬ 1-2
▨ 3-9
▤ >9

Kilometers
0   40   80   120

Fig. 2. Distribution of semipermanent wetlands in eastern South Dakota that were classified as suitable black tern habitat for nesting and foraging. Shade symbols indicate number of suitable wetlands within 25.9-km² cells.

seasonal wetlands by foraging black terns may have led to misclassifications when presence of black terns and observers did not coincide. Problems resulting from misclassifications of semipermanent wetlands were minimal because Naugle et al. (1999) found that significant predictors of black tern occurrence and their order in regression equations were identical regardless of whether nesting or foraging records were used to define wetland use.

Using the discriminant function, we identified wetland area and 2 landscape factors, total semipermanent wetland area and grassland area, that were important in separating suitable and unsuitable semipermanent wetlands (Wilks' $\lambda = 0.78$, $F = 44.17$, df = 3,408, $P \leq 0.001$; Table 2). Wetland area contributed most to the discriminant function. Suitable wetlands were larger ($\bar{x} = 18.9$ ha; SE = 3.6) than unsuitable wetlands ($\bar{x} = 6.0$ ha; SE = 1.2). Wetland suitability was positively related to total areas of semipermanent wetlands and upland grasslands surrounding surveyed wetlands (Table 2). Apparent and jack-knife classification rates were >75% (Table 2).

When the discriminant function model was applied to spatial data, 13,399 (55.6%) of the 24,083 semipermanent wetlands ≥0.2 ha in eastern South Dakota were classified as suitable habitat. Further validation of the discriminant function using a sample of 75 wetlands obtained after model construction indicated that wetlands where black terns were absent during field surveys were correctly classified as unsuitable habitat (Table 2). When easement and fee-

title tracts were combined with suitable wetlands, 5,829 (43.5%) of the 13,399 suitable wetlands were protected.

Number of suitable semipermanent wetlands within 25.9-km² cells was summarized into 4 classes: 1 = 0, 2 = 1–2, 3 = 3–9, and 4 = >9 wetlands (Fig. 2). Suitable black tern habitat was widespread and abundant throughout the northern Prairie Coteau (Fig. 2). Isolated areas of suitable habitat also were identified in the northeastern Missouri Coteau and middle Central Lowlands domains (Fig. 2). Waubay Wetland Management District (WMD), a 5-county federal wetland management area that encompasses the northern Prairie Coteau (Figs. 1 and 2), contained 57.3% (7,675) of suitable semipermanent wetlands in eastern South Dakota. Of the 5,829 suitable, protected semipermanent wetlands in eastern South Dakota, 62.3% (3,632) are located within Waubay WMD.

Local Factors Influencing Black Tern Habitat Suitability

We found interactions between height and density of emergent vegetation at nests and random sites outside the colony ($F = 37.70$, df = 1,16, $P < 0.001$) and at random sites within and outside the colony ($F = 24.61$, df = 1,16, $P <$
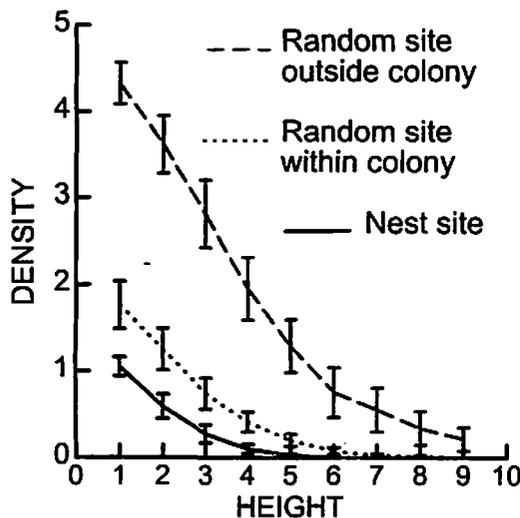
Fig. 3. Relationship between height and density of emergent vegetation at nests and random sites within and outside black tern nesting colonies in semipermanent wetlands in eastern South Dakota. Mean with SE bar.

0.001). Height and density of vegetation was lower at nest sites and random sites within the colony compared to random sites outside the colony (Fig. 3). Density of emergent vegetation at nest sites decreased with increasing vegetation height (Fig. 3). Dominant emergent vegetation at each of 20 randomly selected nest sites was cattail ([*Typha* spp.] 65% of sites), bulrushes ([*Scirpus* spp.] 20%), and bur-reed ([*Sparganium* spp.] 15%).

DISCUSSION

Habitat evaluation across 2 scales enabled us to identify local and landscape factors associated with wetland suitability for nesting and foraging black terns. The importance of landscape factors in the discriminant function indicated that characteristics of entire landscapes, in addition to attributes of individual wetlands, must be considered when assessing habitat suitability. Rather than simply concluding that black terns require large wetlands averaging 18.9 ha without considering landscape-level variability, Naugle et al. (1999) found that size of wetlands used by black terns was related to characteristics of the surrounding wetland complex. Black terns used smaller (6.5 ha) wetlands located in high-density wetland landscapes (landscape type *d*) composed of large and small wetlands more than those in homogeneous landscapes containing predominately large (landscape type *c*; 15.4 ha) or small wetlands (landscape type *b*; 32.6

ha) (Naugle et al. 1999). Low wetland density landscapes (landscape type *a*) composed of primarily small wetlands, where few semipermanent wetlands occur and potential food sources are spread over large distances, were not widely inhabited by black terns (Naugle et al. 1999).

Relationships between landscape factors and habitat suitability for black terns indicated that they typically inhabit wetlands within landscapes where <50% of grasslands had been tilled. Recent advances in the field of landscape ecology (Turner 1989, Turner and Gardner 1991, Forman 1995, Bissonette 1997) have indicated that the matrix (e.g., adjacent uplands) often influences landscape function by altering within-patch (e.g., wetland) dynamics. In northern prairie ecosystems, pesticide and fertilizer runoff and siltation from agricultural lands alters wetland vegetation composition (Kantrud 1986) and reduces invertebrate abundance (Novak 1992, Dunn and Agro 1995). We used grassland abundance in this study as a surrogate measure reflecting the negative impacts of agricultural activities on wetland habitats. Findings of Beintema (1997), who indicated that agricultural tillage decreases diversity of invertebrate forage available to wetland avifauna, reinforce our contention that human-induced modifications in upland habitats influence processes within wetlands.

High correct classification rates (76–100%) for unoccupied wetlands indicated that the model identified unsuitable wetlands using wetland area and landscape-level attributes. Characteristics of entire landscapes must be considered in habitat assessments because wetlands that do not correspond to landscape-scale habitat requirements may not be suitable despite favorable local conditions. Lower correct classification rates (22–78%) for occupied ponds indicated that suitability also is dependent on local vegetative conditions for wetlands which correspond to black tern habitat requirements from a landscape perspective. Our vegetative analysis reconfirms that suitable nesting substrates occur within regenerating or degenerating wetlands (Weller and Spatcher 1965, Weller and Fredrickson 1974, van der Valk and Davis 1978, Hickey and Malecki 1997). Our analyses of local vegetative conditions within wetlands also indicated that vegetation structure, rather than species of emergent vegetation, largely dictates suitability of substrates for nesting black terns. Height and density of emergent

vegetation was lower at random and nest sites within colonies than at random sites outside colonies (Fig. 3), indicating that black terns typically nest in more sparsely vegetated areas. The interaction between vegetation height and density within nest sites also indicated that black terns nest in either short–dense or tall–sparse vegetation. Either type of vegetation structure provides black tern chicks with refuge from aerial predators (Chapman Mosher 1986, Dunn and Agro 1995, Hickey and Malecki 1997), and affords adults rapid aerial access for defending nests. Dense, monotypic stands of cattail, which often form in wetlands in agricultural landscapes (Kantrud 1986), severely reduce wetland habitat suitability at a local scale (Linz and Blixt 1997). Although philopatry in black terns is considered low (Dunn and Agro 1995), wetlands support breeding black terns in consecutive years when favorable marsh conditions persist.

MANAGEMENT IMPLICATIONS

Results from this study indicate that both local and landscape factors influence habitat suitability for nesting and foraging black terns in the PPR. Therefore, acquisition programs that protect individual wetlands without regard to their relationships within wetland complexes and associated upland habitats are likely to meet with limited success. Acquisition programs designed to protect habitat for black terns should maintain the integrity of entire prairie landscapes. GIS databases, when combined with mathematical models that predict locations of suitable habitats, may be valuable tools for conservation planning. Regional summaries generated using the GIS data from our study indicated that wetland protection programs in eastern South Dakota have protected 44% of wetlands suitable for black terns. We suggest that future efforts to secure suitable black tern habitat concentrate on Waubay WMD, a high priority area within the Prairie Coteau physiographic region that encompasses 62% of all the suitable, unprotected black tern habitat.

ACKNOWLEDGMENTS

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