WATERBIRD DISTRIBUTION AND HABITAT IN THE PRAIRIE POTHOLE REGION, U.S.A.

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A

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Abstract

The Prairie Pothole Region (PPR) of north-central North America provides some of the most critical wetland habitat continent-wide to waterbirds. Agricultural conversion has resulted in widespread wetland drainage. Furthermore, climate change projections indicate a drier future, which will alter remaining wetland habitats. I evaluated Black Tern (*Chlidonias niger*) habitat selection and the potential impacts of climate change on the distribution of waterbird species. To examine Black Tern habitat selection, I surveyed 589 wetlands in North and South Dakota in 2008-09, then created multivariate habitat models. I documented breeding at 5% and foraging at 17% of wetlands surveyed, and found local variables were more important predictors of use than landscape variables, evidence for differential selection of wetlands where breeding and foraging occurred, and evidence for a more limited role of area sensitivity (wetland size). To examine the potential effects of climate change, I created models relating occurrence of five waterbird species to climate and wetland variables for the U.S. PPR. Projected range reductions were 28 to 99%, with an average of 64% for all species. Models also predicted that, given even wetland density, the best areas to conserve under climate change are northern North Dakota and Minnesota.

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OVERALL INTRODUCTION

Many waterbird species are of conservation concern due to widespread conversion and degradation of the wetland habitats they rely upon. Climate change effects are likely to cause further impacts on wetland habitats through increased temperatures and evapotranspiration. The Prairie Pothole Region (PPR) of the north-central U.S. and south-central Canada contains many small prairie wetlands that provide some of the most critical habitat continent-wide to migrating and breeding wetland-associated birds (Batt et al. 1989, Beyersbergen et al. 2004). Most of this landscape has already been severely altered due to conversion to cropland. Wetland losses in the Dakotas averaged 42%, and in Minnesota and Iowa have averaged 90% since European settlement began in the late 1700's (Dahl 1990, Johnson et al. 2008). These losses may continue as corn ethanol incentives increase the value of the land for crops (Griffin et al. 2009). Climate projections based on Global Circulation Models (GCMs)/emissions scenarios project, on average, large increases in temperature and moderate increases in precipitation in the PPR, with an overall increase in drought (Ojima and Lackett 2002). This will likely cause reductions and geographic shifts in wetland habitats (Johnson et al. 2010). To address these problems, I took two approaches to investigate the potential changes for waterbirds. The first was to study habitat selection by the Black Tern (*Chlidonias niger*) – a species that is difficult to manage because of low breeding site fidelity (Heath et al. 2009). The second approach was to study the potential effects of future climate change on the distribution of five waterbird species in the PPR of the U.S.

The Black Tern is a migratory species that breeds in freshwater wetlands throughout the northern U.S. and southern Canada. For the PPR, it is listed as a species of high conservation concern (Beyersbergen et al. 2004). Two previous studies of Black Tern habitat requirements in the PPR found that terns used large wetlands and preferred high density wetland landscapes (Brown and Dinsmore 1986, Naugle et al. 2000). However, these results may be confounded by problems associated with passive sampling (Johnson 2001). Their results are also likely to be more applicable to foraging terns because they combined foraging and breeding detections in their models. I modeled habitat selection by terns, examining which characteristics of the landscape and which of the local wetlands were potentially important to breeding and foraging terns. My study design addresses the potential confounding factor of passive sampling.

The few studies that have looked at the potential impacts of climate change on avian species in the PPR have focused on waterfowl. They concluded that habitat for waterfowl would be reduced, and one study predicted that suitable conditions would shift eastward to Minnesota and Iowa (Poiani and Johnson 1991, Sorenson et al. 1998, Johnson et al. 2010). To examine the potential effects of climate change on waterbirds in the PPR, I used species distribution models (SDMs) to look at changes between predicted current and projected future distributions. I chose five waterbird species whose core breeding area is the PPR: American Bittern (*Botaurus lentiginosus*), American Coot (*Fulica americana*), Black Tern, Pied-billed Grebe (*Podilymbus podiceps*), and Sora (*Porzana Carolina*; Beyersbergen et al. 2004). I created SDMs by relating species occurrence records from the Breeding Bird Survey to down-scaled climate and wetland variables. Using these SDMs, I compared current predicted distributions for the five species to several future projections under different climate change scenarios. Additionally, I assessed where the best areas might be for waterbird conservation reserves under a changed climate.

These studies, conducted at a regional level, can provide information to help guide management decisions in the PPR. Many important and long-lasting decisions are currently being made in the PPR about wetland preservation and restoration. The Black Tern study can inform land managers about which habitat characteristics to manage for to mitigate against future population declines. The climate change analysis also gives an indication of the best locations to preserve and restore wetlands for waterbirds in anticipation of a warmer and drier future.

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CHAPTER 1

Wetland Selection by Breeding and Foraging Black Terns in the Prairie Pothole Region of the United States[1]

Abstract. While the Prairie Pothole Region (PPR) of North America provides critical habitat to many wetland-associated birds, most research has focused on the habitat needs of waterfowl species. We examined wetland selection by Black Terns (*Chlidonias niger*), a species that breeds primarily in the PPR, has experienced population declines, and is difficult to manage for because of low site fidelity. To characterize wetland selection by Black Terns in the PPR, we surveyed 589 wetlands in 2008-09 throughout North Dakota and South Dakota. We documented breeding at only 5% and foraging at 17% of the wetlands surveyed. We created predictive habitat models using a machine-learning algorithm, Random Forests, to explore the relative role of local wetland characteristics and those of the surrounding landscape, and to evaluate which characteristics were important to predicting breeding versus foraging terns. We also examined area-dependent wetland selection while addressing the passive sampling bias by replacing occurrence of terns in the models with an index of density. Local wetland variables were more important than landscape variables in predictions of breeding and foraging occurrence. Wetland size was more important to prediction of foraging locations than breeding locations, while floating matted vegetation was more important to prediction of breeding locations than foraging locations. Breeding terns selected for wetlands with an interspersion of open water and emergent vegetation; foraging terns selected wetlands with an expanse of open water. The amount of seasonal wetland in the landscape was the only landscape variable important to both foraging and breeding predictions. We created a density index by dividing the number of terns foraging or breeding in the wetland by the wetland area. Models created using this index indicated

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[1] Steen, V. and A. Powell. 2010. Wetland Selection by Breeding and Foraging Black Terns in the Prairie Pothole Region U.S.A. Prepared for submission to *Condor*.

that wetland selection by foraging terns may be more area dependent than by breeding terns. Terns used wetlands as small as 1.6 ha, which is smaller than previously reported. Our study provides some of the first evidence for differential breeding and foraging wetland selection in Black Terns, and for a more limited role of landscape effects and area sensitivity.

INTRODUCTION

The Prairie Pothole Region (PPR) of north-central North America provides critical habitat to much of the continent's migrating and breeding wetland-associated birds. Since European settlement, the fertile soil of the region, along with manpower, machinery, and economic incentives caused much of this land to be converted to cropland. Between 1780 and 1980, approximately 50% of wetlands in the PPR were converted to cropland (Dahl and Johnson 1991, Dahl and Allord 1996) and, in some areas, nearly all of the native grasslands (Samson and Knopf 1994). Despite the history of habitat loss, waterfowl as well as some waterbirds increased in the 1990's (Niemuth and Solberg 2003, Ringelman 2005). It is estimated that waterfowl populations in the PPR increased 492% from 1990 to 2000 (Ringelman 2005). These increases were attributed primarily to Conservation Reserve Program (CRP) subsidies for farmland which created and preserved large amounts of habitat (both upland and wetland), combined with a period of wet years, which created favorable wetland conditions (Ringelman 2005). However, renewed habitat loss is underway as corn biofuel incentives and mandates have increased commodity prices, resulting in loss of CRP lands and previously untilled lands (Griffin et al. 2009). Furthermore, climate change effects are expected to increase drought and cause loss of wetland habitats (Ojima and Lackett 2002, Johnson et al. 2010).

In the PPR, where greater than 50% of the continent's surveyed populations for eight waterfowl species breed (Batt et al. 1989), waterfowl productivity is of paramount interest. As a result, many habitat conservation decisions are informed by waterfowl research and management initiatives (Beyersbergen et al. 2004). While most waterfowl require grasslands for nesting and wetlands for foraging, habitat requirements for waterbirds may differ. Many waterbirds are more wetland-dependent than waterfowl requiring wetlands for both nesting and foraging, and may not be sensitive to the characteristics of the surrounding uplands. The PPR provides breeding habitat to over 50% of the continental populations of six waterbird species (Beyersbergen et al. 2004). Far less attention has been afforded to these species and recent conservation plans for the PPR have pointed to an information gap for waterbirds (Beyersbergen et al. 2004, Ringelman 2005).

The Black Tern (*Chlidonias niger*) nests and primarily forages in wetlands. It is listed as a species of conservation concern; its core breeding range in North America is the PPR (Beyersbergen et al. 2004). Breeding Bird Survey (BBS) data indicate its North American population declined 61.1% from 1966 to 1996, with the sharpest declines occurring before 1980 followed by a subsequent leveling off; Peterjohn and Sauer 1997, Sauer et al. 2008). As for many birds that breed in the PPR, population declines are attributed to loss and degradation of habitat (Beyersbergen et al. 2004, Heath et al. 2009).

Black Terns exhibit weak inter-annual breeding site fidelity. This is likely due to the dynamic nature of vegetative conditions suitable for breeding (Shealer 2003) and makes understanding the wetland characteristics selected by terns particularly important for their management. Habitat selection is a process that results in the disproportionate use of available habitats. This process is thought to be hierarchical with selection of the broadest spatial scale occurring first (e.g. home range), followed by selection at finer spatial scales (e.g. nest site; Johnson 1980, Jones 2001). In the PPR, where there is a high degree of fragmentation, there is not only heterogeneity at the finer spatial scales but also at the landscape scale. Landscapes may not meet the requirements of the species if the patches contained within are too isolated from other patches, too small, or confer edge effects. For waterbirds, wetlands are thought of as the "patch" of local habitat. Small wetlands may not meet the area requirements of the species, isolated wetlands may not meet the area requirements of vagile species, and edge effects may affect wetland suitability through sedimentation, pesticide and herbicide runoff, grazing, or increased predation.

Most studies of waterbirds breeding in the PPR that have included landscape metrics focused on isolation by measuring wetland composition (i.e. the amount of wetland in the landscape; Brown and Dinsmore 1986, Fairbairn and Dinsmore 2001). However, another study also incorporated upland landscape composition, edge cover, and a measure of grazing intensity (Naugle et al. 1999). Typically the size of the local habitat patch is considered a landscape characteristic because it is a fragmentation metric. However this is only the case for contiguous habitat types such as forest or grassland but typically not for wetlands which vary naturally in size. Thus, the size of the local wetland “patch” might be best thought of as a local characteristic.

Black Terns are considered a vagile species because they often forage away from their breeding locations. As such they may be expected to be sensitive to landscape and patch size effects. Two previous studies that examined either landscape-level habitat associations (Brown and Dinsmore 1986) or both local- and landscape-level habitat associations (Naugle et al. 2000) of Black Terns in the PPR found that they responded positively to the amount of wetland in the landscape and to wetland size. However, the results of both of these studies are confounded by problems associated with passive sampling (Johnson 2001). Combining breeding and foraging detections may also make the results of these studies more difficult to interpret. We address both of these potential confounding factors in this study.

We conducted this study at a regional level, sampling across the PPR of North and South Dakota, so that inferences would be applicable to regional-level management planning. Our specific objectives were to: 1) compare the importance of landscape characteristics (composition and edge) versus local wetland characteristics to breeding and foraging terns, 2) explore which characteristics are important to breeding versus foraging terns, and 3) assess area sensitivity using models that account for potential passive sampling bias. Finally, we offer management recommendations for Black Terns based on our findings.

METHODS

STUDY AREA

The PPR in North and South Dakota covers the area east and north of the Missouri River, an area of approximately 220,000 km^2 (Fig. 1.1). Water-filled glacial depressions termed *potholes* are the characteristically small prairie wetlands that pock-mark this region and reach densities greater than 40 per km^2 in some areas (Kantrud et al. 1989). Three level III ecoregions make up the PPR of North and South Dakota (Omernik 1987): Lake Agassiz Plains is flat and highly cropped with relatively few wetlands; Northern Glaciated Plains is flat to gently rolling, highly cropped, and has lost many small wetlands; and Northwestern Glaciated Plains has a rolling topography, is a mixture of cropland and pasture, and has retained many large and small wetlands (Fig. 1.1).

WETLAND SELECTION

In a GIS, we randomly selected wetlands from a digital wetlands layer throughout the PPR of North and South Dakota (Fig. 1.1). The layer contained wetland basins reclassified from contiguous wetland polygons from the USFWS National Wetlands Inventory layer to single wetland basins following the procedures of Cowardin et al. (1995) and Johnson and Higgins (1997).

Our sampling frame differed between 2008 and 2009 when we surveyed 93 and 496 wetlands, respectively. In 2008, we selected wetlands on lands owned by the USFWS (National Wildlife Refuges and Wetland Management Districts) that were at least three hectares in size and classified as seasonal, semipermanent, or lake. In 2009, we used a two-tiered process to generate a spatially-balanced, size-stratified selection of wetlands. First, we chose 18 primary sampling units based on a systematic random sample to achieve a spatial balance across the study area. These were either counties or 50 x 50 km blocks. Within each primary sampling unit, we randomly selected 40 seasonal or semipermanent size-stratified wetlands - eight wetlands from each of five size strata (very small, 0.2-1.0 ha; small, 1.1-5.0 ha; medium, 5.1-20 ha; large, 20.1-50 ha; and very large, >50 ha). Wetlands were selected irrespective of land ownership (public or private). We made an effort to obtain land access permission for 4-5 wetlands of each size class per primary sampling unit. Neighboring very small and small wetlands were added to offset the underrepresentation in areal coverage of the two smallest size strata. These additional wetlands were selected by randomly choosing up to three additional wetlands smaller than 5 ha within 500 m of an already selected small or very small wetland. Thus the final selection consisted of 20-25 size-stratified wetlands per primary sampling unit plus neighboring small and very small wetlands.

BLACK TERN OCCURRENCE AND DENSITY

We chose survey dates to coincide with peak incubation dates reported for similar latitudes. We used the phenological south-to-north gradient of incubation dates to maximize the length of our field season by beginning in southern South Dakota and ending in northern North Dakota. We tried to revisit wetlands if there was an indication that we were there before incubation began, such as birds acting territorial around potential nest sites or laying eggs. Otherwise, we visited each wetland once to survey for Black Terns and assess local habitat variables. Surveys were conducted from 5-26 June in 2008 and 3 June to 1 July in 2009 during daylight hours but not during inclement weather (high winds or heavy rain).

We estimated the number of foraging terns by recording the maximum count of birds that were exhibiting foraging behavior. These were birds that were seen obtaining prey or those that were making slow and low flights over the wetland typical of foraging behavior. If the wetland was large and all foraging birds could not be seen from a single vantage point, we used a conservative estimate of the total number of birds seen from multiple points. We estimated the number of breeding terns by thoroughly searching the wetland for nests and multiplying the number of nests by two. The precise search strategy depended on wetland size and amount of vegetation. Open water wetlands were surveyed from one or more (depending on wetland size) shoreline vantage points. Vegetation-choked wetlands were surveyed by walking in a zigzag pattern from shoreline to shoreline through the vegetation. We surveyed wetlands with an intermediate amount of vegetation on foot or by kayak (depending on accessibility and water depth). Because Black Terns often nest close together, in areas where we observed nesting or potentially nesting terns, we walked or kayaked transect lines spaced ~20 m apart to thoroughly search for nests. All field data were collected under approval of University of Alaska, Fairbanks IACUC #06-46.

HABITAT VARIABLES

Local Habitat Variables. We described each wetland using seven local habitat variables: four vegetative condition variables, cover type, wetland size, and wetland regime. The vegetative condition variables described the estimated percentage of open water, emergent vegetation, wet meadow, and floating matted vegetation. Open water consisted of areas with standing water and no exposed vegetation. Emergent vegetation consisted of plants that are rooted underwater and exposed above the surface of the water, such as cattails (*Typha* spp.) and rushes (*Scirpus* spp.). Wet meadow described low-stature grasses, rushes, and sedges such as *Carex* species and *Phalaris arundinacea* that often exist along the periphery and other shallow water areas of the wetland. Floating matted vegetation described vegetation that had accumulated to form a mat of rooted or unattached, living or dead vegetation. We used four classes to describe cover type, the spatial pattern of open water and emergent vegetation: type I (vegetation choked, open water less than 5%), type II (open water 5-95%, at least some vegetation in the center of the wetland), type III (central expanse of open water >5%, with peripheral emergent vegetation), and type IV (open water >95%) (Stewart and Kantrud 1971). We estimated wetland size after correcting for current year's water level. To do this, we used a map of the wetland from the digital wetlands layer, corrected the outline of the wetland for current water level, then estimated percent change in wetland size from the original. Wetland regime (temporary, seasonal, semipermanent, or lake) was taken from the digital wetlands layer to describe the permanency of the wet period for that wetland in an average water year (Cowardin et al. 1979).

Landscape and Geographic Variables. We described the landscape around each wetland using four edge cover variables and seven landscape composition variables. We described edge cover of the upland with in a 10-m radius surrounding the high water line as the estimated percentage of four variables: tree/shrub, grass (including pasture), cropland, and other (usually barren cover such as road) cover types.

We used ArcMap 9.2 with the extension Hawth's Tools (Beyer 2004) to calculate the estimated percentage cover of seven landcover classes: prairie, planted, cropland, seasonal wetland, semipermanent wetland, lake, and total wetland (temporary + seasonal + semipermanent + lake + river + water) within a 2-km radius circle around the center point of the wetland. We used a 2-km radius circle to define landscape extent because it was close to the reported average distance Black Terns fly to long-distance foraging sites (2.4 km; Mosher 1986), and because we found, in an early modeling exercise comparing models with varying extents, that a 2-km radius model performed (based on predictive accuracy) as well or better than 1-km or 4-km models (unpubl. data). The remaining landcover classes were not modeled at all (hayland, forest, and urban) or individually (temporary wetland and river) because of their low representation in the landscape.

Data for landscape composition was obtained from a GIS raster layer created by the USFWS (USFWS, Region 6 Habitat and Population Evaluation Team, unpublished data). The raster classified landcover at a 30-m resolution into 13 classes: temporary wetland, seasonal wetland, semipermanent wetland, lake, river, water, prairie, planted, hayland, cropland, forest, urban, and barren based on Landsat Thematic Mapper imagery of scenes from 2000-2003. Prairie described lands that had not been previously cropped and were comprised of generally native grasses, forbs, and small shrubs and often used for cattle grazing. Planted described lands that had previously been cropped and were now planted with a mixture of grasses and forbs. These lands usually lacked the variety and included more introduced species than prairie. They were generally part of the Conservation Reserve Program (CRP) and were not subject to land use such as grazing. Hayland included land planted primarily with alfalfa. These lands were typically hayed at least once per year. Cropland was land planted with crops or fallowed. Accuracy assessment in 2007 for upland classes was above 90% (M. Estey, Pers. Comm.). The National Wetlands Inventory (NWI) layer was used to ascribe wetland regimes. Where water pixels extended beyond NWI polygons, they were labeled as water. For descriptions of the wetland regimes see Cowardin et al. (1979). Finally, we also included two geographic variables, longitude and latitude to look for any remaining spatial trending.

STATISTICAL ANALYSES

We developed four habitat models using the response variables, breeding occurrence, breeding density, foraging occurrence, and foraging density, and the seven local habitat, eleven landscape, and two geographic predictor variables. We developed models for both occurrence and density because they represent different trade-offs for managers. Occurrence data is quicker, easier and cheaper to collect, and is also more comparable to previous studies. However, it may be biased by passive sampling effects. Density data requires more resources to survey a similar number of wetlands but is less biased by passive sampling effects. We developed both foraging and breeding models because it is important for managers to know if recommendations would be different for breeding and foraging terns; these measure also differ in the amount of effort required for data collection.

We defined breeding and foraging occurrence as the presence of at least one breeding or foraging tern, respectively, at a wetland. We defined breeding and foraging density as the count of breeding or foraging terns, respectively, divided by the area (ha) of the wetland (corrected for current water level). For the foraging models, we excluded wetlands where Black Terns were recorded as breeding but not recorded as foraging, because although foraging terns likely forage where they breed they were not always confirmed as doing so. Because the data had a lot of zeros and a few high values we used a fourth square root transformation for both breeding and foraging densities. We grouped predictor variables according to scale of measurement and function: local wetland, edge, surrounding landscape, and geographic.

We also constructed subset models for breeding and foraging occurrence using the following subsets of predictor variables: local wetland, edge, surrounding landscape, landscape effects (edge and surrounding landscape), and geographic. Comparative accuracy assessments of these subsets allowed us to explore the relative role of landscape and local variables in predicting Black Tern occurrence.

We constructed the habitat models using Random Forests, a machine learning algorithm that uses an ensemble of classification or regression trees to examine the patterns between the predictor variables and the response variable (Breiman 2001). We assess model accuracy, variable importance, and partial dependence between predictors and the response. We chose to use Random Forests because it works well with complex ecological datasets, demonstrated by its high predictive ability, and because it provides a measure of variable importance that can reliably rank categorical and continuous predictors variables even when some of the predictor variables are highly correlated (Lawler 2006, Cutler et al. 2007, Hochachka et al. 2007, Oppel et al. 2009). The subsampling used to create trees in Random Forests also reduces the influence of spatial autocorrelation (see Goetz et al. 2010) and handles non-stationarity (Fortin and Melles 2009).

We used the cforest implementation of Random Forests available in the package 'party' in R 2.9.2. We specified 1000 trees, each created with 0.6 of the data without resampling, and with five predictor variables chosen for each split. We calculated the accuracy of predictions to the 0.4 out-of-bag data for the combined and subset models. We evaluated the classification models using the area under the curve of the receiver operating characteristic curve (AUC) to assess model performance and to compare local and landscape models. AUC values range from 0 to 1 and give the probability that, for a randomly selected pair of presence-absence observations, a presence observation has a higher value than an absence observation. AUC values of at least 0.5 discriminate better than random. Values of at least 0.7 are considered acceptable, between 0.8 and 0.9 are considered good, and greater than 0.9 are considered outstanding (Hosmer and Lemeshow 2000). We assessed model performance for the breeding and foraging density models, using R^2 values.

Although a number of methods can be used to rank variables in Random Forests, we used conditional permutation importance done in a conditional inference framework because it has been shown to be unbiased when variables differ in their scale of measurement, number of categories, or when variables are correlated (Hothorn et al. 2006, Strobl et al. 2007, Strobl et al. 2008) and thus provides reliable ranks of variables. Permutation importance is determined by randomly permuting a given predictor variable in the out-of-bag data for a specific tree, then assessing the subsequent decrease in accuracy when the permuted data is run through the tree compared to when the un-permuted data is run through the tree. The decrease in accuracy is averaged over all trees (1000 trees in our case). Conditional permutation importance differs from permutation importance by using a non-bootstrapped subsample to build the tree.

We report relative variable importance, with the most important variable scaled to 100 for ease of interpretation and for allowing comparison across models. We categorize the variables into four classes: very important, important, moderately important, and least important. We used the Jenks optimization method to group the scaled variable ranks by finding natural breaks in the values (Jenks 1967). The Jenks optimization method finds breaks in values to create a specified number of groups based on minimizing the variance within a group and maximizing the mean between groups. This produced the following divisions in the importance value ranks for the four classes: very important (VI), 51 to 100; important (I), 17 to 50; moderately important (MI), 4 to 16; and least important (LI), less than 4. We generated partial dependence plots using package ‘randomForest’ in R 2.9.2 to help interpret the relationship between the predictor variables and the response variable. These plots show this relationship over the full range of values for a given predictor variable using the average value for all other predictor variables. They do not account for any interactions that may exist.

RESULTS

SUMMARY STATISTICS

We surveyed a total of 589 wetlands: 93 in 2008, and 496 in 2009. Most were semipermanent or seasonal wetlands (Table 1.1). Type II (interspersion of open water and emergent vegetation) was the most frequently encountered wetland vegetative state, followed by type I (< 5 % open water; Table 1.1). Mean wetland size was 22.0 ha +/- 45.5 (Table 1.2). Open water and emergent vegetation were the dominant vegetative conditions; wet meadow and floating matted vegetation made up relatively little wetland vegetative condition (Table 1.2). While grass was the most common cover class composing the 10-m edge around wetlands, crop was the most common landcover class (Table 1.2).

We found Black Terns breeding at only 5% (32 of 589) and foraging at 17% (97 of 564) of wetlands surveyed. Size of wetlands where breeding occurred ranged from 1.6 – 234 ha ($\bar{x}$ = 68.6 ha +/- 69.4) while wetlands where foraging occurred ranged from 1.6 – 504 ha ($\bar{x}$ = 54.2 ha +/- 74.6: Table 1.2). The number of nests per breeding wetland ranged from 1 – 64 ($\bar{x}$ = 7.5). The number of terns per foraging wetland ranged from 1 – 125 ($\bar{x}$ = 9.8). Black Tern breeding densities ranged from 0.01 – 11.4 birds wetland^{-1} ha^{-1}, while foraging densities ranged from 0.003 – 5.9 birds wetland^{-1} ha^{-1}.

HABITAT SELECTION MODELS

Model Performance. For the breeding occurrence subset models, the wetland subset model, with only the seven local wetland habitat variables performed nearly as well as the combined model, which included all 20 predictor variables (Table 1.3). The subset models with only landscape, edge, landscape and edge, or geographic variables performed better than random but below the AUC critical value. Likewise, the foraging occurrence wetland subset model performed nearly as well as the combined foraging occurrence model (Table 1.3). The landscape and landscape effects (landscape and edge) subset models narrowly met the AUC critical value. The edge and geographic subsets performed better than random but did not meet the AUC critical value. The R^2 value for the breeding density model was 0.45 and for the foraging density model it was 0.48.

Variable Importance. For Predictions of Black Tern breeding occurrence there were two VI variables and two MI variables, in order of decreasing importance: percentage of floating matted vegetation (VI), wetland size (VI), wetland type (MI), and the amount of seasonal wetland in the landscape (MI; Fig. 1.3). Partial dependence plots (not shown) indicated that breeding terns were positively related to the amount of floating matted vegetation, wetland size, and the amount of seasonal wetlands in the landscape, and selected for type II wetlands. The remaining sixteen variables accounted for little to none of the predictive ability of the model; AUC for a model with the four VI or MI variables was 0.91, which was close to the AUC for the combined model with all variables (0.92; Table 1.3).

For predictions of Black Tern foraging occurrence there were two VI variables, two I variables, and five MI variables. The VI, I, and MI variables, in order of decreasing importance were: wetland size (VI), percentage of floating matted vegetation (VI), latitude (I), wetland type (I), percentage of open water (MI), percentage of emergent vegetation (MI), amount of seasonal wetland in the landscape (MI), 'other' cover in the wetland edge (MI), and amount of prairie in the landscape (MI; Fig. 1.3). Partial dependence plots (not shown) indicated that foraging terns were related positively to wetland size, floating matted vegetation, open water, and seasonal wetland in the landscape. They had two peaks of occurrence by latitude (in the southern and northern ends of the study area), they selected type III and to a lesser extent type IV wetlands, and they dropped off above 65% emergent vegetation. They were related negatively to 'other' in the edge and prairie in the landscape. The remaining eleven other variables accounted for little to none of the predictive ability of the model; AUC for a model with the nine VI, I, and MI variables was 0.88, which was the same as the AUC for the combined model with all variables (0.88; Table 1.3).

Our density models, used to ameliorate the passive sampling bias which can inflate the importance of patch size, did reduce the importance of wetland size in predicting wetlands where terns were breeding. It was downgraded from I to MI, similar in importance to the amount of seasonal wetland in the surrounding landscape and to wetland type. Wetland size was still VI to predicting wetlands where terns foraged. All other variable importance levels remained the same with the exception of two in the foraging density model: seasonal wetland in the landscape was downgraded from MI to LI, and total wetland in the landscape was upgraded from LI to MI.

DISCUSSION

RELATIVE IMPORTANCE OF LANDSCAPE AND LOCAL CHARACTERISTICS

Variable importance ranks from occurrence and density models indicate a strong predictive influence of local wetland characteristics on wetland selection by foraging and breeding Black Terns in the PPR. Also, subset occurrence models, which compared predictive abilities of the local and landscape variables, showed that the local variables we considered were far better at predicting tern foraging and breeding occurrence. Although, in general, landscape variables were least important, the amount of seasonal wetland in the landscape was moderately important in three of the four models. One other study assessed similar landscape variables and found that the amount of semipermanent wetland in the landscape was important in discriminating suitable from unsuitable wetlands (Naugle et al. 2000). Our result may correspond to their result as seasonal wetlands can function more like semipermanent wetlands in wet years; this describes 2009, when most of our surveys were conducted.

Thematically, our findings of a larger relative role of local characteristics are in contrast with the two major previous studies in the PPR. Brown and Dinsmore (B; 1986) controlled for local characteristics and concluded that wetland size and the amount of wetland in the landscape were positively related to Black Tern occurrence. Naugle et al. (N; 2000) assessed a number of local and landscape characteristics and found that suitable and unsuitable wetlands were separated mostly by landscape characteristics. N found that a higher amount of grassland and semipermanent wetland in the landscape and one local characteristic, wetland size, were important.

While B only considered landscape characteristics, N considered the same numbers of local and landscape variables as we did (seven and 11; by our definition of local and landscape). A number of methodological differences existed between our study and that of N, and may explain the differences in findings. This includes differences in definition of the response variables, landscape variable scale, spatial coverage, sample size, and predictor variables used. N modeled foraging and breeding detections together which would be expected to bias the results toward foraging occurrence, the more common occurrence type. We measured landscape variables in a 12.5 km^2 area, a smaller scale than the 25.9 km^2 used by N. Our scale was biologically based, with the 2-km distance from the wetland center selected on the basis of Black Tern foraging distances. Our spatial coverage and sample size were larger than that of N. Although both studies were located in the PPR, we covered North and South Dakota, while N covered just South Dakota. A potentially important difference in the predictor variable suite was the lack of any measure of floating matted vegetation by N, a high-ranking variable in our models likely due to its use as a nesting substrate. If this variable explains much of the variability in wetland selection, as indicated by our predictive models, its omission in previous studies could be an important source of model error (Barry and Elith 2006).

DIFFERENTIAL BREEDING AND FORAGING WETLAND SELECTION

Our study provides some of the first quantitative evidence that Black Terns select differently for foraging and breeding wetlands. Naugle et al. (2000) found that wetland area, amount of grassland in the landscape, and amount of semipermanent wetland in the landscape were the first, second, and third most important variables, for breeding and foraging terns (using forward stepwise regression and discriminant function analysis). In contrast, our analysis of tern density indicated that wetland size was more important to foraging than breeding terns. Additionally, breeding and foraging terns selected different wetland types. Breeding terns selected for wetlands with an interspersion of open water and emergent vegetation (type II wetlands), whereas foraging terns selected for open water wetlands (type IV wetlands) and those with a central expanse of open water and vegetation on the periphery (type III wetlands). The amount of floating matted vegetation was important in both models.

Floating matted vegetation was probably the most important modeled variable in the selection of breeding wetlands because of its importance as a nest substrate. Black Terns do not build nests from scratch, but rather rely on floating matted vegetation, vacated nests of other floating-nest waterbirds, muskrat structures, or mud patches (Heath et al. 2009). Most nests found in our study were located on floating matted vegetation.

The preference for breeding wetlands with an interspersion of open water and emergent vegetation (type II wetlands) may be related to the nest-site preference for an intermediate amount of emergent vegetation that is not close to shore while accessible to open water (Heath et al. 2009). The percentage cover of open water or emergent vegetation, however, was not important in predicting use of wetlands by breeding terns.

The preference for foraging wetlands with a higher amount of floating matted vegetation is likely related to the overlap in foraging and breeding wetlands; Black Terns often forage where they breed. It is also possible that these wetlands support higher levels of prey species as many invertebrates benefit from plant litter (Murkin et al. 1982, Magee 1993). Larger wetlands may provide more foraging opportunities for Black Terns; fish distribution is related to wetland size in the PPR where smaller and shallower wetlands more frequently dry up or freeze during winter (Herwig et al. 2010). The preference for foraging in wetlands with a central expanse of open water and a peripheral band of emergent vegetation (type III wetlands) makes sense in light of Black Terns' preference for foraging in open water areas (Mosher 1986). Type IV wetlands also provide open water areas while lacking most of the emergent vegetation. The presence of emergent vegetation in type III wetlands may relate to higher levels of prey species: wetland vegetation appears to support higher numbers of aquatic invertebrates (Krull 1970, Zimmer et al. 2000).

AREA SENSITIVITY AND PASSIVE SAMPLING

Previous studies in the PPR concluded that the Black Tern is an area-sensitive species (Brown and Dinsmore 1986, Naugle et al. 2000). Brown and Dinsmore found that Black Tern occurrence was positively related to wetland size and in their size-stratified sample of 30 wetlands they did not find terns in any wetlands smaller than 5 ha. Naugle et al. (2000) surveyed 412 randomly selected semipermanent wetlands and found that Black Terns occupied large wetlands ($\bar{x} = 18.9$ ha) and that wetland size was important in discriminating between used and unused wetlands in a habitat suitability model. However, because neither of these studies accounted for the passive sampling bias, the conclusion that the Black Tern is an area-sensitive species remains unqualified (Johnson 2001).

Passive sampling occurs when a larger area is surveyed in a larger patch, effectively allocating a disproportionate survey effort to larger patches (Connor and McCoy 1979). The occurrence rate of a species, especially if it is uncommon, is expected to increase simply as the search area increases (Johnson 2001), thus passive sampling can result in the appearance of area-sensitivity. One way to control for this bias is to survey equal areas in patches of different sizes. However, this is rarely practical in wetland studies in the PPR, because it would mean surveying less than 1% of large wetlands. Another option to control for the effects of passive sampling is by modeling density rather than occurrence. However, estimating densities of Black Terns is difficult because they do not meet the assumptions for fixed distance sampling, and because it is difficult to define the appropriate area to use for density calculations. However, we were able to use an index of density in our models that at least ameliorated the effect of passive sampling.

Our density models indicated that foraging terns were area-sensitive but breeding terns had low area-sensitivity. Wetland area was important to foraging terns regardless of whether occurrence or density was used as the response variable. In the breeding density model however, wetland size was only marginally important. Also, we found terns breeding in four small wetlands that were from 1.6 to 5.0 ha. This indicates that small wetlands can provide breeding habitat.

DETECTION PROBABILITY

We did not estimate detection probability in this study for a number of reasons. The primary reason is that both foraging and breeding Black Terns are highly detectible given a thorough search of the wetland. Although roadside surveys or shoreline point surveys may underestimate counts of terns, especially of breeding terns, at larger wetlands and those with denser vegetation, thorough searches of wetlands should remove most of that bias. Additionally, estimating detection probability is more costly because repeat surveys are required. Also, the assumption of closure is violated for foraging

Black Terns because they move between wetlands, making it difficult, if not impossible to estimate detection probability. That said, it is possible that there was a bias in detection probabilities that influenced counts of breeding and foraging terns. For breeding terns, there may have been a slight bias towards underestimating breeding counts at larger wetlands. This is consistent with our finding of less area sensitivity in selection of wetlands for breeding. However, we do not believe that it explains this result given that the bias was likely small. For foraging terns, it is possible that there was a bias towards higher counts of foraging terns at wetlands where we spent disproportionately (per unit area) more time because foraging terns move in and out of wetlands. These were usually wetlands with more vegetation and type II and I wetlands, and likely had less to do with wetland size. This is not consistent with our variable importance ranks or our conclusion about area sensitivity.

MANAGEMENT IMPLICATIONS

While Black Terns likely benefit from waterfowl conservation programs that conserve landscapes with a high density of wetlands and grasslands, many suitable breeding wetlands will not be covered by these efforts. The results of our study suggest that small wetlands surrounded by cropland also provide breeding habitat for terns. Our findings also indicate that availability of nesting substrate is very important to wetland selection by terns. In drier climates where cattail growth is not checked by periodic flooding, cattail management has been shown to increase nest sites and benefit terns (Linz et al. 1994, Linz and Blixt 1997). Furthermore, the options for managing cattails are numerous, and include herbicide application, cattle grazing, and fostering muskrat populations (Sojda and Solberg 1993), although the precise benefit of the latter two have not been studied for Black Terns. In flooded wetlands where little natural nesting substrate is available, artificial nesting platforms can benefit terns (Shealer et al. 2006). As wetland loss is likely to continue, especially of smaller wetlands in crop-growing areas, it may be possible to compensate for loss of these habitats by creating and managing for nesting substrate elsewhere.

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Table 1.1. Frequencies of categorical predictor variables. These are shown for surveys conducted in the Prairie Pothole Region where Black Terns were absent, breeding, or foraging, 2008-09.

	Frequency			
Wetland Variable	Wetlands Surveyed (n = 589)	Absent (n = 471)	Breeding (n = 32)	Foraging (n = 93)
Type:				
I	0.22	0.27	0.03	0.01
II	0.42	0.39	0.84	0.42
III	0.17	0.15	0.13	0.30
IV	0.19	0.19	0.0	0.27
Regime:				
Temporary	0.05	0.06	0.0	0.01
Seasonal	0.36	0.42	0.16	0.14
Semipermanent	0.56	0.50	0.81	0.82
Lake	0.02	0.02	0.03	0.03

Table 1.2. Means (± SD) for continuous predictor variables. Variables are grouped into wetland habitat, edge cover, and landscape composition variables, and shown for surveys conducted in the Prairie Pothole Region 2008-09 where Black Terns were absent, breeding, or foraging. Wetland habitat and edge cover variables were measured in the field; landscape composition variables were measured using a GIS landcover layer. Units are percentages for all variables except Wetland Size.

	All Wetlands (*n* = 589)		Absent (*n* = 471)		Breeding (*n* = 32)		Foraging (*n* = 93)	
Variable	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Wetland Habitat								
Wetland Size (ha)	22.0 ± 45.5	0.01-504	13.3 ± 29.3	0.01-231.4	68.6 ± 69.4	1.6-234.6	54.2 ± 76.1	1.6-504
Open Water	46.4 ± 37.4	0-100	43.2 ± 38.2	0-100	43.3 ± 26.9	4-90	62.5 ± 31.9	0-99
Emergent Vegetation	35.4 ± 35.1	0-100	36.6 ± 36.8	0-100	45.7 ± 27.2	5-96	26.9 ± 26.4	0-96
Wet Meadow	14.9 ± 26.7	0-100	16.9 ± 28.7	0-100	7.2 ± 16.3	0-78	7.1 ± 13.8	0-58
Floating Mat	0.6 ± 1.5	0-18	0.3 ± 0.9	0-10	2.7 ± 2.4	0-10	1.3 ± 2.5	0-18
Edge Cover (within 10-m of wetland)								
Crop	22.9 ± 34.9	0-100	24.3 ± 36.3	0-100	13.0 ± 24.6	0-93	18.7 ± 30.0	0-100
Grass	71.5 ± 34.9	0-100	70.1 ± 36.1	0-100	81.1 ± 28.6	0-100	75.3 ± 30.5	0-100
Tree/Shrub	2.7 ± 7.1	0-70	2.5 ± 6.8	0-70	1.5 ± 2.1	0-8	3.8 ± 9.1	0-70
Other	1.7 ± 5.7	0-54	1.9 ± 6.1	0-54	1.1 ± 3.6	0-20	0.7 ± 1.7	0-9
Landscape Composition (landcover within 2000-m)								
Planted	12.8 ± 11.6	0-57	12.4 ± 11.0	0-51	13.5 ± 13.6	1-53	14.2 ± 14.0	0-57
Prairie	21.1 ± 18.0	0-86	22.3 ± 18.6	0-86	19.5 ± 17.8	1-55	15.5 ± 13.6	1-69
Crop	50.4 ± 24.2	0-96	50.2 ± 25.0	0-96	47.0 ±18.8	10-78	52.5 ± 21.9	6-91
Seasonal Wetland	3.5 ± 2.7	0-19	3.3 ± 2.6	0-19	4.8 ± 3.3	0-12	4.1 ± 3.2	0-17
Semiperm. Wetland	5.1 ± 4.8	0-38	4.6 ± 4.4	0-35	7.8 ± 6.0	0-23	7.0 ± 6.0	0-38
Lake	2.1 ± 5.6	0-57	2.1 ± 5.8	0-57	2.0 ± 5.0	0-20	1.9 ± 4.4	0-20
Total Wetland	13.7 ± 8.5	0-63	12.9 ± 8.7	0-63	17.2 ± 5.7	9-30	16.1 ± 7.7	3-46

Table 1.3. Model assessment using area under the curve (AUC) values. AUC values are shown for combined and subset models predicting occurrence of breeding and foraging Black Terns in the Prairie Pothole Region, 2008-09. Model accuracies were assessed using predictions to out-of-bag data. AUC critical value = 0.70.

Model	Breeding	Foraging
Combined[a]	0.92	0.88
Wetland subset[b]	0.87	0.85
Edge subset[c]	0.60	0.56
Landscape subset[d]	0.64	0.71
Landscape & Edge[e]	0.67	0.73
Geography subset[f]	0.55	0.65

[a] Combined: Wetland, Landscape, Edge, and Geography subsets.

[b] Wetland subset: emergent vegetation, floating mat, open water, wet meadow, type, regime, wetland size.

[c] Edge subset: grass, crop, tree/shrub, other

[d] Landscape subset: prairie, planted, crop, seasonal, semipermanent, lake, total wetland

[e] Landscape & Edge: Landscape and Edge subsets

[f] Geography subset: Latitude, Longitude

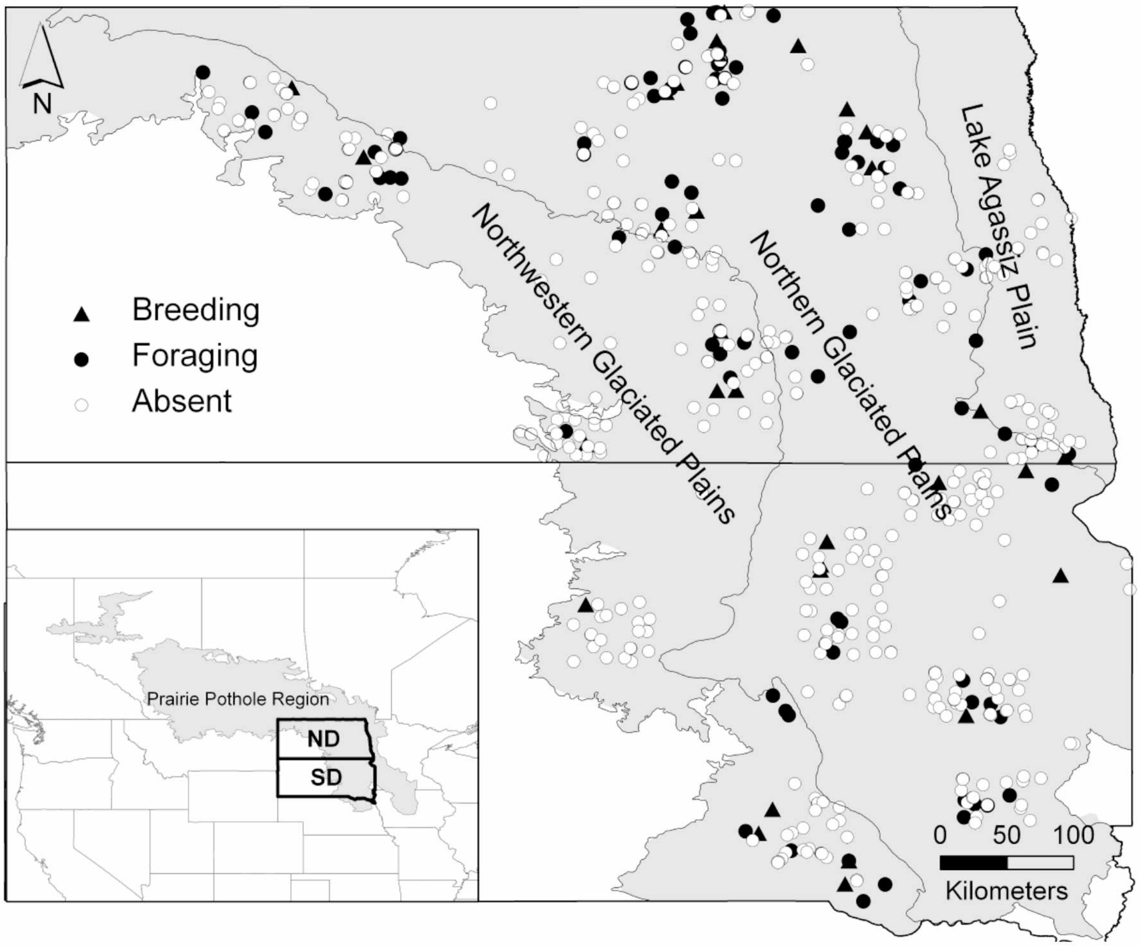

Figure 1.1. Map of Black Tern survey results. Symbols show locations of 589 wetlands across three level III ecoregions in the Prairie Pothole Region of North and South Dakota that were surveyed in 2008-09 where terns were breeding, foraging, or absent. Wetlands where terns were breeding and foraging are shown as breeding wetlands. Inset shows the location of the PPR with the area shown by the map outlined in black.

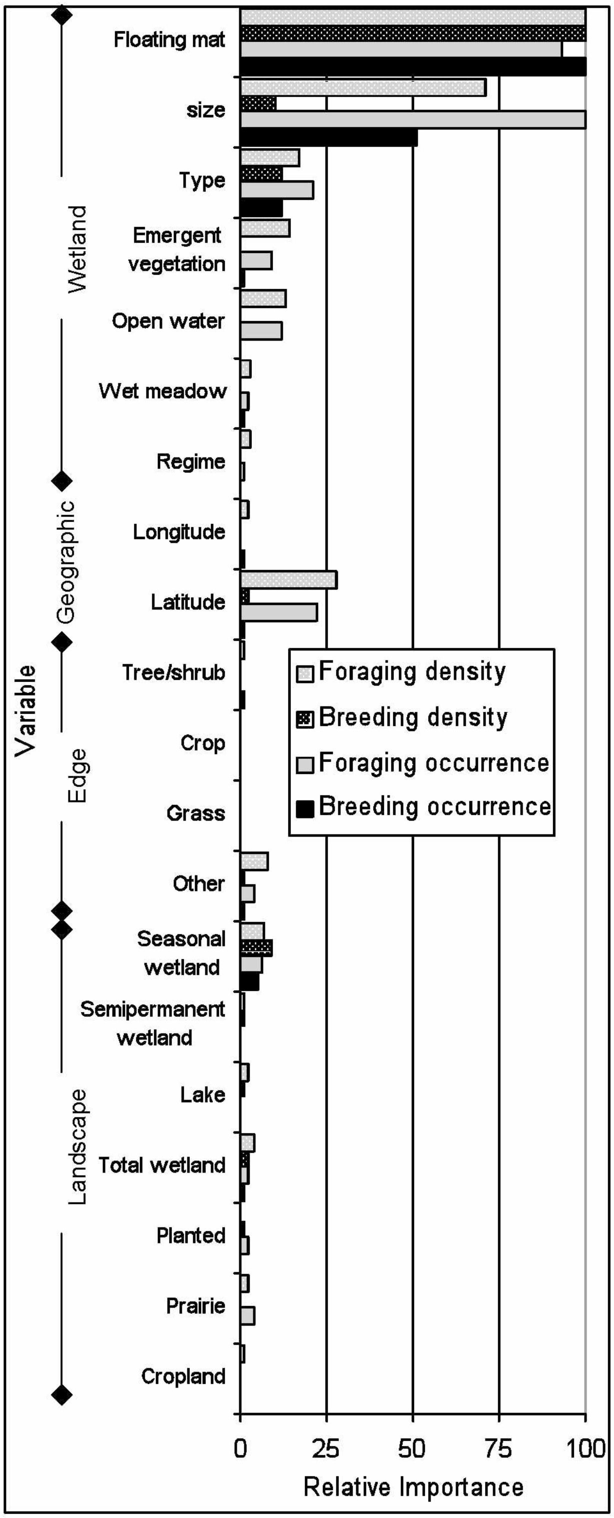

Figure 1.2. Relative importance of variables. This is shown for four models predicting selection of wetlands by Black Terns in the Prairie Pothole Region: foraging density, breeding density, foraging occurrence, and breeding occurrence.

CHAPTER 2

Potential Effects of Climate Change on the Distribution of Waterbirds in the Prairie Pothole Region, U.S.A.[2]

Abstract.-Freshwater wetlands and wetland-dependent birds are considered at particularly high risk for negative climate change effects. We predicted current and future distributions of five waterbird species common in the Prairie Pothole Region (PPR) using bioclimatic species distribution models (SDMs). We created fine-scale SDMs for the U.S. PPR using breeding bird survey occurrence records for 1971-2000 and wetland and climate parameters. For each waterbird species we predicted current distribution and projected four potential future distributions: all combinations of two Global Circulation Models (GCMs; CGCM and MIROC) and two emissions scenarios (B1 and A2), and an ensemble projection that averaged these four. Averaged for all five species, range reduction for the ensemble projections was 64%. However, individual species projections varied widely with some species projected to be more severely impacted than others. Differences among projections of GCM/emissions scenarios for an individual species were small. We also projected future distribution to an artificial landscape where wetlands were numerous and constant to highlight areas suitable as conservation reserves under future climate scenarios. While one GCM/emissions scenario indicated that suitable habitat would shift eastward for some species, the ensemble model indicated that northern North Dakota and Minnesota would be the best area for conservation reserves within the U.S. PPR under these conditions.

INTRODUCTION

Modern global climate change (Karl and Trenberth 2003) is expected to contribute to anthropogenic stresses on ecological systems resulting in the further loss of populations, species, and general biodiversity. With a 0.74 °C increase in global mean surface temperature over the past century (1906-2005; IPCC 2007), a response is

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[2] Steen, V. and A. Powell. 2010. Potential Effects of Climate Change on the Distribution of Waterbirds in the Prairie Pothole Region, U.S.A. Prepared for submission to *Waterbirds*

discernable across plant and animal species (Root et al. 2003). Global climate warming is projected to be between 1.1 and 6.4°C by 2100 (IPCC 2007), with significant consequences for global biodiversity predicted (Thomas et al. 2004). Much of our ability to mitigate against species losses will lie in our ability to anticipate the effects of climate change (Heller and Zavaleta 2009).

One major anticipated effect of climate change on avian species is distributional shifts. Birds may respond to climate change directly by tracking shifts in temperature or precipitation clines to stay within their physiological tolerances. They may also respond indirectly by tracking shifts in habitat features such as nesting locations, food, or other resources that shift in response to climate change (Wormworth 2006). Bioclimatic models are often used to project these shifts. These models are a form of species distribution model (SDM) that relate climate variables to current species distributions and then use projected climate variables from Global Circulation Models (GCMs) and emissions scenarios to predict future species distributions. This approach is considered simplistic because it does not account for dispersal capability, biotic interactions, or adaptation (Dormann 2007, Wiens et al. 2009). However, bioclimatic models can provide a useful first measure of approximated climate change effects and indicate where to direct more in depth research and conservation efforts (Pearson and Dawson 2003, Wiens et al. 2009).

Landcover correlates, when available, can increase the utility of bioclimatic models. While at broader spatial scales climate variables explain most of the variation in species occurrence patterns (Currie 1991), at finer spatial scales landcover variables also become important (Pearson et al. 2004, Luoto et al. 2007). Although climate usually forms the bounds of the broader fundamental niche of a species, many species are further restricted by habitat, which often forms the bounds of the realized niche. Thus, including landcover variables in bioclimatic models enables finer scale predictions at the regional scale, the scale at which management decisions are generally made.

Freshwater wetland habitats have suffered directly from anthropogenic land conversion activities and are also expected to be dramatically affected by climate change through changes in temperature and precipitation. Because these wetlands are considered to be at particularly high risk for negative climate change effects, wetland-dependent bird species are also at high risk (Wormworth 2006). In the PPR of the north-central U.S. and south-central Canada, numerous small wetlands provide some of the most critical wetland habitat for breeding and migrating wetland-associated birds (Batt et al. 1989, Beyersbergen et al. 2004). The hydrology of these typically shallow wetlands is especially susceptible to climate change effects. Periods of relatively low precipitation and warmer temperatures reduce the ratio of wet/dry periods for ephemeral wetlands, reduce the size and hydroperiod of wetlands, and affect the amount and spatial arrangement of emergent vegetation (Larson 1995, Poiani et al. 1995, Poiani et al. 1996). Climate projections based on GCM/emissions scenarios predict, on average, large increases in temperature and moderate increases in precipitation in the PPR, and overall, an increase in drought conditions (Ojima and Lackett 2002). Because waterbird numbers are related to the number of water-holding basins (Niemuth and Solberg 2003), we expect waterbird populations to decrease as wetland areas decrease. However, it is not simply the presence of wetlands that may affect bird use: wetland variables such as amount of emergent vegetation and wetland size are also related to habitat suitability for wetland birds (Brown and Dinsmore 1986, Poiani and Johnson 1991).

We use climate and wetland variables to create bioclimatic SDMs to project future distribution of five waterbird species in the U.S. portion of the PPR under future climate scenarios. Because climate interacts with wetlands to create complex habitat conditions, we use an advanced machine learning method (Random Forests), which has the ability to model unspecified interactions, to create our SDMs. While 39 waterbird species breed in the PPR, five waterbird species and one colonial waterbird species (Franklin's Gull; *Leucophaeus pipixcan*) breed primarily in the PPR. We selected the five species to look how climate change might impact waterbirds in the PPR: American Bittern (*Botaurus lentiginosus*), American Coot (*Fulica americana*), Black Tern (*Chlidonias niger*), Pied-billed Grebe (*Podilymbus podiceps*), and Sora (*Porzana carolina*). Our specific objectives were to (1) illustrate with maps and index (shift in center of range, range reduction, and change in relative index of occurrence) the change between predicted current distribution and projected future distributions under GCM/emissions scenarios; and (2) assess the value of wetland conservation reserves under GCM/emissions scenarios and a landscape with high, uniform wetland density. These assessments can provide resource managers an indication of the relative potential severity of climate change impacts in the U.S. PPR on different waterbird species and help inform future research on strategies to mitigate against negative climate change effects.

METHODS

STUDY AREA

The study area was the PPR within four states, North Dakota, South Dakota, Minnesota, and Iowa, an area of approximately 320,000 km^2 (Fig. 2.1). The study was restricted to these four states because consistent landcover and downscaled climate data were available. Water-filled glacial depressions termed *potholes* are the characteristic small prairie wetlands that pock-mark this region and reach densities greater than 40 per km^2 in some areas (Kantrud et al. 1989). Since European settlement, these wetlands have been converted to cropland with wetland losses greatest in the eastern portion of the PPR. Concordantly, the PPR in Minnesota and Iowa have experienced the greatest wetland losses, 85% and 95% respectively, while North and South Dakota have retained many more wetlands, with losses of 49% and 35% respectively (Dahl 1990, Johnson et al. 2008). Losses of surrounding prairie habitats have been even greater than wetland losses (Beyersbergen et al. 2004).

SPECIES OCCURRENCE

We obtained species occurrence (presence/absence) data from the North American Breeding Bird Survey (BBS; Sauer 2007) for the five focal species. The BBS consists of >3000 routes located on secondary roads throughout the continental U.S. and southern Canada. Routes are surveyed once annually during June between 0500 and 1000. Route locations remain the same year after year, although some routes may not be surveyed in a given year. Each route is 39.4 km long and includes five ten-stop sections, with all stops spaced 0.8 km apart. Three-minute point-count surveys are conducted at each stop.

We used data from high-quality surveys (reported by the BBS as "run type 1") for the years 1971-2000 for the 87 routes in our study area. We chose not to use route-level survey totals because of the potential loss of information when aggregating to a broader scale. We instead used one 10-stop section total for each route. We used the first section for species whose detection rate was significantly higher in this section. This was true for all species except Black Terns. For Black Terns we used the middle section (third section). To reduce the influence of temporal autocorrelation we included, at most (some routes were not surveyed consecutive years), every second year of surveys of a given BBS route. The number of years of survey results included for a given route ranged from two to 15. The number of survey routes included for a given year ranged from 14 to 31.

WETLAND DATA

We obtained wetland variables for North and South Dakota from a GIS raster layer created by the U.S. Fish and Wildlife Service (USFWS; USFWS, Region 6 Habitat and Population Evaluation Team, unpublished data), and for Minnesota and Iowa from a GIS polygon layer created by the USFWS (USFWS, Region 3 Habitat and Population Evaluation Team, unpublished data). Both layers contained wetland basins reclassified from contiguous wetland polygons by the USFWS National Wetlands Inventory (NWI) layer to single wetland basins. They followed the procedures of Cowardin et al. (1995) and Johnson and Higgins (1997) to describe each wetland basin by its most permanent water regime: temporary, seasonal, semipermanent, lake, and river. NWI data is based on aerial photographs taken in the late 1970's and early 1980's. For descriptions of the wetland regimes see Cowardin et al. (1979).

We used ArcMap 9.2 with the extension Hawth's Tools (Beyer 2004) to calculate wetland composition in a 2-km radius buffer around each 10-stop survey segment. We calculated seven wetland variables (Table 2.1) that represented composition in the landscape. Total wetland was the combined composition of temporary, seasonal, semipermanent, lake, and river; total ephemeral wetland was temporary, seasonal, and semipermanent.

CLIMATE DATA

We obtained historic and projected monthly temperature and precipitation data from the USDA Forest Service (Coulson et al. 2009, Coulson and Joyce 2010). Using these we calculated 20 climate variables (Table 2.1). We delineated seasons as summer (June-August), fall (September-November), winter (December-February), and spring (March-May). We calculated mean temperatures by averaging the minimum and maximum monthly temperatures over the given time period. We included seasonal and annual variables because seasonal and annual climate have been shown to be important in explaining variation in the number of PPR wetlands holding water (Larson 1995). Current year's wet wetland count is also related to the previous year's count (Larson 1995) and this is related to longer term climate so we included five-year and ten-year variables as proxies. We also included the variances in five-year and ten-year precipitation and temperature, and five-year and ten-year temperature ranges, because larger values of these variables may indicate that wetlands are cycling through wet and dry phases, an important factor in creating dynamic vegetative conditions (Johnson et al. 2010). Climate data from 1971-2000 were used to construct the SDMs and data from 1981-2000 and 2081-2100 were used to create current and future predictions, respectively, using the SDMs.

Projected climate data were obtained from output from two GCMs: CGCM3.1MR (Canadian Centre for Climate Modeling and Analysis Third Generation Coupled Global Climate Model Version 3.1, Medium Resolution) and MIROC3.2MR (Japanese Centre for Climate System Research, University of Tokyo; National Institute for Environmental Studies and Frontier Research Center for Global Change Model for Interdisciplinary Research on Climate Version 3.2 Medium Resolution) each forced with two IPCC emissions scenarios (Nakicenovic et al. 2000), A2 and B1. The two GCMs represent the two extremes of high and low projections. MIROC tends to project more extreme changes than other GCMs, while CGCM tends to project less extreme changes. The A2 and B1 emissions scenarios represent mid-high and low range emissions scenarios, respectively. For our study area and time periods, MIROC predicts a 6.6°C and 3.9°C increase in mean temperature and an 8.6 mm and 4.9 mm decrease (18% and 10% respectively) in monthly precipitation under scenarios A2 and B1, respectively. The CGCM predicts a 5°C and 2.7°C increase in mean temperature and a 3.6 mm and 1.1 mm increase (7% and a 2%, respectively) in monthly precipitation under scenarios A2 and B1, respectively.

Historical climate data were developed using PRISM (PRISM, Parameter-elevation Regressions on Independent Slopes Model) data. Projected climate data were developed using change factors from the GCMs and the historical climate data. Following the methods of Price et al. 2004, monthly change factors for minimum temperature, maximum temperature, and precipitation were computed and downscaled to the five arc minute grid level (grid points spaced 8-km apart across the study area for a total of 4957 points) using an interpolation technique. Finally, the change factors were imposed on 30-year baseline climatology (1961-1990; PRISM) to correct for bias in the GCM projections. PRISM data at the 2.5 arc minute scale were aggregated to the 5 arc minute grid scale to produce the historical data.

SPECIES DISTRIBUTION MODELS

We constructed an SDM for each of the five waterbird species by relating 742 BBS species occurrence records (772 for Black Tern) to current climate data for 1971-2000 from the 8-km climate grid points nearest the BBS routes and wetland predictor variables from within a 2-km buffer of the 10-stop route segment. We used a non-parametric machine learning approach, Random Forests, because of its high predictive ability, ability to model unspecified interactions, and demonstrated use for bioclimatic SDMs (Lawler et al. 2006, Prasad et al. 2006). Random Forests uses an ensemble of classification and regression trees, each built with a subset of the data, to model the pattern between predictor variables and the response variable. We used permutation importance to assess variable importance. This is based on the reduction in predictive accuracy to internally withheld data when values of a given variable are randomly permuted. We report the top ten variables for each model. Although the choice of the number of variables to report is arbitrary, we expect it to provide an adequate basis for comparing models.

We used the RandomForests package in R 2.9.2 to create our models (Breiman 2001). We specified 3000 trees. Each tree was constructed with a bootstrapped subsample of two-thirds of the data rows and a subsample of six predictor variables tried at each split. We maintained equal sample sizes for presence/absence by selecting 25 10-stop route segments for each year where the species was present and another 25 10-stop route segments where the species was absent. We built the models with all of the data points but assessed performance of the classification models' predictions to a 30% withheld split. We report confusion matrix values and the area under the receiver operating characteristic curve (AUC). From the confusion matrix, we report the counts of true positives, false positives, true negatives, false negatives and overall classification accuracy based on a 0.5 threshold for determining presence. Overall classification accuracy is calculated by dividing the number of correctly predicted presences and absences by total predictions. AUC is a threshold free assessment of model performance. AUC values range from zero to one and give the probability that, for a randomly selected pair of presence-absence observations, a presence observation has a higher value than an absence observation. AUC values of at least 0.7 are considered acceptable, between 0.8 and 0.9 are considered good, and greater than 0.9 are considered outstanding (Hosmer and Lemeshow 2000).

PROJECTED DISTRIBUTIONAL CHANGES

We created current predictions and future projections of the relative index of occurrence for each of the five species by applying the SDMs to the current wetland and climate data (the 20-year period for current climate data being 1981-2000), and to current wetland and future climate data (the 20-year period 2081-2100). Twenty-year time periods were chosen to mitigate the influence of smaller scale variations in climate. A 100-year period between current and future time periods was used to allow fuller divergence among GCM/emissions scenarios and current conditions. We also created an ensemble future relative index of occurrence for each species by averaging the relative index of occurrence for the four GCM/emissions scenarios.

We created current and future predictive distribution maps for each species in ArcMap 9.2 based on determination of grid point locations as suitable or unsuitable. A grid points was determined suitable if the average index of occurrence (over the 20-year time period for the data) was greater than 0.5. A threshold of 0.5 was used because we set sample sizes of presence/absence points to be equally subsampled in the Random Forests model, so the expected number of occurrences was 0.5 (see Liu et al. 2005). We used inverse distance weighting interpolation (IDW) with a search radius of 12 points and a power of 2 to create a smoothed surface from the grid of predictions. We also created an ensemble future predictive map for each species by averaging the predictions (relative index of occurrence) for each species for the four GCM/emissions scenarios.

We index changes between predicted current and projected future distributions using three measures: i) shifts in geographic center of distribution, ii) change in distribution, and iii) change in relative index of occurrence (following methods similar to Virkkala et al. 2008). To calculate shifts in geographic center of distribution we measured the distance between the centroids of predicted suitable locations for the current and future distributions. To calculate change in distribution, we calculated the percent loss in the number of suitable grid points. Finally we calculated change in the relative index of occurrence we subtracted the current relative index of occurrence from future relative index of occurrence for each grid point location and then averaged the results over all grid points.

ARTIFICIAL WETLAND RESTORATION

We created current and future species occurrence and distribution projections for a restored landscape where wetlands were numerous, in order to evaluate the potential benefits of wetland restoration. These current and future projections used the same climate data as above, but used artificial wetland data that were based on current wetland conditions that could support all five species (i.e. high species richness). To determine the composition of this artificially restored wetland landscape, we selected each location where all five species were predicted to be present in the current species SDMs and imported these locations into a GIS. We then chose a spatially-balanced random subset of 21 locations from which we calculated the average composition of each wetland variable within a 2-km buffer of each location. The resulting compositions (as % of landscape) were: temporary (1.9%), seasonal (3.7%), semipermanent (5.5%), lake (5.5%), river (0.1%), total ephemeral (11.1%) and total wetland (15.6%). These wetland compositions were used as the wetland data for all grid points in all years. We created current and future species occurrence and distribution projections as otherwise described above in section "Current Predictions and Future Projections of Species Occurrence and Distribution."

RESULTS

SPECIES DISTRIBUTION MODELS

Performance. SDM performance was good to outstanding as assessed by how well models predicted species presence/absence to a withheld test set using AUCs (Table 2.2). Overall accuracies were also good although the rank order was not always consistent with the AUC value for a given species (Table 2.2).

Important Variables. Although wetland variables represented only 26% of the variables used in the Random Forests model, they represented 56% of the top-ten most important variables for the five SDMs (Table 2.3). Each wetland variable was included in at least two SDMs' top-ten variables. Of the climate variables (Table 2.3), temperature variables represented a disproportionately large, and precipitation a disproportionately small, proportion of the top-ten most important variables. Among climate variables, summer temperature, five-year average temperature, and ten-year precipitation were included in four SDMs' top-ten ranks.

PROJECTED DISTRIBUTIONAL CHANGES

The SDMs predicted that all five waterbird species will become less common in the U.S. PPR by the end of this century as a result of climate change. Two indices of change, range reduction and change in relative index of occurrence, suggested future declines of all five species in all four GCM/emissions scenarios (Table 2.4). Overall average projected distribution change was -64%, and overall average change in relative index of occurrence was -0.12. The models projected that Sora and Black Tern will be most severely affected, followed by Pied-billed Grebe and American Coot; American Bittern will be least affected (Table 2.4). Black Tern and Sora also showed relatively large projected distributional shifts (Table 2.4), while distributional shifts for the other species were negligible.

Although the four GCM/emissions scenarios represented a wide range of future climate conditions, the indexed changes in projected waterbird distributions indicated only small differences by severity of future climate change (Table 2.4). Furthermore, the relative severity of those projected changes was sometimes counterintuitive (Table 2.4). The SDMs for future climate conditions indicated that Black Tern and American Bittern may experience smaller reductions under the mildest GCM/emissions scenario, CGCM B1 (Table 2.4). However, the models predicted that Pied-billed Grebe and American Coot may experience smaller reductions under the worst GCM/emissions scenario, MIROC A2 (Table 2.4).

Ensemble projections suggest that areas of suitable habitat for these five species in the U.S. PPR may be reduced by approximately 30% to almost 100% and that currently unsuitable areas will not become suitable by the end of this century (Fig. 2.2). Areas of suitable habitat for American Bittern, American Coot, and Pied-billed Grebe will still exist, but will be reduced in availability within currently suitable areas. For Black Tern, only very small areas of suitable habitat are projected to exist in north-central and north-eastern North Dakota. Almost no suitable habitat is projected to exist for Sora, except very small areas in north-central and north-eastern North Dakota.

WHERE TO RESTORE WETLANDS IN ANTICIPATION OF CLIMATE CHANGE

Predictive distributions under wetland restoration conditions, where wetlands are numerous across the landscape, indicate that under current climate conditions, there is a northward gradient of higher relative index of occurrence for all five species (Fig. 2.3). This gradient is steepest for Black Tern and Sora with relative index of occurrence increasing by about 0.4 from southern Iowa to northern North Dakota and northern

Minnesota. Under future climate conditions the ensemble results indicate this gradient shifts north or northeastward with the highest relative index of occurrence for all five species still in northern North Dakota and Minnesota. However, the most severe GCM/emissions scenario, MIROC A2, indicates a more eastward shift for American Bittern, Black Tern, and Pied-billed Grebe.

DISCUSSION

PROJECTED DISTRIBUTIONAL CHANGES

Our SDMs and the GCM/emissions scenarios we used predicted that within the U.S. PPR, by the end of the century suitable habitat will be reduced for five of the most common waterbird species in the PPR, with negative effects disproportionately impacting some species. Differences in projections among different future climate projections (GCM/emissions scenarios) were small. Our predicted reductions of suitable habitats are similar, at least qualitatively, to previous studies of the impacts of climate change on the ecologically similar waterfowl in the PPR. For example, Larson (1995) extrapolated from a model relating current climate (precipitation and temperature variables) to future wetland density, and suggested that suitable habitat for waterfowl would be reduced under those conditions. Poiani and Johnson (1991) used a process-based wetland vegetation cover-cycle simulation model and concluded that habitat conditions for waterfowl would diminish. Sorenson et al. (1998) extrapolated from a model relating a drought index (Palmer Drought Severity Index) and wetland number to estimate waterfowl populations under a number of future climate change projections for the North-central U.S. For precipitation and temperature projections similar to our ensemble (+4.6°C and -5% precipitation) they predicted that waterfowl populations would fall to zero, while we estimated a 64% range reduction for waterbird populations.

For a given species we found only small differences in projected occurrence rate and change in index of occurrence among the GCM/emissions scenarios we used, even though the scenarios represented a range in temperature increase (2.7 to 6.6°C) and change in precipitation (-8.6 mm to +3.6 mm). This may be because an asymptote was reached for these species in their response to climate change with the milder

GCM/emissions scenarios, and any additional change in climate variables had little additional effect. It may also be that the SDMs are doing a poor job of extrapolating outside the sampling space. It is likely that some of the temperature and precipitation values in the future climate projections are outside the range of variation used to create the SDMs. Random Forests holds the last known value constant when a data point is beyond the sampled data (Elith and Graham 2009). If all the GCM/emissions scenarios approach or exceed the limits of the current data, then all four future scenarios would be expected to produce similar results.

Our model predictions suggested that Black Tern and Sora would be more affected by climate change than the other three species we considered. Suitable wetland habitat for Black Terns and Sora may be more climate-dependent than for the other species; there were more climate variables in the top-ten variables for these two species (Table 2.3). Thus we would expect Black Tern and Sora would be more affected by climate change. Two aspects of the analysis methodology may also have contributed to this finding. It is possible that the poorest performing models (Black Tern and Sora) predicted the greatest change as an artifact of model performance. Virkkala et al. (2008) suggested this as a possible explanation for differences in predicted changes among species. However, they suggested it was an unlikely explanation for their results because this pattern did not apply to their results. It does not consistently apply to our results either. Although the AUC-based assessment displays this pattern, the overall accuracy-based assessment does not. Furthermore, differences among model performances were fairly small.

Another possibility for these results is that differential species detectability caused biases in occurrence records that were incorporated into the SDMs. The BBS was designed for surveying passerines and is thought to do a poorer job of censusing waterbirds for a number of reasons (Johnson et al. 2009). Waterbirds are generally in wetlands while the survey is conducted from land. Furthermore, some waterbirds are inconspicuous and vocalize infrequently. If waterbirds are simply underestimated, our models probably underestimated current distribution and future distribution. The relative difference would likely remain the same and this would have little effect on our indices of change. However, if there is some systematic bias related to the predictor variables, predicted occurrences would carry this bias. This may have little effect on the change indices, or could cause them to be skewed positive or negative. In general, Sora and American Bittern are the most inconspicuous of the five species we looked at. As Sora was a species with relatively large and American Bittern a species with relatively small projected changes, there does not seem to be a systematic bias in regards to projected change with species detectability.

WHERE TO RESTORE WETLANDS IN ANTICIPATION OF CLIMATE CHANGE

Our projections of future distribution across a restored wetland landscape suggest that the northern-most portions of the study area (northern North Dakota and Minnesota) are generally the best locations to protect and restore wetlands for all five waterbird species under the future climate change scenarios we examined. A northward shift is consistent with expectations, findings, and projections of poleward range shifts for species of many taxa including birds (Peters and Darling 1985, Peterson 2003, Huntley et al. 2006, Parmesan 2006).

In contrast to our projections of a northward shift, Johnson et al. (2005, 2010) extrapolated from process-based models of wetland dynamics to conclude that under three projected climate change scenarios, the best wetland conditions for waterfowl in the PPR will shift eastward. They predicted that in a drier climate, wetlands with the best conditions for waterfowl will shift from the Dakotas to Minnesota and Iowa, areas that historically received too much rain to generate the dynamic wet-drying that produce wetlands with suitable vegetative conditions. They applied three uniform climate shifts (+2°C, +4°C, and +4°C and +10% precipitation for the 2010 study). These shifts covered a milder range (with overlap) of changes than the four GCM/emissions scenarios we examined. However, the drier scenarios may have played a larger role in their results. The driest scenario (MIROC A2) from our results projected a more easterly shift for three of the species we considered (Fig. 2.3), and was more in line with Johnson et al. (2005, 2010).

Broadening the SDM approach may offer insight into the range of possible outcomes for wetland-associated birds in the PPR. A number of papers have acknowledged and reviewed the methodological sources of variability in predictions among various SDMs (Diniz et al. 2009, Buisson et al. 2010, Mbogga et al. 2010). The consensus so far is that modeling method is the largest source of variance, followed by choice of GCM; the interaction between the two also seems to be important. We used one modeling method, Random Forests, to model predicted distributions of five species, according to climate projections from four GCM/emissions scenarios, across a portion of the PPR. A more comprehensive modeling effort using additional GCMs, greater geographical coverage, alternative analysis methods, and additional species including waterfowl would be useful for comparing to process-based projections.

To date, the most important and pressing issue for conservation of avian species in the PPR has been widespread habitat destruction, primarily a result of conversion of wetland and grassland to cropland. Climate change projections indicate a drier climate for this region, which has strong implications for the labile pothole wetlands and avian species that rely on them. Although bioclimatic SDMs have numerous uncertainties, they provide an effective way of looking into the future for the sake of conservation and resource management (Wiens et al. 2009). Our study provides a regional assessment of potential climate change impacts on waterbirds given current landcover, and of the value of protecting and restoring wetlands, by spatial location, under climate change scenarios.

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Table 2.1. Twenty seven climate and landcover variables used in species distribution models. Temperature calculations were based on the average monthly minimum and maximum. Precipitation calculations were based on monthly totals. Wetland landcover is based on percent composition in the landscape of wetland regimes. Total ephemeral wetland includes temporary, seasonal, and semipermanent wetlands. Total wetland includes the ephemeral regimes and lake and river.

Climate		Landcover
Temperature	Precipitation	Wetland
Yearly	Yearly	Temporary
Winter	Winter	Seasonal
Summer	Summer	Semipermanent
Spring	Spring	Lake
Fall	Fall	River
5-year	5-year	Total ephemeral
10-year	10-year	Total wetland
5-year variance	5-year variance	
10-year variance	10-year variance	
5-year range		
10-year range		

Table 2.2. Assessments of species distribution models. Confusion matrix and area under the curve (AUC) values are based on predictions to a 30% withheld dataset. Results of confusion matrix are given as counts of true positives, false positives, true negatives, and false negatives of presence and absence predictions (based on a 0.5 threshold). Overall accuracy equals the proportion of true positives and negatives. AUC critical value = 0.70.

Species	Classification Matrix					AUC
	True positive	False positive	True negative	False negative	Overall accuracy (%)	
American Coot	48	35	133	7	81	0.89
American Bittern	43	43	131	6	78	0.92
Black Tern	29	41	156	6	80	0.85
Pied-billed Grebe	37	32	146	8	82	0.88
Sora	41	36	129	17	76	0.84

Table 2.3. Variable importance for five bioclimatic species distribution models. Top ten variables are shown in descending order of rank. Variable categories are denoted by W (wetland), P (precipitation), and T (temperature).

Rank	Variables by species distribution model				
	American Bittern	American Coot	Black Tern	Pied-billed Grebe	Sora
1	W-total	W-total	W-ephemeral	W-total	W-total
2	W-semi.	W-semi.	W-total	W-semi.	P-10 yr.
3	W-ephemeral	W-ephemeral	W-seas.	W-ephemeral	T-10 yr. range
4	W-temp.	W-lake	W-temp.	W-lake	W-ephemeral
5	W-seas.	W-seas.	W-semi.	T-10 yr. var.	W-semi.
6	W-lake	W-river	P-5 yr.	W-seas.	T-10 yr. var.
7	P-10 yr.	P-10 yr.	P-10 yr.	T-10 yr. range	W-seas.
8	T-summer	T-spring	T-5 yr.	T- summer	T-5 yr.
9	T-yr.	T-5 yr.	T-10 yr.	W-river	T-summer
10	P-winter	W-temp.	T-summer	T-5 yr. ave.	T-10 yr.

Table 2.4. Species distribution change assessments. Projected shifts, range reduction, and change in relative index of occurrence are given for five waterbird species in the Prairie Pothole Region, U.S.A. Projections were made using bioclimatic species distribution models, four global circulation model (GCM)/emissions scenarios, and an ensemble average of the four. "Current" is based on 1981-2000 climate data; "future" is based on 2081-2100 climate data. Projections were made to 4957 8-km grid points (locations). Shift was calculated as the distance from the current geographic mean of suitable locations to the future ensemble geographic mean of suitable locations. Change in distribution was calculated as the percent loss in number of suitable locations from current to future. Change in relative index of occurrence was calculated by subtracting the current relative index of occurrence from the future relative index of occurrence for each location. "C" denotes GCM CGCM; "M" denotes GCM MIROC.

Species	Shift (km)	Change in distribution (%)					Change in relative index of occurrence				
	Ensemble	C B1	C A2	M B1	M A2	Ensemble	C B1	C A2	M B1	M A2	Ensemble
American Bittern	12	-23	-29	-27	-36	-29	-0.07	-0.09	-0.08	-0.10	-0.08
American Coot	11	-39	-38	-44	-37	-39	-0.12	-0.12	-0.11	-0.11	-0.11
Black Tern	170	-89	-98	-97	-100	-97	-0.12	-0.14	-0.12	-0.12	-0.13
Pied-billed Grebe	16	-58	-49	-61	-47	-54	-0.10	-0.08	-0.10	-0.08	-0.09
Sora	191	-99	-99	-98	-100	-99	-0.20	-0.19	-0.19	-0.18	-0.19

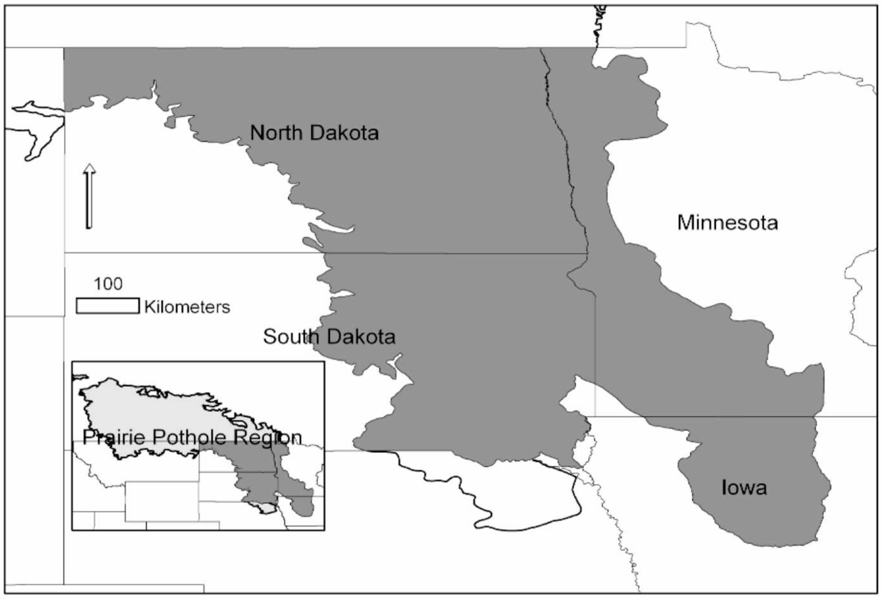

Figure 2.1. Map of the study area. Data for this study were derived from the PPR within North Dakota, South Dakota, Minnesota, and Iowa (the area shown in dark grey)

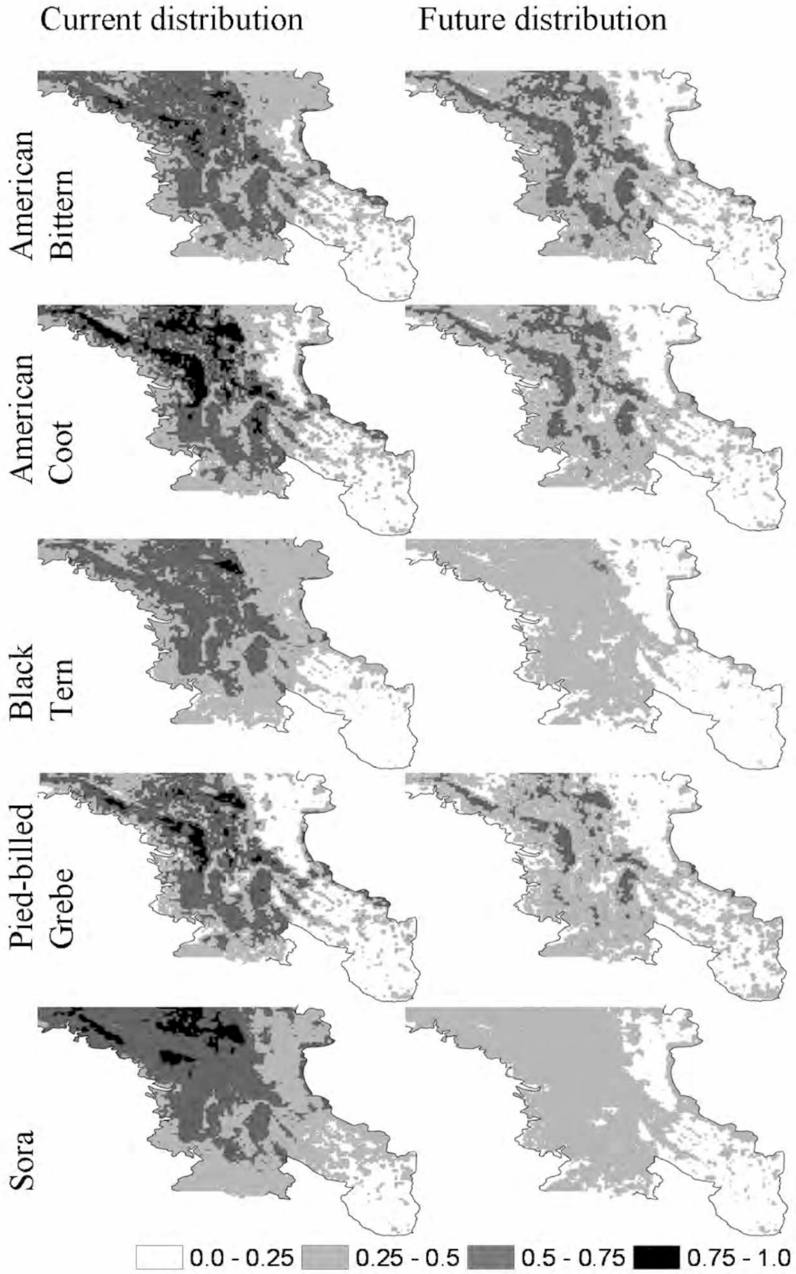

Figure 2.2. Predicted current and future distributions for five waterbird species. Current predictions were based on climate records for 1981-2000. Future projections were based on the ensemble average of four Global Circulation Model/emissions scenarios for 2081-2100. Maps show four levels of relative index of occurrence with darker colors indicating higher probability and lighter colors indicating lower probability.

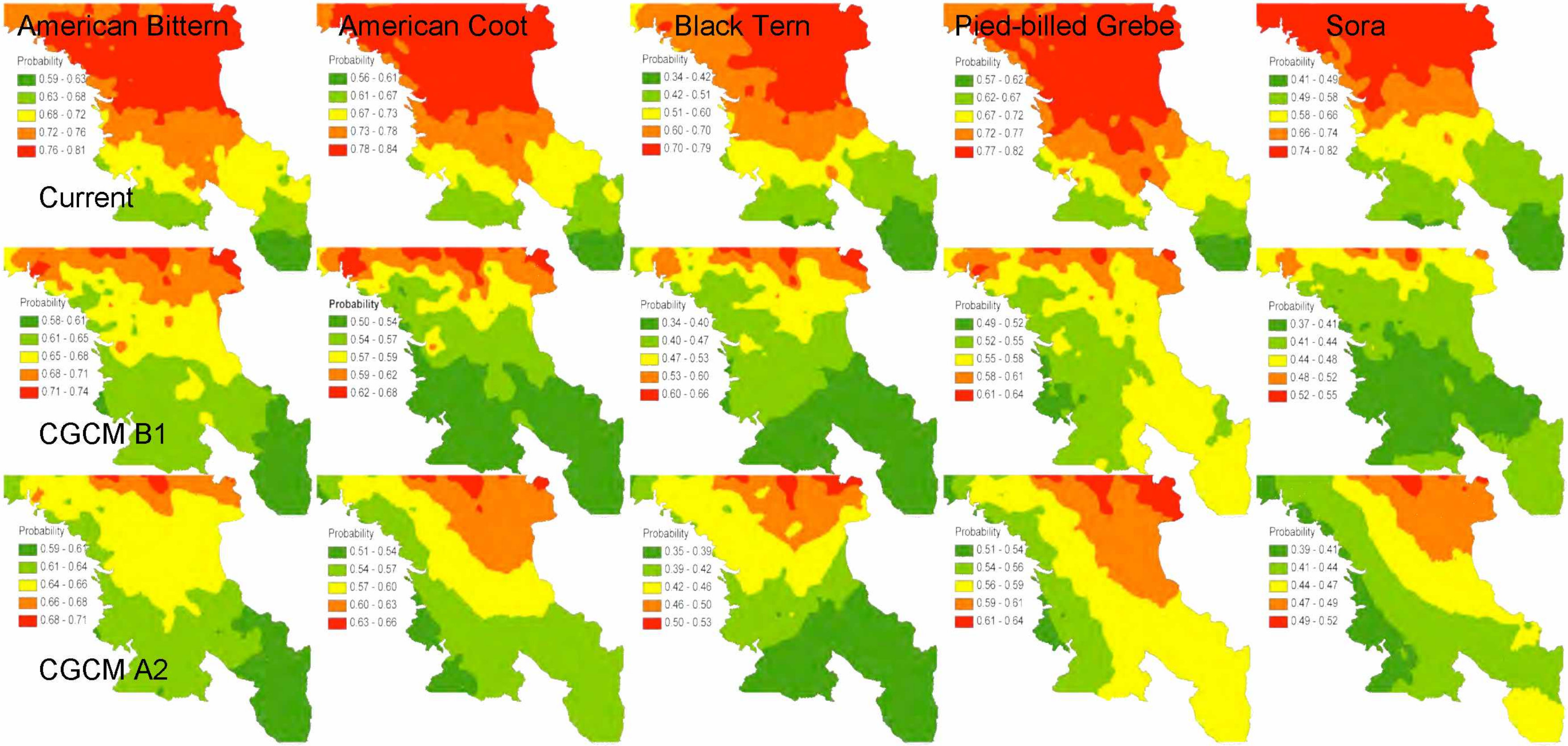

Figure 2.3. Predicted current and future distributions for five waterbird species with a “restored” landscape. The “restored” landscape consists of a uniform high-density of wetlands. Current predictions were based on climate records for 1981-2000. Future projected distributions are shown for 2081-2100 for four Global Circulation Model/emissions scenarios and an ensemble average of the four. Maps show five levels of relative index of occurrence. Note that the scale differs among the maps. Continued on next page.

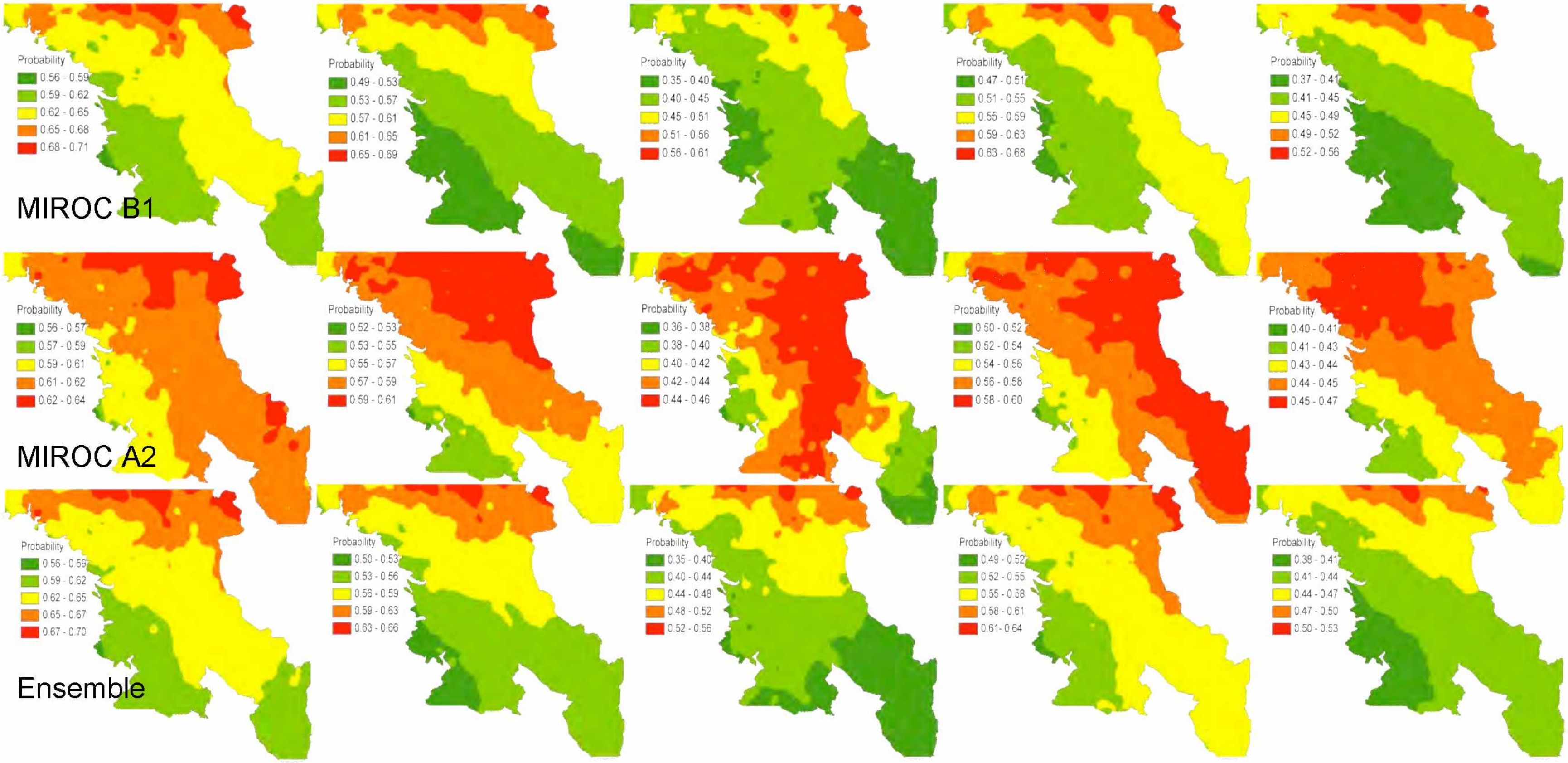

Fig. 2.3. Continued from previous page.

OVERALL CONCLUSION

This thesis addresses information needs for waterbirds that breed in the PPR of the U.S. Previous studies of habitat selection by Black Terns in the PPR concluded that the Black Tern is an area sensitive species, requiring large wetlands, and prefering high density wetland landscapes and wetlands surrounded grass rather than cropped lands (Brown and Dinsmore 1986, Naugle et al. 2000). However, these results could be confounded by problems associated with passive sampling (Johnson 2001) and by grouping breeding and foraging detections. I could not fully address the passive sampling problem but was able to use an index of density to ameliorate its effects. I modeled occurrence and density of both breeding and foraging terns, and I examined the relative role of local wetland and surrounding landscape characteristics in habitat selection.

Breeding terns appear less area sensitive than previously thought. The occurrence models showed wetland size was very important to selection of wetland habitat by both breeding and foraging terns. However, the density models, which at least partly address passive sampling, found wetland size was only moderately important to selection of breeding wetlands. The density model used a fourth-square root transformation of the original density data. This transformation substantially reduced a lot of the high values in the dataset; values that primarily corresponded to small wetlands. Thus, although the original values might overestimate densities (because a tern's home range encompasses an area beyond its wetland), especially for small wetlands, some passive sampling bias likely still remained. It is possible that if the passive sampling bias could be fully addressed, breeding selection would not be dependent on wetland size. Furthermore, this study documented breeding in smaller wetlands (four between 1.6 and 5.0 ha) than previously reported (5.3 ha; Heath et al. 2009).

This study provided the first empirical evidence for differential selection of wetlands by breeding and foraging terns in the PPR. The amount of floating matted vegetation (a nest substrate) in the wetland was more important to selection of breeding than foraging wetlands. Wetland size was a more important characteristic for determining where terns foraged than bred. Breeding terns selected wetlands with an interspersion of open water and emergent vegetation while foraging terns selected wetlands with a central expanse of open water; this is consistent with observations of microsite preferences for nesting amongst dispersed vegetation and foraging over open water, and with observations of terns commuting from nesting wetlands to foraging wetlands with more open water (Mosher 1986).

Local wetland characteristics were relatively more important than landscape characteristics in predicting wetland selection by Black Terns in the PPR. This is in contrast to previous studies which concluded that landscape characteristics very important (Brown and Dinsmore 1986, Naugle et al. 2000). The local wetland variable subset had most of the predictive power for breeding and foraging models. There was general concurrence with variable importance ranks for breeding and foraging models. The amount of floating matted vegetation, a local wetland variable and an often used nesting substrate, was a very important variable in all of the models. This could be an important source of the different findings as this variable was not included in the previous studies (Barry and Elith 2006).

Because of the relatively high importance of local characteristics and because Black Terns use small wetlands, populations may continue to decline even if only smaller wetlands in cropped landscapes are lost. Because the amount of floating matted vegetation is very important to terns, especially as a nesting substrate for breeding terns, it may be possible to compensate for habitat loss in some areas by managing for this habitat element elsewhere. In areas with dense emergent vegetation, cattail management has been shown to increase nest sites and benefit terns (Linz et al. 1994, Linz and Blixt 1997). In flooded wetlands where little natural nesting substrate is available, artificial nest platforms can benefit terns (Shealer et al. 2006).

In the second chapter, I used bioclimatic species distribution models (SDMs) for five waterbird species in the PPR to predict the potential impacts of climate change. The SDMs projected that within the U.S. PPR, suitable habitat will be reduced for five waterbird species common in the PPR and climate change may disproportionately affect some of these species. The SDMs suggested that Black Tern and Sora would be more affected by climate change than American Bittern, American Coot, or Pied-billed Grebe using three indices of change: shift in distribution (distance), change in distribution (area), and change in index of occurrence. I used four different GCM/emissions scenarios that represented a range of severity of projections. However, projections differed little between milder scenarios and more severe scenarios.

I also examined projections to an artificially created landscape with a high density of wetlands that approximated wetland restoration. The ensemble projections indicated that northern North Dakota and Minnesota would provide the highest climatic suitability for waterbirds in the U.S. portion of the PPR. These areas would be the best locations to conserve and restore in anticipation of future climate change. This study did not address the Canadian portion of the PPR. That is something that should be addressed in future studies as Canada may become even more important in the future to species that breed in the PPR.

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