Habitat associations and conservation of wetland-obligate birds

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Abstract

A basic understanding of species-specific habitat associations is a prerequisite for the effective management of at-risk species. Many wetland-dependent birds in the Upper Midwest are at-risk due to habitat loss and degradation. To investigate the habitat associations of wetland-dependent birds, I: 1) determine the relative importance of habitat heterogeneity vs. wetland area for biodiversity and species abundance, 2) develop species-specific models of habitat associations for eight declining obligate wetland bird species that use coastal wetland habitat in the Great Lakes basin, and 3) provide general habitat models for these species that are useful across multiple regions. The central hypothesis of this work is that populations of wetland-dependent birds are influenced by a combination of landscape and proximate habitat features, regionally specific hydrologic conditions, and anthropogenic stressors. Findings from the analysis of habitat heterogeneity indicated support for a tradeoff between area and habitat heterogeneity but highlight the importance of wetland area as the primary driver of variation in species richness and abundance. Species-specific combinations of habitat heterogeneity and other wetland characteristics provided additional explanatory power. Findings from hierarchical multi-scale occupancy models for coastal wetland birds in the Great Lakes basin indicated that the eight focal species are eurytopic, with little variation in occupancy despite differences in remotely sensed landscape characteristics, including anthropogenic disturbance. These species use a high proportion of the coastal wetlands in at least some years. Thus, wetland loss is problematic for these species and conservation planning should focus on protecting as many wetlands as possible. Finally, the regional comparison showed that these species have regionally specific habitat associations, but in most cases, associations estimated in one region can be informative when applied to other regions. In conclusion, habitat associations of wetland birds in the Upper Midwest are both species- and region-specific. Conservation of these species will depend primarily on protecting wetlands across a gradient of habitat characteristics at multiple scales and on reversing ongoing trends of wetland loss.

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Chapter 1: The relative importance of wetland area versus habitat heterogeneity for promoting species richness and abundance of wetland birds in the Prairie Pothole Region, USA

SYNOPSIS

Recent work has suggested that a trade-off exists between habitat area and habitat heterogeneity, with a moderate amount of heterogeneity supporting greatest species richness. Support for this unimodal relationship has been mixed and has differed among habitats and taxa. I examined the relationship between habitat heterogeneity and species richness after accounting for habitat area in glacially formed wetlands in the Prairie Pothole Region in North America at both local and landscape scales. I tested for area-habitat heterogeneity trade-offs in wetland bird species richness, the richness of groups of similar species, and in species' abundances. I then identified the habitat relationships for individual species and the relative importance of wetland area versus habitat heterogeneity and other wetland characteristics. I found that habitat area was the primary driver of species richness and abundance. Additional variation in richness and abundance could be explained by habitat heterogeneity or other wetland and landscape characteristics. Overall, avian species richness responded unimodally to habitat heterogeneity, suggesting an area-heterogeneity trade-off, whereas group richness and abundance metrics showed unimodal or linear relationships with habitat heterogeneity. Habitat heterogeneity indices at local and landscape scales were important for some species and avian groups, but not for all. Both abundance of individual species and species richness of most avian groups were higher on publicly owned wetlands than on privately owned wetlands, on restored wetlands than natural wetlands, and on permanent wetlands than on wetlands of other classes. However, I found that all wetlands examined, regardless of ownership, restoration status, and wetland class, support wetland obligate birds. Thus, protection of all wetland types could potentially contribute to species conservation. My results do support conventional wisdom that protection of large wetlands is a priority but also indicate that maintaining habitat heterogeneity will enhance biodiversity and support higher populations of individual species.

KEYWORDS

abundance; area-habitat heterogeneity trade off; biodiversity; habitat heterogeneity; Prairie Pothole Region; species-area relationship; species richness; wetland bird

INTRODUCTION

Biodiversity is an important element of ecosystem resilience, with ecosystems that have higher biodiversity being less susceptible to the negative impacts of environmental fluctuations (Wang & Loreau 2014; Oliver et al. 2015; Oehri et al. 2017). Similarly, larger populations tend to be more stable than smaller populations, all else being equal, and are better able to withstand environmental fluctuations (Soulé 1987; Traill et al. 2007). Because large areas of contiguous habitat are key to supporting biodiversity, the goals of many local and regional conservation efforts are to conserve and maintain blocks of contiguous habitat above some minimum threshold size (Soulé & Terborgh 1999; Mittermeier et al. 2003; Bakker 2005; Brice et al. 2017; Brown et al. 2019), often in the form of patches of native vegetation that retain elements of structural complexity and landscape connectivity (Fischer et al. 2006).

A large body of theory and empirical evidence—primarily founded in the theory of island biogeography—indicates that that species-area relationships are best modeled as convex upward curves (or sometimes sigmoidal curves), with more species present in larger areas (MacArthur & Wilson 1967; Connor & McCoy 1979; Tjørve 2003). Larger areas of habitat are also typically preferable for individual species because certain species display area-sensitivity (i.e. preferring large areas over small areas; Johnson & Igl 2001; Horn et al. 2007; Ribic et al. 2009), require large home ranges (Cardillo et al. 2005; Barton et al. 2015), or are habitat specialists (Dennis et al. 2013; Rösch et al. 2015).

The mixture of habitat types available at a site is also expected to influence diversity and abundance of species at that site. Specifically, species richness is expected to be greater where there is a considerable degree of habitat heterogeneity available to meet the various niche requirements of many different species. However, Allouche et al. (2012) postulated a negative quadratic relationship between species richness and habitat heterogeneity, reflective of a trade-off between area and habitat heterogeneity. The more diverse the habitat is, the smaller the area of any individual patch is likely to be, thus reducing the suitable area for individual species. Allouche et al. (2012) demonstrated such unimodal relationships using simulation, empirical data, and a meta-analysis of island datasets. Furthermore, an extensive body of literature has documented that such unimodal relationships exist for some plants (Redon et al. 2014; Yang et al. 2015), zooplankton (Schuler et al. 2017), invertebrates (Hernandez et al. 2006; Almada & Sarquis 2017), fish (Paxton et al. 2017), and birds (Rahbek 1997; Allouche et al. 2012; Chocron et al. 2015; Tuanmu & Jetz 2015).

However, the evidence for unimodal relationships is controversial (Carnicer et al. 2013; Hortal et al. 2013; Stein et al. 2014). Not all studies addressing the nature of habitat heterogeneity-species richness relationships have found evidence of unimodal relationships (e.g., Bar-Massada & Wood 2014; Stein et al. 2014; Lorenzón et al. 2016; Lee & Martin 2017). Furthermore, most of the studies that have found unimodal relationships for birds have examined avian communities generally across large regions (e.g., North American Breeding Bird Survey data as in Chocron et al. 2015 and Tuanmu & Jetz 2015), across multiple ecosystems (e.g., Bar-Massada & Wood 2014), and have used elevation (e.g., Allouche et al. 2012; Chocron et al. 2015) or land cover to define habitat heterogeneity (e.g., Chocron et al. 2015; Tuanmu & Jetz 2015; Lee & Martin 2017). Few studies have limited the scope to a single ecosystem type and quantified habitat heterogeneity at a local scale (e.g., within-ecosystem habitat heterogeneity). Thus, the relationship between habitat heterogeneity and species richness may be masked by confounding factors in some of these studies.

Allouche et al. (2012) also hypothesized that more heterogeneous habitats would have smaller average population sizes because of reduced effective habitat area. However, as with their predictions regarding species richness, support for Allouche et al.'s hypothesis regarding abundance has been mixed. While Allouche et al. found a significantly negative relationship between mean avian species abundances and elevation range as predicted, Bar-Massada and Wood (2014) found that a significantly negative relationship between mean avian species abundance and foliage height diversity lost its statistical significance when a factor for habitat type (grassland, savanna, or woodland) was added to the model. Bar-Massada and Wood's research also showed no relationship between cover diversity and mean species abundance. Lorenzón et al. (2016a) found that abundances of individual bird species most often showed positive or no relationships with the number of habitat types within a plot. To further complicate the issue, Paxton et al. (2017) actually found a unimodal relationship between abundances of individual fish species and habitat complexity. Thus, no universal relationship appears to exist between species abundances and habitat heterogeneity. Different taxa will need to be assessed individually for evidence of an area-habitat heterogeneity tradeoff if this information is to be useful for developing tailored conservation and management recommendations.

Herein, I identify the nature of diversity and abundance relationships with area and habitat heterogeneity for wetland bird communities in the Prairie Pothole Region of North America. Prairie pothole wetlands are an excellent system in which to test for such species-habitat relationships because they represent a fairly discrete habitat type with substantial variability in zonation patterns of vegetation (Stewart & Kantrud 1971) and birds (Weller & Spatcher 1965). I can quantify within-wetland (i.e. local) habitat heterogeneity as well as land cover heterogeneity within the surrounding landscape and thus can test for such relationships at two scales. This specificity will allow us to assess the relationships and apply them to regional wetland bird conservation efforts and wetland restoration efforts.

The importance of wetlands and the need to conserve them is supported by their ecological and economic values. In addition to providing key habitat for breeding and migrating birds, wetlands offer a variety of other ecosystem services including flood mitigation, improving water quality, nutrient cycling, and human recreation (Gopal & Junk 2000). Despite these important functions, wetlands are an imperiled ecosystem and wetland loss is an ongoing national, continental, and global issue (Gopal & Junk 2000; Ma et al. 2010; Dahl 2014; Davidson 2014). Wetlands are directly lost to human development and agricultural expansion, frequently accompanied by significant disruption of hydrologic regimes. In addition, they receive inputs from their watersheds, and thus bear the brunt of anthropogenic activities. For example, conversion of grassland habitat in the Prairie Pothole Region to agricultural production degrades adjacent wetlands through increased sediment and agricultural chemical inputs (Wright & Wimberly 2013).

Little research has been conducted on the habitat heterogeneity-species richness relationships in wetlands in general (Fairbairn & Dinsmore 2001; Gonzales-Gajardo et al. 2009; Lorenzón et al. 2016; see reviews in Tews et al. 2004; Stein et al. 2014), despite the fact that wetlands are a major source of biodiversity (Gopal & Junk 2000). For example, Igl and Johnson (1997) recognized 51 obligate wetland-breeding bird species in North Dakota. In addition to supporting high levels of biodiversity, wetlands are also highly productive ecosystems (Gopal & Junk 2000). The Prairie Pothole Region is considered the "Duck Factory" of North America (Wentz 1981; Thomas 1990; Ballard et al. 2014; McLean et al. 2016), and it is estimated that 50-80% of the North American waterfowl population is produced here (Batt et al. 1989), supporting a $3 billion (USD) waterfowl hunting industry (Carver 2015). Although conservation efforts in the Prairie Pothole Region are not aimed at biodiversity conservation, *per se*, 96% of the species that I include in my study are either mentioned in state and regional conservation planning documents or are expected to be negatively impacted by future climate conditions (Table 1). Furthermore, the primary aims of most planning documents (e.g., NAWMP 2018) are to support "abundant and resilient" populations of birds, regardless of their current population status. One of the necessary steps to promote such healthy populations is to identify those wetland features that best provide habitat for these species during the breeding season. Unsurprisingly, most conservation plans also set goals to protect and maintain appropriate habitat for their focal species. By understanding the nature of the relationship between habitat heterogeneity and species richness in this particular ecosystem type in this particular region, regionally specific conservation and management recommendations can be developed that help prioritize wetlands for protection and that take into account the relative importance of wetland area versus habitat heterogeneity.

Kadmon and Allouche (2007) found that the predicted effects of area on species richness were unaffected by the incorporation of habitat heterogeneity into integrated models. In contrast, they found that predictions regarding the effects of habitat heterogeneity were not independent of area, except in a few rare cases such as when area is large and immigration rates are very high. Given this relative importance of habitat area, I expected that controlling for area would be important to understand the independent contributions of area and habitat heterogeneity towards wetland biodiversity. My primary objectives in this study are first to identify the relationship between habitat heterogeneity and species richness in wetlands after accounting for habitat area, and then to evaluate whether this relationship is the same 1) for groups of similar species 2) for species abundances, and 3) at two different scales of habitat heterogeneity (i.e. local within-wetland scale and landscape scale).

While understanding the relationships of wetland bird richness and abundance with wetland area and habitat heterogeneity may be useful for prioritizing wetlands for protection, it is also important to keep in mind the biological and logistical context of wetlands being considered for protection. For instance, public versus private ownership explains variability in abundance of bird species in the Prairie Pothole Region beyond that explained by local and landscape-level variables (Ahlering et al. 2019). Although birds clearly do not select habitat based on land ownership, land-use goals for economic income are likely to employ different management practices and thereby create different vegetation structures than goals for conservation and public use. Ownership-specific patterns in vegetation composition, patch isolation, and patch size may also contribute to bird’s apparent response to land ownership (Cunningham 2005). Similarly, wetland class (Naugle et al. 2000; Igl et al. 2017), restoration status (Fletcher & Koford 2003; Begley et al. 2012; Igl et al. 2017), geographic location (Steen 2010), wetland vegetation and cover (Naugle et al. 2000; Fairbairn &

Dinsmore 2001; Steen 2010; Igl et al. 2017), and surrounding land use and land cover can influence the suitability of a particular wetland (Naugle et al. 2000; Fairbairn & Dinsmore 2001; Forcey et al. 2011, 2014; Igl et al. 2017). I therefore added the secondary objective to summarize the relationship of habitat composition patterns to bird diversity and abundance, and to compare the relative importance of heterogeneity and other habitat characteristics to wetland area for the purposes of developing guidance that can be targeted for particular conservation goals ranging from overall biodiversity to abundances of individual species.

I expected that overall avian species richness would respond unimodally to habitat heterogeneity once area was accounted for, consistent with the habitat heterogeneity-area trade-off (Allouche et al. 2012). In addition, I expected that the richness of groups of similar species and the abundances of individual wetland-associated species would respond more strongly to individual habitat components because an individual animal is more likely to be present if there is an adequate area of its preferred habitat. I also expected that these species would respond more strongly to within-wetland habitat heterogeneity than to landscape-level heterogeneity because the vast majority of these species are wetland obligates and thus are likely to depend on habitat within the extent of a single isolated wetland. However, I expected that the nature of the relationship (whether positive linear, negative linear, or unimodal) would depend on the particular species being assessed. I expected a species-specific mixture of wetland and landscape features to be most suitable for each of my focal species and each species group. Finally, I expected that biodiversity and abundance would respond most strongly to wetland area rather than to wetland heterogeneity and other habitat characteristics because many species will use sub-optimal habitat, but wetland area would seem to be a baseline habitat requirement for those species that are considered wetland obligates.

METHODS

Bird Surveys

In the Prairie Pothole Region of North America, 1,097 different wetlands were surveyed for breeding birds from 1995 to 1997 (Fig. 1-1), with 209 wetlands surveyed in

1995, 465 wetlands surveyed in 1996, and 607 wetlands surveyed in 1997. Of these wetlands, 919 were surveyed in a single year, 172 were surveyed in two years, and 6 were surveyed in all three years of the study for a total of 1281 wetland-year combinations. During the site-selection process, wetlands were chosen with the goal of obtaining diversity in geographic distribution (Fig. 1-1), as well as wetland class, size, and restoration status (Igl et al. 2017). Having a range of explanatory variable values is the best way to find associations between response and explanatory variables because greater variation in an explanatory variable results in more precise regression coefficients (Lock et al. 2016). Wetlands were selected from both private and public (Federal) owners.

The study design and bird-survey methodology were described in detail in Igl and Johnson (1997) and Igl et al. (2017). Birds were surveyed with total area counts using slightly modified versions of the methods described by Stewart and Kantrud (1972) and Igl and Johnson (1997). Survey methods included counting waterfowl with a spotting scope, walking the perimeter of the wetland to obtain better views, flushing birds if emergent vegetation obstructed the view, and broadcast calling to identify birds aurally (i.e. American Coot [*Fulica americana*], Pied-billed Grebe [*Podilymbus podiceps*], American Bittern [*Botaurus lentiginosus*], Least Bittern [*Ixobrychus exilis*], Sora [*Porzana carolina*], and Virginia Rail [*Rallus limicola*]; Igl et al. 2017). These techniques allowed us to increase the detection probabilities of secretive marsh birds and rare species. Data quality was ensured with careful training of field personnel (Igl et al. 2017).

Sites were visited once or twice per breeding season. The first visits occurred between 3 May and 30 May of each year. The second visits occurred between 12 June and 3 July of each year. Wetlands that were visited just once were sampled between 17 May and 2 July of each year. I limited observations of each species to a single sampling visit. In instances where a wetland was visited twice in a single season, I used only the count data from the visit that occurred closest to the middle of the breeding season (mid-June).

Total species richness was calculated as the sum of the number of wetland-dependent species observed at each wetland site/year based on the recorded occurrence of each species on the visit that fell closest to the middle of the breeding period. I then divided the wetland-dependent species into avian groups based on phylogenetic or behavioral traits (Table 1) and calculated avian group richness (number of species from that avian group present at the site). These groupings reflect primarily qualitative relationships between species, though they may overlook differences in habitat association patterns related to more specific foraging behaviors (e.g., diving waterfowl versus dabbling waterfowl) and nest-site selection (e.g., upland nesting shorebirds vs. shorebirds that nest in the vegetation of wetter areas). Blackbirds, including Red-winged Blackbird (*Agelaius phoeniceus*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), and Great-tailed Grackle (*Quiscalus mexicanus*), were separated from the other passerine species because as a group they were far more abundant than the other passerines and their responses to the environmental covariates could swamp any patterns that existed for other passerines. I also examined the habitat models for individual species in recognition of the fact that the avian groupings may not be representative of the habitat associations of all members of that group. Total abundance was calculated as the sum of all indicated breeding pairs (e.g., singing male or observed pair) observed at a site, and represents a minimum total abundance, given that some individuals may not have been detected. Individual species abundances were the sum of the number of indicated breeding pairs of that species observed at each site during its peak breeding period.

Environmental Covariates

For my metrics of heterogeneity wetland area was either estimated by field personnel, obtained from the U.S. Geological Survey's Northern Prairie Wildlife Research Center, or determined from the U.S. Fish and Wildlife Service's National Wetlands Inventory (NWI) database (Igl et al. 2017). Field personnel also classified wetlands using the Stewart and Kantrud (1971) classification system during site visits. Wetlands in the Prairie Pothole Region represent different wetland classes primarily defined across a gradient of water permanency. These classes include temporary wetlands with the shortest hydroperiods and generally the greatest amount of interannual variability; seasonal wetlands with intermediate hydroperiods and high interannual variability; semi-permanent wetlands with longer hydroperiods and lower interannual variability; and permanent wetlands with the greatest area, longest hydroperiods, and least interannual variability (Niemuth et al. 2010). In addition, alkali wetlands are a special class defined by a highly dominant intermittent-alkali zone, with highly saline shallow water. These alkali wetlands are large, relatively rare, with high variability but often retain water despite drought (Kantrud & Stewart 1984). In this region, both wetland area and wetland classification, for a given wetland, may fluctuate between years due to changes in water availability and wetland conditions. Thus, it was important to record wetland area and classification at the time of the visit.

Within a wetland, habitat-cover characteristics, including percentages of open water, emergent vegetation, wet meadow, and shoreline/mudflat, were estimated visually during each site visit. During site visits field personnel also estimated percentages of land cover of the surrounding landscape within 400 m ofthe wetland. Chocron et al. (2015) found land cover heterogeneity measures taken within a 400-m buffer distance of survey locations provided more explanatory power for avian species richness than did comparable measures taken within a 5-km buffer. Therefore, I am confident that these observer-generated estimated 400-m land cover types are an adequate measure of the land cover surrounding these wetlands. The land cover types I focused on included grassland, hayland, planted cover, woodland, wetland, shrubland, cropland, feedlots, and road/railroad rights-of-way.

For my metrics of heterogeneity, I calculated two Inverse Simpson Diversity Indices for each wetland, with one index representing heterogeneity at the local scale (based on the percentages of within-wetland land cover) and the other representing heterogeneity at the landscape scale (based on the percentages of land cover and land use within 400 m). Inverse Simpson Diversity indices (λ^{-1}) were calculated using the following formula for lambda:

$$\lambda = \sum_{i=1}^{R} p_i^2$$

where *R* is the total number of *i* habitat types at the given scale and p_i is the arithmentic mean of the proportional abundances of the *i*th habitat type. A higher index value is associated with a greater heterogeneity of cover types at a scale. The local heterogeneity index was based on the four local habitat covariates, and the landscape heterogeneity index was based on only the natural land cover covariates. Land cover types including cropland, feedlots, and road/railroad rights-of-way were excluded from the landscape heterogeneity index because I expect that birds will respond negatively to these potential stressors while my interest is in how these wetland-dependent birds respond to heterogeneity at the landscape-level. Instead I considered these agricultural and non-agricultural human-dominated land uses as separate explanatory variables.

Modeling

Models were developed for overall species richness of 57 wetland-dependent bird species, richness of avian groups, total abundance of all 57 wetland-dependent species on a wetland, and individual species abundance for species that occurred on at least 30 different wetlands (Table 1). Only species with occurrences on at least 30 different wetlands were modeled individually because species distribution models based on a sample size of less than 30 are rarely consistent enough to be used in conservation planning (Wisz et al. 2008).

I used a two-tiered modeling approach to allow us to examine the additional contribution of habitat heterogeneity to species richness and abundance of individual species above and beyond that contribution explained by the wetland area. I first developed area models to calculate expected species or avian group richness or individual species abundance. For each of these response variables, I constructed linear mixed effects models using package lme4 (Bates et al. 2015) that included a random effect for site to account for wetlands that were surveyed in more than one year. Candidate models also included a single fixed effect of either wetland area, the log-transformed wetland area, or the square root of wetland area. I calculated the marginal R-squared value for these candidate area models using package MuMIn (Barton 2018) in R (R Core Team 2015). I then identified the single-variable candidate model with the highest adjusted marginal R-squared value and report that as my top-performing area model for each response variable. Adjusted marginal R-squared values identify the amount of variation explained by the fixed effects of the model while accounting for the number of terms in the model.

From these top-performing area models, I calculated the residuals of the richness or abundance values for each site and used these residuals as the response variables in a second set of habitat models. This two-tiered approach allowed me to incorporate the effects of sampled area, which was important because one would generally expect higher abundances at larger sites as an artifact of a greater amount of sampling effort ("passive sampling"; Johnson 2001). Specifically, the residuals from the models of richness correct the richness values for area. Similarly, the residuals from the models of abundance represent an area-corrected abundance, similar to density. However, this area correction method has the advantage of allowing a non-linear relationship between abundance and area, rather than prescribing a linear relationship as is done when dividing abundance by area to calculate a density.

The resulting habitat models of the residuals included a random effect of site and fixed effects for the local heterogeneity metric, the landscape heterogeneity metric, wetland class, ownership, restoration status, and latitude. I also considered the inclusion of the raw percentages of wetland, grassland, woodland, and cropland and the combined percentage of all non-agricultural anthropogenic land uses based on expectations that these land cover types would have an especially strong effect on habitat use by wetland birds. In the Prairie Pothole Region of Iowa, Fairbairn and Dinsmore (2001) found that the presence and abundance of at least some wetland birds were related to wetland cover within 3 km. Some species of wetland birds use neighboring grasslands for nesting habitat (Greenwood et al. 1995; Skagen & Thompson 2000). Woodland (Greenwood et al. 1995; Thompson et al. 2014), cropland (Greenwood et al. 1995) and other anthropogenic disturbances (DeLuca et al. 2004; Anderson 2017; Glisson et al. 2017) may deter certain species from using nearby habitat. Furthermore, Glisson et al. (2017) found that including such anthropogenic disturbances improved the performance of habitat models for wetland bird occupancy.

I used a restrictive threshold-based pre-selection of Pearson's product moment correlation coefficient $|r| \geq 0.60$ to assess for collinearity among my covariates (Dormann et al. 2013). I did not find any pairs of variables with $|r| \geq 0.60$ and therefore included all variables of interest within my set of candidate models. From each set of candidate models, I selected the habitat model with the highest adjusted marginal R-squared value.

I then examined the nature of the heterogeneity relationship to determine whether there was evidence of a habitat heterogeneity-area trade-off (Allouche et al. 2012). If a heterogeneity term was included in the selected habitat model, I tested whether the inclusion of the quadratic heterogeneity term resulted in a further increase in the adjusted marginal R-squared value. If so, the quadratic term was included in the final habitat model. Simple linear relationships suggested that a species group or individual species may not experience such a trade-off. A convex unimodal relationship—as indicated by a negative quadratic relationship—supported the theory that a trade-off existed.

I evaluated my final habitat models through cross validation. I constructed habitat models using about two-thirds of the data (n = 845 wetland-year combinations), which I randomly selected from the 1281 wetland-year combinations used for the construction of the area models. I held the remaining one-third of the data (n = 436 wetland-year combinations) in reserve for model evaluation. I re-ran my top-performing habitat models using the withheld data to determine whether the habitat models were overfit, as would be indicated if the amount of variation explained was not consistent with the original habitat models. Area models were created with the entire dataset and not subjected to this model evaluation technique because they contained only a single explanatory variable and thus were not likely to be overfit.

RESULTS

I recorded a total of 33,525 indicated breeding pairs of 57 wetland-dependent species on 1097 wetlands (1281 wetland-year combinations) surveyed between 1995 and 1997 (Table 1). Of these species, 38 occurred on at least 30 different wetlands. Mean overall species richness was 7.25 (±5.33 SD) species per wetland, and mean total abundance was 26.17 (±41.13 SD) indicated breeding pairs (Table 2). The surveyed wetlands ranged in area from 0.01 to 204.26 hectares, with a mean area of 4.09 (±12.94 SD) hectares. The preponderance of small wetland basins is representative of the distribution of wetland sizes in the Prairie Pothole Region (Cowardin et al. 1995)

Of the 1097 wetlands, 592 wetlands (702 wetland-year combinations) were on privately owned lands and 505 (579 wetland-year combinations) were on federal Waterfowl Production Areas (WPAs) or National Wildlife Refuges. Publicly owned wetlands had a larger mean size than privately owned wetlands ($t(1279) = -6.26$, $p < 0.01$) and had correspondingly higher mean species richness ($t(1279) = -9.64$, $p < 0.01$) and mean total avian abundance ($t(1279) = -9.29$, $p < 0.01$).

The surveyed wetlands included 365 restored wetlands (424 wetland-year combinations) and 732 natural wetlands (857 wetland-year combinations). The restored wetlands averaged smaller in size than the natural wetlands that had not been restored ($t(1279) = -4.44$, $p < 0.01$), and had lower mean species richness ($t(1279) = -3.02$, $p < 0.01$) and mean total avian abundance ($t(1279) = -4.08$, $p < 0.01$).

The surveyed wetlands included temporary wetlands ($n = 157$), seasonal wetlands ($n = 359$), semipermanent wetlands ($n = 498$), permanent wetlands ($n = 41$), and alkali wetlands ($n = 42$). Welch's analysis of variance tests showed that classes of wetlands were significantly different in size ($F(4, 168.90) = 33.69$, $p < 0.01$), species richness ($F(4, 170.66) = 131.14$, $p < 0.01$), and mean total avian abundance ($F(4, 170.60) = 72.83$, $p < 0.01$). Post hoc Games-Howell tests showed that alkali wetlands were significantly larger than all but permanent wetlands, and mean overall species richness (14.5 species ± 6.3 SD versus 16.2 species ± 6.3 SD, respectively) and mean total avian abundances (100.2 indicated breeding pairs ± 87.9 SD versus 70.1 ± 68.5 SD) were highest on these two wetland classes.

Overall, local heterogeneity showed a very slight positive relationship with wetland area ($R^2 = 0.02$; Fig. 1-2A). In contrast, landscape heterogeneity was not related to wetland size overall (R^2 = 0.00; Fig. 1-2B). These relationships did not differ by wetland class.

Species Richness

The model with log-transformed wetland area performed best for all avian groups except shorebirds. Area models explained the greatest amount of variation (7-63%) in species richness among the wetlands (Table 3). Overall species richness showed an especially strong positive linear relationship with log-transformed wetland area (R^2 = 0.63; Fig. 1-3A). The habitat models based on variables including local heterogeneity, landscape heterogeneity, wetland classification, wetland ownership, restoration status, latitude, surrounding wetland cover, grassland cover, woodland cover, agricultural cover, and/or human-dominated land cover explained a small amount of additional variation in species richness (2-20%). Wetland permanence classification was the most consistently important of these metrics, explaining additional variation in the richness residuals of all eight avian groups. Closely following in consistency was local heterogeneity, which was included in the habitat models of seven of the avian groups. Latitude and percentages of grassland cover and human land use within 400 m each explained additional variation in the richness residuals of six of the eight avian groups; restoration status explained additional variation in five models; ownership, wetland cover, agricultural cover, and landscape heterogeneity were included in the top models of four avian groups; and woodland cover explained additional variation in three avian groups.

Based on my best habitat model, overall species richness is lowest on alkali wetlands and highest on permanent wetlands (Table 4). Permanent wetlands also have the greatest numbers of waterfowl, grebe, rail, wading bird, and other colonial waterbird species. Largest numbers of blackbirds and other passerine species are found on semipermanent wetlands. The greatest numbers of shorebird species are found on alkali wetlands. Overall species richness and richness of waterfowl, wading birds, blackbirds, and other passerines are higher on publicly owned wetlands than on privately owned wetlands. Indeed, no avian group showed higher species richness on privately owned wetlands. In contrast, while overall species richness and richness of waterfowl, rails, blackbirds, and other passerines is higher on restored wetlands, grebe richness is higher on natural wetlands.

The local heterogeneity showed unimodal (negative quadratic) relationships with species richness for overall species richness (Fig. 1-4A), waterfowl, grebes, and blackbirds whereas landscape heterogeneity showed unimodal (negative quadratic) relationships for other colonial waterbirds (Table 4). Rails, shorebirds, passerines, and other colonial waterbirds showed positive linear relationships with local heterogeneity. Overall species richness, waterfowl, grebes, and blackbirds showed positive linear relationships with landscape heterogeneity.

Abundance

Similar to species richness, abundance was particularly sensitive to wetland area. The square root of wetland area best explained variation in species abundances for 16 of the 38 species modeled, log-transformed wetland area best explained abundances of another 15 species, and abundances of seven species were best modeled by untransformed wetland area (Table 5).

Total abundance showed a positive non-linear relationship with square root of wetland area ($R^2 = 0.54$; Fig. 1-3B) and explained 54% of variation. The area model explained at least as much variation as the top habitat model for 36 of the 38 species modeled. The mean percentage of variation explained by the area model for individual species was 13 (±11 SD) %, with a minimum of 1% and a maximum of 39%. The habitat models explained a mean of 4 (±2 SD) % of the variation in abundances of individual species, with a minimum of 0.4% (rounded in Table 5 to <1%) and a maximum of 11%.

Of the top habitat models for individual species, wetland class was included for 37 species. The percentage of grassland cover was included for 24 individual species. Local heterogeneity was included in 20 top habitat models, and 20 top habitat models included landscape heterogeneity as a covariate. Latitude was included in 19 top habitat models, and ownership and human land use were each included for 16 species. Percentage of woodland cover and restoration status were each included for 14 species, and percentages of wetland and agricultural cover were each included for 13 species.

For all species, abundance was positively correlated with wetland area (Table 6). Of the 37 species that varied by wetland class, 57% were most abundant on permanent wetlands, 30% were most abundant on alkali wetlands, 8% were most abundant on semipermanent wetlands, 5% were most abundant on temporary wetlands, and none was most abundant on seasonal wetlands (Table 7). Of the 24 species that had percentage of grassland cover in the top habitat model, 42% showed a positive linear relationship and 58% had a negative linear relationship, although in almost every case the coefficients were negligibly small. Of the 16 species that had ownership in the top habitat model, 81% had higher abundance on publicly owned wetlands. Of the 16 species that had percentage of non-agricultural human land use in the top habitat model, 62% showed a negative linear relationship and 38% showed a positive linear relationship. Of the 14 species that had percentage of woodland cover in the top habitat model, 71% showed a negative linear relationship and 29% showed a positive linear relationship. Of the 13 species that had restoration status in the top habitat model, 92% had higher abundances on restored wetlands than on natural wetlands. Of the 13 species that had percentage of wetland cover in the top habitat model, 62% showed a negative linear relationship and 38% showed a positive linear relationship. Of the 13 species that had percentage of cropland cover in the top habitat model, 46% showed a positive linear relationship and 38% showed a negative linear relationship (although, again, many of the coefficients were so small as to be negligible).

Total avian abundance showed a positive linear relationship with my heterogeneity metrics (Fig. 1-4B), and individual species abundances showed both convex unimodal and concave relationships with heterogeneity. The abundances of four species showed convex unimodal (negative quadratic) relationships with local heterogeneity, five species showed concave (positive quadratic) relationships, 11 species showed positive linear relationships, and two species showed negative linear relationships. Two species showed negative quadratic relationships with landscape heterogeneity, two species showed positive quadratic relationships, nine species showed positive linear relationships, and seven species showed negative linear relationships.

Model evaluation

Applying my top habitat models to the withheld data showed that the models were not overfit (Tables 3 and 4) because the amount of variation explained by the models (as determined by the adjusted marginal R-squared values) were very similar to those obtained with data used for constructing the models. The mean difference in explained variation was an absolute value of 2%.

DISCUSSION

Overall species richness in prairie pothole wetlands during the breeding season responded somewhat unimodally to habitat heterogeneity within wetlands after accounting for wetland area, a result that is consistent with the habitat heterogeneity-area trade-off relationship described by Allouche et al. (2012). Overall species richness was best described by a unimodal relationship with heterogeneity at the local scale. Unimodal relationships have been found for bird communities across North America with heterogeneity in elevation, foliage height, and land cover (Bar-Massada & Wood 2014; Chocron et al. 2015; Tuanmu & Jetz 2015). A study of wetland bird communities in Argentina, however, identified a positive linear relationship rather than a unimodal relationship between species richness and habitat heterogeneity (Lorenzón et al. 2016a). Similarly, I found a positive linear relationship between overall species richness and landscape-scale heterogeneity. The metric of heterogeneity used by Lorenzón et al. (2016a) included percentages of eight habitat types within 200 m of single point count locations and thus potentially included both within-wetland (local) habitat features and surrounding landscape features, depending on the configuration of the wetland. Therefore, the two scales of habitat heterogeneity that I distinguished were confounded in their study. Furthermore, their findings were confined to fluvial wetlands, and different hydrologic regimes may drive species-habitat relationships in other types of wetlands.

Although I did find support for the habitat heterogeneity-area trade-off relationship at the level of overall species richness and local scale habitat heterogeneity, my findings were less clear at the level of avian groups. Four groups (not including overall species richness) included a quadratic term for local or landscape habitat heterogeneity. The remaining four groups did not include a quadratic term but three of these groups did include a linear term for at least one scale of habitat heterogeneity. The exception was wading birds, perhaps because they are likely to use shallow-water portions of a wetland (Lantz et al. 2010), and thus may be settling in wetlands based on water level rather than heterogeneity of habitat types.

The predominant trend suggests that while some groups respond unimodally as expected to habitat heterogeneity, others increase linearly with increasing habitat heterogeneity, but in most cases at least a small amount of variation in group richness can be explained by habitat heterogeneity. Similarly, Bar-Massada and Wood (2014) found a combination of unimodal and positive linear relationships between species richness and various measures of habitat heterogeneity at several spatial scales. Bar-Massada and Wood (2014) concluded that the relationship between species richness and habitat heterogeneity is not fixed and depends on the scale, habitats, and heterogeneity metrics being assessed. To this I would add that the nature of this relationship is species-specific.

Likewise, I found mixed evidence of an area-heterogeneity trade-off when I examined the relationships between species abundances and habitat heterogeneity after controlling for area. Combined abundance of all species showed a positive linear relationship with the square root of wetland area (Fig. 3B), 13 species showed evidence of a unimodal relationship between abundance and habitat heterogeneity at either scale, and 25 species showed evidence of simple linear relationships with habitat heterogeneity at one or both scales. Lorenzón et al. (2016a) found evidence of positive linear relationships between individual species abundances of wetland birds and habitat heterogeneity. In contrast, Bar-Massada and Wood (2014) found no relationship between mean species abundance and local heterogeneity, but a negative relationship between mean species abundance and foliage height heterogeneity. Surprisingly, seven species in my study showed evidence of a concave relationship rather than a convex unimodal relationship. Such a relationship would indicate that intermediate values of heterogeneity may be less suitable for these species than more extreme values of heterogeneity. Again, my results highlight the species- and avian group-specific nature of the relationships between abundance and habitat heterogeneity.

Wetland area metrics explained a considerable amount of variation in species richness and abundance (Fig. 3). For overall species richness and seven of the eight avian groups, richness was best explained by log-transformed wetland area. Richness of shorebirds, the only exception, was best modelled by square root of area, which is a proxy for wetland perimeter (exact if a wetland is circular). These results are consistent with the fact that most shorebirds forage in the shallow water often associated with wetland edge (Skagen & Thompson 2000). For species abundances, square root of wetland area was the most frequently model-selected area metric (total abundance and 16 individual species). I speculate that many of these species may be nesting near the wetland edge, and thus more edge allows for a greater number of nesting territories. Log-transformed area best explained the abundance of an additional 15 species. Finally, untransformed wetland area was the best area metric for seven species, suggesting that the number of these species is simply proportional to the size of the wetland, typical of a standard species-area relationship (MacArthur & Wilson 1967).

Importantly, my results suggest that wetland area is the primary driver of wetland bird species richness and abundance. The overall species richness model shows this pattern most strongly: 63% of variation in overall species richness was explained by log-transformed area alone, whereas only 10% of variation was explained by the habitat models. The area models also explained more variation in species richness than did the habitat models for all eight avian groups. Servat et al. (2017) similarly found evidence that area was more important than habitat heterogeneity in accounting for variation in avian species richness at high-elevation wetlands in Peru. Fairbairn and Dinsmore (2001) found that area was the most important variable for explaining wetland bird species richness and in combination with cover of emergent vegetation explained 60% of variation in species richness, similar to the degree of variation explained by my area-only model for overall species richness. Likewise, my area models generally explained more variation in total abundance and individual species abundances than did the habitat models. Crozier and Niemi (2003) found that area explained 12-72% of variation in abundances of 38 species, versus just 4-11% of variation explained by measures of habitat heterogeneity. However, as expected the abundance of individual species generally responded less strongly to wetland area than did measures of richness, as indicated by the lower amounts of variation explained.

Although wetland area was the primary driver of species richness, I also found that species did respond to habitat heterogeneity at local and landscape scales. Equal numbers of species responded to each scale of habitat heterogeneity. Of the 32 species that responded to habitat heterogeneity, 12 responded only to local-scale habitat heterogeneity, 11 responded only to landscape-scale heterogeneity, and 9 species responded to heterogeneity at both scales. In contrast, Brandolin and Blendinger (2016) found that the abundances of more wetland bird species responded to within-wetland habitat features than to features of the surrounding landscape. However, Naugle et al. (1999) found that wetland species in the Prairie Pothole Region may respond to different scales, and especially wide-ranging species such as Black Terns are expected to respond to landscape-scale habitat characteristics and heterogeneity.

Like Brandolin and Blendinger (2016) and Elphick (2008), I found that phylogenetically similar species responded to many of the same habitat characteristics. For instance, many waterfowl (7 out of 15 species) and colonial waterbirds (3 out of 5 species) included wetland ownership as an explanatory variable in the top model of abundance residuals. Top models for both grebe species, both rail species, shorebirds (4 out of 5 species), passerines (5 out of 5 species, plus both blackbird species), and colonial waterbirds (3 out of 5 species) included grassland cover. Top models for waterfowl (10 out of 15 species) included woodland cover. Both blackbird species, other passerines (3 out of 5 species), and shorebirds (3 out of 5 species) included wetland cover in their top models. Human land use was included in the top models for waterfowl (7 out of 15 species), both rail species, and colonial waterbirds (3 out of 5 species). Agricultural cover was included in the top models for passerines (4 out of 5 species) and shorebirds (3 out of 5 species). Restoration status was included in the top models for waterfowl (7 out of 15 species) and passerines (4 out of 5 species). Latitude was included in the top models for waterfowl (9 out of 15 species), both rail species, and passerines (3 out of 5 species).

It is worth noting, however, that in a number of these cases, the directionality of these relationships differed among some of the phylogenetically similar species, and furthermore, individual species abundances did not always follow the associated avian group richness trends with regards to certain habitat characteristics. For instance, while other colonial waterbird richness showed a positive linear relationship with local heterogeneity, Ring-billed Gull abundance showed a negative linear relationship with local heterogeneity. These differences in directionality are most likely due to species-specific habitat use patterns, and in the latter case to such behavioral habitat use patterns that were not accounted for in my choice of avian groupings. For most management purposes, the individual species abundances and overall species richness are likely to be the most valuable of my findings.

The different avian groups and individual species also responded differently to land use and land cover. I found a mix of positive and negative linear relationships between avian group richness or species abundances and percentages of wetland, grassland, agriculture, and non-agricultural human land uses, and between species abundances and percentages of woodland, though many of the individual coefficient values are so small as to make the directionality of these relationships irrelevant. However, these results again most likely reflect differences in the habitat use of many of these species for nest site selection in the matrix of habitat surrounding the wetland and the influences of surrounding vegetation on foraging behavior. For example, previous literature has documented the propensity of Killdeer to nest in row crop agricultural land, whereas most species avoid nesting in these human-dominated landscapes (Best et al. 1997; Fletcher & Koford 2003).

I found that both abundance and species richness were typically higher on publicly owned wetlands than on privately owned wetlands, with the only exceptions being American Wigeon, Ring-billed Gull, and American White Pelican. Previous work on grassland bird responses to land ownership found that Henslow's Sparrow and Bobolink (Ahlering et al. 2019) and Song Sparrow (Cunningham 2005) were also most abundant on publicly owned land. Publicly owned wetlands in my study were generally larger than privately owned wetlands, with considerably less adjacent cropland, more open water, and less wet meadow and shoreline/mudflat habitat. These differences in habitat characteristics, in combination with different management goals and practices (Cunningham 2005; Ahlering et al. 2019), may explain some of the difference in species richness and abundance between ownership types.

Similarly, both abundance and species richness were typically higher on restored wetlands than on natural wetlands. This indicates that wetland restoration is an effective method of improving the quality of habitat for most species, as is being pursued under the Prairie Pothole Joint Venture Implementation Plan for waterfowl (Brice et al. 2017). Similar to my study, Fletcher and Koford (2003) found increases in the abundances of two out of six wetland obligate species on restored wetlands after restoration at prairie pothole wetlands in Iowa. Other studies have found that richness of wetland-dependent species was comparable between natural and restored wetlands (Begley et al. 2012; Anderson 2017). My results may indicate that restoration may result in higher aquatic productivity that attracts wetland birds (Ratti et al. 2001) or that the natural wetlands in my study were generally degraded habitat. It is worth noting, however, that grebe richness and Black Tern abundance were significantly lower on restored wetlands than on natural wetlands, so natural wetlands still offer important habitat for some species.

Finally, I found that the most consistent habitat variable for determining both richness and abundance was wetland class. Both richness and abundances were highest on permanent wetlands. However, all types of wetlands in the Prairie Pothole Region served as the most or second most important habitat type for at least one species (for example, seasonal wetlands hosted the second greatest diversity of shorebirds and the second highest abundances of ten individual species). This suggests that wetlands of all classes—including the generally small and shallow temporary and seasonal wetlands that are particularly targeted for drainage and agricultural conversion (Niemuth et al. 2010)—have a role to play in enhancing biodiversity and supporting higher populations of individual species in this region.

Conclusions

These findings can inform prioritization of conservation activities, based on the goals of specific projects. In particular, my results support the existing order of priorities outlined in the Prairie Pothole Joint Venture Implementation Plan (Prairie Pothole Joint Venture 2017). Increasing the overall area of natural wetlands that are protected will have the single biggest benefit to both breeding wetland bird species richness and abundance of individual species. However, larger wetlands may not always have the highest conservation value given the context in which they occur. For instance, location on the landscape (whether it falls within a broader network of wetlands or exists in isolation) and surrounding land cover and land use may also influence the biodiversity of a given wetland. Furthermore, my results show that the ownership of a wetland may influence its conservation value, presumably as a reflection of the management goals that have been pursued at the site. My results indicate that protected public lands are especially important for maintaining wetland bird populations. Thus, some methods of obtaining wetlands for protection (land acquisition versus easements) may be more successful than others in achieving conservation goals. However, patterns of ongoing wetland loss (Dahl 2014; Lark et al. 2015) and predominantly private land ownership (Cowardin et al. 1995; Cunningham 2005; Ciuzio et al. 2013) emphasize that conservation efforts in this region will most likely need to promote appropriate stewardship of privately owned wetlands. Such biological and logistical concerns should be considered as part of evaluating any wetland for protection or restoration.

Many factors that drive heterogeneity in these ecosystems, such as wetland water levels and vegetation patterns, are highly dynamic and result in fluctuations in heterogeneity over time. While these changes are important contributors to the functioning of these ecosystems and their resulting productivity, many historic biological and abiotic drivers of disturbance that once maintained a mosaic of wetland habitat types appropriate for various species—such as the short vegetation and mudflat habitat ideal for foraging shorebirds—have been lost in the Prairie Pothole Region (Skagen & Thompson 2000). Throughout the selection process, and once a wetland has been targeted for protection, an emphasis should be placed on maintaining a diversity of wetland successional stages across the landscape. Habitat succession becomes problematic when mosaics of wetlands at various successional stages are not present nearby to provide alternative habitat for stenotopic wetland species that tolerate only a limited range of habitat characteristics. Thus, keeping landscape, state, and regional contexts in mind is imperative to developing a matrix of wetlands that support the greatest possible biodiversity. Specifically, management actions that limit invasion by undesirable plant species and guide habitat succession towards goals appropriate for the site or the landscape and regional context of the wetland may be necessary. In some situations, maintaining heterogeneous wetlands will involve efforts to manage vegetation cover, such as through restoration, at a given wetland and in other cases it may involve targeting certain wetlands for protection over others.

If there are particular species of concern, such as those listed in state wildlife action plans (South Dakota Department of Game Fish and Parks 2014; Dyke et al. 2015; Murano 2017; North Dakota PPJV Planning Team 2017), the abundance of such species can be managed at multiple scales based on species-specific responses to wetland and landscape features. My results identify important features for a variety of wetland-obligate species in the Prairie Pothole Region, many of which have been identified as species of conservation concern in state and regional conservation plans (Brice et al. 2017; Murano 2017; North Dakota PPJV Planning Team 2017). In particular, given that wetlands of different classes can be expected to support somewhat different species assemblages, efforts to protect wetlands should incorporate a diverse range of wetland types.

An important caveat of these findings is that measures of species richness and abundance alone do not indicate that the habitat being used represents habitat that is successfully contributing to supporting healthy populations in the long term. Additional research should also consider the implications of heterogeneous wetlands, wetland ownership, and restoration status on the vital rates of wetland-obligate species and examine how these parameters compare to my results for biodiversity and abundance.

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TABLES

Table 1. Avian species of interest, by group; number of wetlands on which each species was observed; and total number of indicated breeding pairs of each species. Bolded numbers indicate the total number of indicated breeding pairs of the entire functional group.

Avian group	Scientific name	Conservation status	N wetlands where species occurred		Total number of indicated breeding pairs
			Total number of different wetlands occupied	Total number of occupied wetland-years	
Waterfowl					**15616**
Canada Goose	*Branta canadensis*	[1,12]	65	67	150
Wood Duck	*Aix sponsa*	[1,4,12,13]	36	38	71
Blue-winged Teal	*Spatula discors*	[1,4,12]	781	919	4356
Northern Shoveler	*Spatula clypeata*	[1,4,12,14]	347	378	906
Gadwall	*Mareca strepera*	[1,4,12,14]	521	603	1965
American Wigeon	*Mareca americana*	[1,12,14]	62	66	132
Mallard	*Anas platyrhynchos*	[1,4,12,14]	555	635	1964
Green-winged Teal	*Anas crecca*	[1,12]	134	141	244
Northern Pintail	*Anas acuta*	[1,4,11,12]	212	230	415
Canvasback	*Aythya valisineria*	[1,4,11]	65	67	178
Redhead	*Aythya americana*	[1,4,12,14]	217	244	692
Ring-necked Duck	*Aythya collaris*	[1,4,14]	63	65	130

Lesser Scaup	*Aythya affinis*	1,4,11,13	130	148	479
Bufflehead	*Bucephala albeola*	1,14	9	11	21
Hooded Merganser	*Lophodytes cucullatus*	1	5	5	6
Ruddy Duck	*Oxyura jamaicensis*	1,4	235	269	956
American Coot	*Fulica americana*	7,12	569	655	3101
Grebes					**1471**
Pied-billed Grebe	*Podilymbus podiceps*	7,12	261	291	478
Horned Grebe	*Podiceps auritus*	5,10,14	29	32	79
Red-necked Grebe	*Podiceps grisegena*	7,14	6	6	7
Eared Grebe	*Podiceps nigricollis*	6,14	51	58	890
Western Grebe	*Aechmophorus occidentalis*	5,14	12	12	17
Rails					**743**
Virginia Rail	*Rallus limicola*	6	111	123	205
Sora	*Porzana carolina*	7,12	295	313	538
Wading Birds					**521**
American Bittern	*Botaurus lentiginosus*	5,10,12	92	97	120
Least Bittern	*Ixobrychus exilis*	6,14	3	3	3
Great Blue Heron	*Ardea herodias*	6,12	12	12	13
Cattle	*Bubulcus ibis*	7	7	7	61

Egret					
Black-crowned Night-Heron	*Nycticorax nycticorax*	[6,14]	59	66	316
White-faced Ibis	*Plegadis chihi*	[7]	2	2	8
Shorebirds					**1150**
American Avocet	*Recurvirostra americana*	[2,4,11,14]	24	29	113
Piping Plover	*Charadrius melodus*	[2,4,9,11,14]	7	10	20
Killdeer	*Charadrius vociferus*	[3,4]	273	295	492
Marbled Godwit	*Limosa fedoa*	[2,4,9,10,12,14]	43	44	81
Wilson's Snipe	*Gallinago delicata*	[3,12]	59	63	75
Spotted Sandpiper	*Actitis macularius*	[3,13]	4	4	8
Willet	*Tringa semipalmata*	[3,4,9,11,12,14]	87	93	134
Wilson's Phalarope	*Phalaropus tricolor*	[2,4,9,10,12,14]	105	115	227
Blackbirds					**8747**
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	[12,14]	428	498	4645
Red-winged Blackbird	*Agelaius phoeniceus*		869	1023	4101
Great-tailed Grackle	*Quiscalus mexicanus*		1	1	1

Passerines					**3036**
Willow Flycatcher	*Empidonax traillii*	[8,13]	35	39	72
Sedge Wren	*Cistothorus platensis*	[12,13]	127	132	208
Marsh Wren	*Cistothorus palustris*	[12,13]	215	241	1315
LeConte's Sparrow	*Ammospiza leconteii*	[4,9,14]	46	48	81
Nelson's Sparrow	*Ammospiza nelsoni*	[10]	18	19	21
Swamp Sparrow	*Melospiza georgiana*	[13]	28	29	49
Common Yellowthroat	*Geothlypis trichas*	[12]	467	521	1290
Harriers					**24**
Northern Harrier	*Circus hudsonius*	[11,14]	22	22	24
Other colonial waterbirds					**2068**
Franklin's Gull	*Leucophaeus pipixcan*	[5,10,12,13]	42	46	308
Ring-billed Gull	*Larus delawarensis*	[7,12,14]	55	58	175
Forster's Tern	*Sterna forsteri*	[7,13]	7	7	15
California Gull	*Larus californicus*	[7]	10	10	12
Common Tern	*Sterna hirundo*	[6,13]	1	1	1
Black Tern	*Chlidonias niger*	[9,10,12,13]	286	312	1298
Double-	*Phalacrocorax*	[7,12,13]	36	38	95

crested Cormorant	*auritus*				
American White Pelican	*Pelecanus erythrorhynchos*	[6,11,14]	30	31	164

[1] NAWMP-listed species (NAWMP 2018)

[2] NP/PPRSP species of concern (Skagen & Thompson 2000)

[3] NP/PPRSP regional priority level 3 (Skagen & Thompson 2000)

[4] PPJV Implementation Plan priority species (Brice et al. 2017; Fields & Barnes 2017)

[5] Waterbird species mentioned in PPJV Implementation Plan – high priority (Niemuth 2017)

[6] Waterbird species mentioned in PPJV Implementation Plan – moderate priority (Niemuth 2017)

[7] Waterbird species mentioned in PPJV Implementation Plan – low priority (Niemuth 2017)

[8] 2005 PPJV Implementation Plan – Landbird Plan priority species (Casey 2005)

[9] SD SGCN (South Dakota Department of Game Fish and Parks 2014; Murano 2017)

[10] ND SGCN – Conservation Priority Level 1 (Dyke et al. 2015; North Dakota PPJV Planning Team 2017)

[11] ND SGCN – Conservation Priority Level 2 (Dyke et al. 2015; North Dakota PPJV Planning Team 2017)

[12] Predicted to decline under future climate scenarios (Steen et al. 2014)

[13] Climate threatened (Langham et al. 2015)

[14] Climate endangered (Langham et al. 2015)

Table 2. Means, standard deviations (in parentheses) and ranges (below) of avian community metrics and wetland characteristics for 1281 wetland-year combinations surveyed in 1995-1997, as well as means and standard deviations broken down by ownership, restoration, and wetland classification. Sample sizes (n) represent number of wetland-years in each category. Wetland characteristics are reported for wetland years rather than for individual wetlands because there is a high degree of annual variation in habitat characteristics.

Variable	All wetlands (n = 1281)	Ownership		Restoration status		Wetland classification				
		Private (n = 702)	Public (n = 579)	Restored (n = 424)	Natural (n = 857)	Permanent (n = 50)	Semi-permanent (n = 580)	Seasonal (n = 426)	Temporary (n = 181)	Alkali (n = 44)
Avian community										
Overall species richness	7.3 (5.3)	6.0 (4.4)	8.8 (5.9)	6.6 (4.5)	7.6 (5.7)	16.2 (6.3)	8.2 (4.7)	6.0 (4.2)	3.0 (2.9)	14.5 (6.3)
	0-29	0-25	0-29	0-22	0-29	0-29	0-23	0-27	(0-19)	(1-25)
Waterfowl richness	3.5 (2.9)	2.9 (2.5)	4.3 (3.1)	3.2 (2.6)	3.7 (3.0)	7.9 (3.1)	3.8 (2.6)	3.1 (2.6)	1.4 (1.8)	7.4 (3.1)
	0-14	0-13	0-14	0-13	0-14	0-14	0-12	0-12	(0-10)	(0-13)
Grebe richness	0.3 (0.6)	0.2 (0.5)	0.4 (0.7)	0.2 (0.4)	0.4 (0.6)	1.1 (0.9)	0.4 (0.6)	0.2 (0.4)	0.0 (0.2)	0.9 (1.1)
	0-4	0-2	0-4	0-2	0-4	0-3	0-2	0-2	(0-1)	(0-4)
Rail richness	0.3 (0.6)	0.3 (0.5)	0.4 (0.6)	0.3 (0.6)	0.3 (0.6)	0.6 (0.8)	0.4 (0.6)	0.2 (0.5)	0.2 (0.4)	0.3 (0.6)
	0-2	0-2	0-2	0-2	0-2	0-2	0-2	0-2	(0-2)	(0-2)
Wading bird richness	0.1 (0.4)	0.1 (0.3)	0.2 (0.5)	0.1 (0.4)	0.2 (0.4)	0.6 (0.7)	0.2 (0.5)	0.1 (0.3)	0	0.3 (0.5)
	0-3	0-2	0-3	0-2	0-3	0-2	0-3	0-2	(0-0)	(0-2)
Other colonial waterbird richness	0.4 (0.7)	0.3 (0.6)	0.5 (0.8)	0.3 (0.5)	0.5 (0.7)	1.3 (0.9)	0.4 (0.7)	0.3 (0.5)	0.1 (0.3)	1.2 (1.3)
	0-7	0-7	0-4	0-3	0-7	0-3	0-5	0-3	(0-1)	(0-7)
Shorebird	0.5 (0.9)	0.5 (0.8)	0.6 (1.0)	0.4 (0.7)	0.6 (0.9)	1.3 (1.1)	0.4 (0.7)	0.4 (0.8)	0.3 (0.6)	2.3 (1.8)

richness	0-7	0-5	0-7	0-5	0-7	0-5	0-4	0-4	(0-3)	(0-7)
Other passerine	0.8 (1.0)	0.6 (0.9)	1.0 (1.1)	0.9 (1.0)	0.7 (1.0)	1.6 (1.3)	1.0 (1.1)	0.6 (0.8)	0.4 (0.7)	0.9 (1.0)
richness	0-5	0-4	0-5	0-4	0-5	0-5	0-5	0-5	(0-4)	(0-3)
Blackbird	1.2 (0.7)	1.1 (0.7)	1.4 (0.7)	1.2 (0.7)	1.2 (0.7)	1.7 (0.6)	1.4 (0.6)	1.1 (0.6)	0.6 (0.6)	1.1 (0.7)
richness	0-3	0-2	0-3	0-2	0-3	0-2	0-3	0-2	(0-2)	(0-2)
Total avian	26.2 (41)	16.8	37.6	19.5	29.4	100.2	29.7	16.8	5.7 (9.9)	70.1
abundance		(22.8)	(53.7)	(26.7)	(46.3)	(87.9)	(38.5)	(23.4)		(68.5)
	0-505	0-220	0-505	0-246	0-505	0-505	0-283	0-174	0-103	4-301
Wetland characteristics										
Wetland area	3.9 (12.2)	1.9 (6.9)	6.2 (16.1)	1.7 (5.2)	4.9	21.4	3.3 (8.4)	1.6 (5.0)	0.5 (0.9)	26.6
(ha)					(14.3)	(24.6)				(38.8)
	0.01-204	0.01-72	0-204	0-64	0-204	0.3-130	0-72	0-75	0-6.4	0-204
Landscape characteristics										
Grassland (%)[1]	15.5	18.1	12.3	14.3	16.1	20.8	15.1	14.1	14.1 (24.1)	33.3
	(26.2)	(28.9)	(22.2)	(27.1)	(25.8)	(24.9)	(27.2)	(25.0)		(28.9)
	0-95	0-95	0-90	0-95	0-95	0-80	0-95	0-90	0-95	0-85
Hayland (%)[1]	7.4 (16.5)	10.0	4.2 (10.6)	11.4	5.4	1.0 (4.6)	8.0 (17.1)	8.7	5.2 (13.0)	2.3 (7.3)
		(19.7)		(21.4)	(12.9)			(18.1)		
	0-95	0-95	0-76	0-95	0-90	0-30	0-90	0-95	0-60)	(0-35)
Planted cover	30.8	21.0	42.7	31.7	30.3	34.2	30.8	32.1	30.6 (28.0)	14.3
(%)[1]	(27.7)	(27.8)	(22.6)	(29.0)	(27.1)	(28.5)	(27.1)	(28.7)		(19.0)

	0-100	0-95	0-100	0-95	0-100	0-97	0-100	0-97	0-95	0-65
Cropland (%)	19.7 (24.6)	25.6 (28.3)	12.8 (16.8)	16.1 (20.7)	21.6 (26.2)	17.3 (21.8)	20.0 (24.6)	18.6 (22.9)	24.3 (29.4)	12.6 (20.5)
	0-98	0-98	0-85	0-90	0-98	0-83	0-98	0-90	0-98	0-80
Woodland (%)[1]	2.3 (4.7)	2.2 (4.9)	2.4 (4.4)	3.0 (4.6)	2.0 (4.7)	1.5 (4.0)	2.6 (4.6)	2.3 (4.6)	1.9 (5.7)	1.7 (3.4)
	0-60	0-60	0-40	0-30	0-60	0-20	0-40	0-50	0-60	0-10
Rights-of-way (%)[2]	2.2 (2.9)	1.9 (2.9)	2.6 (2.9)	2.0 (2.5)	2.4 (3.1)	2.4 (3.7)	2.0 (2.6)	2.4 (2.9)	2.1 (3.5)	3.2 (3.6)
	0-25	0-20	0-25	0-10	0-25	0-15	0-12	0-15	0-25	0-10
Barren (%)	2.4 (3.4)	2.4 (3.3)	2.3 (3.5)	2.4 (2.9)	2.3 (3.6)	1.3 (2.5)	1.9 (2.5)	2.8 (3.5)	2.3 (3.4)	6.1 (8.0)
	0-50	0-30	0-50	0-15	0-50	0-10	0-15	0-30	0-20	0-50
Wetland (%)[1]	18.2 (11.8)	16.9 (11.9)	19.7 (11.5)	17.4 (11.5)	18.5 (11.9)	17.7 (15.1)	18.0 (11.1)	17.5 (10.9)	18.6 (12.7)	25.3 (17.5)
	0-75	0-70	0-75	0-75	0-75	0-75	0-75	0-65	0-50	0-60
Shrubland (%)[1]	0.2 (1.7)	0.2 (2.0)	0.2 (1.4)	0.2 (1.3)	0.2 (1.9)	0.3 (1.6)	0.2 (1.4)	0.2 (2.4)	0.1 (0.7)	0.2 (1.5)
	0-45	0-45	0-20	0-15	0-45	0-10	0-20	0-45	0-10	0-10
Feedlot (%)[2]	0.2 (1.2)	0.2 (1.5)	0.1 (0.8)	0.2 (1.8)	0.1 (0.9)	0.5 (2.1)	0.1 (1.4)	0.1 (1.1)	0.1 (1.0)	0.1 (0.5)
	0-30	0-30	0-10	0-30	0-10	0-10	0-30	0-10	0-10	0-3
Other (%)	1.2 (3.7)	1.6 (4.3)	0.7 (2.8)	1.3 (2.8)	1.1 (4.1)	3.0 (9.6)	1.1 (3.4)	1.2 (3.5)	0.7 (1.9)	1.0 (2.2)
	0-50	0-50	0-40	0-20	0-50	0-50	0-40	0-50	0-10	0-10
Local characteristics										
Open water (%)	37.4 (31.4)	29.5 (28.7)	47.1 (31.8)	29.4 (28.9)	41.4 (31.8)	61.2 (21.9)	42.3 (30.3)	33.7 (30.6)	17.6 (26.0)	64.6 (28.1)
	0-100	0-100	0-100	0-95	0-100	0-95	0-98	0-95	0-95	0-100

Emergent vegetation (%)	23.4 (27.6)	23.0 (28.3)	24.0 (26.7)	27.9 (29.5)	21.2 (26.3)	19.9 (17.3)	29.9 (25.9)	19.4 (28.6)	16.2 (29.4)	12.0 (19.9)
	0-100	0-100	0-100	0-100	0-100	0-95	0-100	0-100	0-100	0-85
Wet meadow (%)	35.1 (33.6)	42.3 (34.9)	26.3 (29.8)	39.4 (34.6)	32.9 (33.0)	13.2 (12.0)	25.5 (25.9)	43.5 (35.9)	56.8 (39.6)	14.9 (18.3)
	0-100	0-100	0-100	0-100	0-100	0-50	0-100	0-100	0-100	0-90
Shoreline Mudflat (%)	3.7 (11.2)	4.8 (14.0)	2.3 (5.9)	2.9 (9.3)	4.1 (12.0)	4.6 (4.4)	1.9 (5.9)	3.1 (8.8)	9.5 (22.9)	8.4 (8.2)
	0-100	0-100	0-50	0-100	0-100	0-15	0-90	0-95	0-100	0-30
Heterogeneity indices										
Local heterogeneity	1.8 (0.6)	1.8 (0.7)	1.8 (0.6)	1.8 (0.6)	1.8 (0.6)	2.1 (0.7)	2.0 (0.6)	1.7 (0.6)	1.5 (0.7)	1.8 (0.7)
	1-3.8	1-3.8	1-3.8	1-3.8	1-3.8	1.1-3.4	1-3.8	1-3.8	1-3.8	1-3.5
Landscape heterogeneity	1.9 (0.6)	1.8 (0.6)	2.1 (0.6)	1.9 (0.6)	1.9 (0.6)	1.9 (0.6)	1.9 (0.6)	1.9 (0.6)	1.9 (0.6)	1.9 (0.6)
	1-4.2	1-3.9	1-4.2	1-3.9	1-4.2	1-3.9	1-4.2	1-3.6	1-3.6	1-3.5

[1] Landscape variables that I included as natural land cover and are incorporated in the landscape heterogeneity metric

[2] Landscape variables that are included as non-agricultural human land uses

Table 3. Amount of variation in species richness (total species richness or functional group richness) explained by models of log wetland size (area) and variation explained by best performing habitat models for residuals of species richness from the area models explained by covariates of the Inverse Simpson diversity index of proximate cover (Local), Inverse Simpson diversity index of landscape-scale habitat heterogeneity (Land), wetland classification (Class), wetland ownership (Ownership), restoration status (Restoration), latitude (Latitude), and percentages of wetland (Wetland %), grassland (Grass%), woodland (Wood%), agricultural land (Ag%), and human land use (Human%) within a 400-m buffer of the wetland. Both area models and habitat models include a random site effect. Sites were randomly assigned to model or validation data sets for the habitat model testing. After best-performing habitat models were generated using model data sets, each best-performing habitat model was evaluated using the validation dataset. Differences in the amount of variation in species richness explained did not differ substantially when models were applied to the validation dataset, indicating that models were not overfit.

Species richness	Area model	Variation explained by area model (%)	Best habitat model	Variation explained by best habitat model (%)	
				Model data	Validation data
Overall species richness	Log area	63	Class + Ownership + Restoration + Wetland% + Wood% + Human% + Local + Local^2 + Land	10	7
Waterfowl	Log area	50	Class + Ownership + Restoration + Latitude + Wood% + Human% + Local + Local^2 + Land	9	3
Grebes	Log area	44	Class + Restoration + Wetland% + Local + Local^2 + Land	2	<0.1
Rails	Log area	7	Class + Restoration + Grassland% + Human% + Local	5	3

Wading birds	Log area	20	Class + Ownership + Latitude + Grass% + Ag%	4	4
Shorebirds	Square root area	19	Class + Latitude + Grass% + Wood% + Ag% + Human% + Local	9	12
Passerines	Log area	13	Class + Ownership + Restoration + Latitude + Wetland% + Grass% + Ag% + Human% + Local	10	13
Blackbirds	Log area	21	Class + Ownership + Restoration + Latitude + Wetland% + Grass% + Wood% + Ag% + Human% + Local + Local^2 + Land	20	21
Other colonial waterbirds	Log area	33	Class + Latitude + Wetland% + Grass% + Human% + Local + Land + Land^2	3	1

Table 4. Regression coefficients and SE (in italics) for best habitat models explaining variation in species richness and species group richness. Values are given only if variable is included in the best habitat model. All values are multiplied by 100 for clarity of presentation. Best habitat models are presented in an effects parameterization and therefore habitat intercepts represent the reference value for privately owned, non-restored, alkali wetlands (where ownership, restoration status, and wetland class are included in the best habitat model). If one or more of these three categorical variables is not included in the best habitat models (as in the case of grebes, rails, wading birds, shorebirds, and other colonial waterbirds), the intercept represents the value for a wetland of the remaining categorical variables' reference levels (in the case of grebes and rails, this translates to the expected mean value for a restored, alkali wetland; in the case of wading birds, the intercept value is the expected mean value for a privately owned, alkali wetland; in the case of shorebirds and other colonial waterbirds, the intercept is the expected mean value for an alkali wetland). Means of other wetland classes and privately owned wetlands can be obtained by adding the intercept with the factor coefficients of interest. Variables are abbreviated as follows: Int = Intercept, Temp = temporary wetlands, Seas = seasonal wetlands, Semi = semipermanent wetlands, Perm = permanent wetlands, Pub = publicly owned wetlands, Rest = restored wetlands, Lat = latitude, Wet = percentage of wetland cover, Grass = percentage of grassland cover, Ag = percentage of agricultural land use, Human = percentage of non-agricultural human land use, Local = local-scale heterogeneity, Local^2 = quadratic term for local -scale heterogeneity, Land = landscape-scale heterogeneity, Land^2 = quadratic term for landscape-scale heterogeneity. Coefficients for percentages of land cover are reported to the tenths place due to the number of coefficient values <1. All other coefficients are rounded to the nearest whole number.

Group	Int	Temp	Seas	Semi	Perm	Pub	Rest	Lat	Wet	Grass	Wood	Ag	Human	Local	Local^2	Land	Land^2
Overall species richness	-375	-120	-49	-40	56	55	83		-1.0		-6.6		-3.3	294	-52	40	
	102	*60*	*57*	*56*	*71*	*20*	*21*		*0.8*		*2.0*		*2.9*	*87*	*21*	*17*	
Waterfowl	-934	-76	-5	-39	27	38	47	15			-4.9		-2.8	148	-27	36	
	245	*39*	*37*	*37*	*46*	*14*	*14*	*5*			*1.3*		*1.9*	*56*	*14*	*11*	
Grebes	-37	10	8	5	21		-5		-0.2					27	-5	3	
	14	*8*	*8*	*8*	*10*		*3*		*0.1*					*12*	*3*	*2*	
Rails	-35	18	15	25	26		8			-0.1			-0.6	9			

	10	*10*	*9*	*9*	*12*		*3*			*0.1*			*0.5*	*3*			
Wading birds	144	6	4	7	11	4		-3		-0.1		-0.1					
	41	*7*	*7*	*7*	*8*	*2*		*1*		*0.0*		*0.0*					
Shorebirds	123	-56	-52	-58	-55			-2		0.3	-0.4	0.2	0.7	3			
	51	*9*	*8*	*8*	*10*			*1*		*0.1*	*0.3*	*0.1*	*0.4*	*2*			
Passerines	172	6	-2	16	14	8	20	-4	-0.5	-0.2		-0.3	-0.7	9			
	73	*12*	*12*	*12*	*15*	*5*	*4*	*2*	*0.2*	*0.1*		*0.1*	*0.6*	*3*			
Blackbirds	178	11	21	31	26	4	4	-5	-0.2	-0.1	-0.9	0.1	-0.6	37	-8	6	
	45	*7*	*7*	*7*	*8*	*3*	*3*	*1*	*0.1*	*0.0*	*0.2*	*0.1*	*0.3*	*10*	*3*	*2*	
Other colonial waterbirds	-142	-3	-3	1	11			3	0.3	0.1			1.6	4		15	-5
	71	*12*	*11*	*11*	*14*			*1*	*0.2*	*0.1*			*0.6*	*3*		*17*	*4*

Table 5. Amount of variation in species abundance (total number of indicated breeding pairs for a given species) explained by models of log wetland size (area) and variation explained by best habitat models for residuals of abundance from the area models explained by covariates of the Inverse Simpson diversity index of local scale habitat heterogeneity (Local), Inverse Simpson diversity index to landscape-scale habitat heterogeneity (Land), wetland classification (Class), wetland ownership (Ownership), restoration status (Restoration), latitude (Latitude), and percentages of wetland (Wetland %), grassland (Grassland%), woodland (Woodland%), agricultural land (Agriculture%), and human land use (Human%) within a 400-m buffer of the wetland. Both area and habitat models include a random effect of site. Sites were randomly assigned to model or validation data sets for the habitat model testing. After best-performing habitat models were generated using model data sets, each best-performing habitat model was evaluated using the validation dataset. Differences in the amount of variation in species richness explained did not differ substantially when models were applied to the validation dataset, indicating that models were not overfit. Only species with occurrences on ≥ 30 unique wetlands were modeled individually.

Species	Area Model	Variation explained by area model (%)	Best Habitat Model	Variation explained by best habitat model (%) Model data	Validation data
Overall abundance	Root	54	Class + Ownership + Restored + Latitude + Grassland% + Woodland% + Local	7	5
Waterfowl					
Canada Goose	Root	4	Class + Human% + Local + Local^2	1	<1
Wood Duck	Log	3	Class + Latitude + Woodland% + Land	3	3
Blue-winged Teal	Log	39	Class + Ownership + Restored + Latitude + Woodland% + Local + Land	7	2
Northern Shoveler	Area	22	Class + Ownership + Restored + Latitude + Wetland% + Woodland% + Human% + Local	6	4

Gadwall	Root	32	Class + Ownership + Restored + Latitude + Woodland% + Agriculture% + Land	4	7
American Wigeon	Area	20	Class + Ownership + Grassland% + Local	1	12
Mallard	Log	24	Class + Ownership + Restored + Latitude + Woodland% + Human% + Land	2	6
Green-winged Teal	Area	8	Class + Ownership + Latitude + Woodland% + Human% + Land	2	<1
Northern Pintail	Log	5	Class + Restored + Woodland% + Agriculture% + Human% + Local + Local^2 + Land	3	2
Canvasback	Root	17	Class + Restored + Latitude + Wetland% + Human% + Local	2	2
Redhead	Root	22	Class + Ownership + Restored + Latitude + Grassland% + Woodland% + Local + Local^2	6	3
Ring-necked Duck	Root	9	Class + Wetland% + Grassland%	2	<1
Lesser Scaup	Root	21	Class + Grassland% + Wetland% + Woodland% + Human% + Land	7	4
Ruddy Duck	Root	25	Class + Wetland% + Grassland% + Local + Local^2	2	<1
American Coot	Root	35	Class + Latitude + Grassland% + Woodland% + Agriculture% + Local + Local^2 + Land	7	8
Grebes					
Pied-billed Grebe	Root	31	Class + Latitude + Grassland% + Local + Local^2	6	6
Eared Grebe	Root	6	Class + Grassland%	<1	1
Rails					

Virginia Rail	Log	5	Class + Latitude + Grassland% + Agriculture% + Human% + Local + Land	6	5
Sora	Log	10	Class + Restored + Latitude + Grassland% + Human% + Land	3	3
Wading Birds					
American Bittern	Log	12	Class + Ownership + Agriculture% + Local	1	5
Black-crowned Night-Heron	Log	1	Ownership + Restored + Land	<1	<1
Shorebirds					
Killdeer	Root	12	Class + Latitude + Wetland% + Grassland% + Agriculture% + Human%	6	5
Marbled Godwit	Area	4	Class + Ownership + Wetland% + Agriculture%	1	2
Wilson's Snipe	Log	1	Class + Grassland% + Local	2	5
Willet	Log	6	Class + Latitude + Grassland% + Woodland% + Agriculture% + Land + Land^2	6	11
Wilson's Phalarope	Area	12	Class + Wetland% + Grassland% + Land	3	8
Blackbirds					
Yellow-headed	Log	20	Class + Ownership + Wetland% + Grassland% + Local + Land + Land^2	6	3

Blackbird					
Red-winged Blackbird	Log	32	Class + Latitude + Wetland% + Grassland% + Human%	6	11
Passerines					
Willow Flycatcher	Area	9	Class + Ownership + Wetland% + Grassland% + Human% + Local + Land + Land^2	3	2
Sedge Wren	Root	3	Class + Restored + Latitude + Wetland% + Grassland% + Agriculture% + Land	3	5
Marsh Wren	Log	9	Class + Ownership + Restored + Grassland% + Agriculture% + Local + Local^2 + Land	5	4
LeConte's Sparrow	Root	3	Class + Restored + Latitude + Grassland% + Agriculture% + Local + Local^2 + Land	2	1
Common Yellowthroat	Log	13	Class + Restored + Latitude + Wetland% + Grassland% + Woodland% + Agriculture% + Human% + Local	11	11
Other colonial waterbirds					
Franklin's Gull	Root	2	Class + Woodland% + Agriculture% + Human%	1	7
Ring-billed Gull	Root	8	Class + Ownership + Human% + Local	5	4
Black Tern	Log	12	Class + Ownership + Restored + Latitude + Grassland% + Local + Land	3	5

Double-crested Cormorant	Area	8	Class + Grassland% + Woodland% + Local + Local^2	1	3
American White Pelican	Root	5	Class + Ownership + Grassland% + Human% + Land + Land^2	1	1

Table 6. Regression coefficients and SE (in italics) for area models for variation in abundances. All values are multiplied by 100 for clarity of presentation. Only species with occurrences on ≥ 30 unique wetlands were modeled individually.

Species	Intercept	Area Coefficient
Overall abundance	42.0	1,999.9
	104.7	*53.6*
Waterfowl		
Canada Goose	-3.0	11.6
	3.0	*1.5*
Wood Duck	5.0	4.8
	1.1	*0.8*
Blue-winged Teal	312.6	229.2
	10.9	*8.2*
Northern Shoveler	43.8	6.9
	4.9	*0.4*
Gadwall	-11.4	128.6
	10.4	*5.3*
American Wigeon	-0.1	2.7
	2.0	*0.2*
Mallard	139.5	113.2
	7.6	*5.7*
Green-winged Teal	11.5	2.0
	2.3	*0.2*
Northern Pintail	30.3	16.1
	2.8	*2.1*
Canvasback	-13.5	22.6
	2.9	*1.5*
Redhead	-10.1	50.0
	5.3	*2.7*
Ring-necked Duck	-3.0	10.4
	1.9	*0.9*
Lesser Scaup	-20.2	45.0
	4.9	*2.5*
Ruddy Duck	-37.1	87.8
	8.5	*4.3*

American Coot	-28.8	213.9
	16.5	*8.4*
Grebes		
Pied-billed Grebe	-8.7	36.3
	3.1	*1.6*
Eared Grebe	-86.4	121.6
	27.7	*14.1*
Rails		
Virginia Rail	14.3	10.2
	1.6	*1.2*
Sora	39.7	24.6
	2.9	*2.2*
Wading Birds		
American Bittern	8.3	9.3
	1.0	*0.7*
Black-crowned Night-Heron	17.5	21.1
	9.6	*7.1*
Shorebirds		
Killdeer	10.5	22.2
	3.3	*1.7*
Marbled Godwit	2.7	0.9
	1.7	*0.1*
Wilson's Snipe	5.6	2.2
	0.8	*0.6*
Willet	9.6	8.4
	1.3	*0.9*
Wilson's Phalarope	7.8	2.4
	2.4	*0.2*
Blackbirds		
Yellow-headed Blackbird	321.8	367.0
	28.7	*21.4*
Red-winged Blackbird	299.9	172.6

	9.7	*7.3*
Passerines		
Willow Flycatcher	1.9	1.0
	1.1	*0.1*
Sedge Wren	8.4	6.4
	2.2	*1.1*
Marsh Wren	91.9	80.9
	9.9	*7.4*
LeConte's Sparrow	0.3	4.9
	1.5	*0.8*
Common Yellowthroat	94.1	50.2
	5.1	*3.8*
Other colonial waterbirds		
Franklin's Gull	-18.4	33.7
	12.6	*6.4*
Ring-billed Gull	-16.3	23.7
	4.3	*2.2*
Black Tern	93.9	92.3
	9.8	*7.3*
Double-crested Cormorant	1.0	1.6
	1.9	*0.2*
American White Pelican	-8.6	18.0
	4.6	*2.4*

Table 7. Regression coefficients and SE (in italics) for best habitat models for variation in abundances. Values are given only if variable is included in the best habitat model. All values are multiplied by 100 for clarity of presentation. Only species with occurrences on ≥ 30 unique wetlands were modeled individually. Best habitat models are presented in an effects parameterization and therefore habitat model intercepts represent the reference value for privately owned, non-restored, alkali wetlands (where ownership, restoration status, and wetland class are included in the best habitat model). Means of other wetland classes and privately owned wetlands can be obtained by adding the intercept with the factor coefficients of interest. Variables are abbreviated as follows: Int = Intercept, Temp = temporary wetlands, Seas = seasonal wetlands, Semi = semipermanent wetlands, Perm = permanent wetlands, Pub = publicly owned wetlands, Rest = restored wetlands, Lat = latitude, Wet = percentage of wetland cover, Grass = percentage of grassland cover, Ag = percentage of agricultural land use, Human = percentage of non-agricultural human land use, Local = local-scale heterogeneity, Local2 = quadratic term for local -scale heterogeneity, Land = landscape-scale heterogeneity, Land2 = quadratic term for landscape-scale heterogeneity. Coefficients for percentages of land cover are reported to the tenths place due to the number of coefficient values <1. All other coefficients are rounded to the nearest whole number.

Species	Int	Temp	Seas	Semi	Perm	Pub	Rest	Lat	Wet	Grass	Wood	Ag	Human	Local	Local^2	Land	Land^2
Overall abundance	1,015	427	549	623	1,654	296	191	-50		-4.8	-15.6			367			
	1,932	*327*	*315*	*312*	*385*	*112*	*115*	*39*		*2.0*	*10.3*			*82*			
Waterfowl																	
Canada Goose	60	-22	-16	-25	11								-1.2	-53	16		
	34	*21*	*20*	*20*	*25*								*1.0*	*30*	*7*		
Wood Duck	115	4	3	4	-6			-3			0.3					3	
	38	*6*	*6*	*6*	*8*			*1*			*0.2*					*2*	
Blue-winged Teal	1,224	-95	-29	-145	112	31	53	-28			-5.6			24		51	

	401	*66*	*64*	*63*	*79*	*23*	*23*	*8*			*2.2*			*17*		*18*
Northern Shoveler	-353	-96	-73	-101	-110	14	12	8	0.8		-1.3		-2.6	23		
	165	*28*	*27*	*27*	*33*	*10*	*10*	*3*	*0.4*		*0.9*		*1.4*	*7*		
Gadwall	777	-76	-78	-110	96	32	37	-17			-5.4	0.4				39
	374	*61*	*59*	*59*	*73*	*22*	*22*	*8*			*2.0*	*0.4*				*17*
American Wigeon	20	-9	-7	-16	1	-6				0.2				-5		
	17	*16*	*15*	*15*	*19*	*5*				*0.1*				*4*		
Mallard	426	-17	-2	-22	23	27	36	-11			-2.1		-3.1			34
	281	*46*	*44*	*44*	*55*	*16*	*16*	*6*			*1.5*		*2.2*			*13*
Green-winged Teal	-117	-30	-19	-31	-24	7		3			-0.5		0.7			7
	86	*14*	*14*	*14*	*17*	*5*		*2*			*0.5*		*0.7*			*4*
Northern Pintail	-29	-35	-29	-56	-39		17				-0.9	0.2	-1.5	54	-12	7
	35	*20*	*19*	*19*	*24*		*7*				*0.7*	*0.1*	*1.0*	*30*	*7*	*6*
Canvasback	-73	-11	-12	-14	3		3	2	-0.2				-0.4	2		
	40	*7*	*7*	*7*	*8*		*2*	*1*	*0.1*				*0.3*	*2*		
Redhead	-511	101	102	121	159	23	14	9		-0.2	-1.3			-32	15	
	173	*28*	*27*	*27*	*33*	*10*	*10*	*3*		*0.2*	*0.9*			*41*	*10*	
Ring-necked Duck	-30	22	24	28	47				0.2	0.1						
	10	*10*	*10*	*10*	*12*				*0.1*	*0.1*						

Lesser Scaup	92	-106	-109	-119	-34				-0.5	0.2	-2.0		-1.3			14
	25	*23*	*22*	*22*	*27*				*0.3*	*0.1*	*0.8*		*1.1*			*6*
Ruddy Duck	51	-24	-23	-27	-4				0.5	-0.4				-50	17	
	45	*27*	*26*	*26*	*33*				*0.4*	*0.2*				*40*	*10*	
American Coot	-523	141	169	161	279			7		-0.5	-2.9	0.4		-61	27	23
	280	*45*	*43*	*43*	*53*			*6*		*0.3*	*1.5*	*0.3*		*65*	*16*	*13*
Grebes																
Pied-billed Grebe	40	39	42	40	63			-2		-0.1				24	-4	
	55	*10*	*9*	*9*	*11*			*1*		*0.1*				*14*	*3*	
Eared Grebe	134	-109	-125	-133	-126					-0.7						
	75	*81*	*78*	*77*	*97*					*0.5*						
Rails																
Virginia Rail	149	15	11	15	21			-4		-0.1		-0.1	0.5	4		2
	40	*7*	*6*	*6*	*8*			*1*		*0.0*		*0.0*	*0.3*	*2*		*2*
Sora	-184	26	27	27	48		9	3		-0.2			-1.1	10		-8
	91	*15*	*14*	*14*	*18*		*5*	*2*		*0.1*			*0.7*	*4*		*4*
Wading Birds																
American	-18	11	11	9	8	2						-0.1		5		

Bittern																
	8	*7*	*7*	*7*	*8*	*2*						*0.0*		*2*		
Black-crowned Night-Heron	1					16	19								-8	
	14					*9*	*9*								*7*	
Shorebirds																
Killdeer	263	-27	-22	-35	6			-6	0.2	0.3		0.4	1.5			
	74	*13*	*12*	*12*	*15*			*2*	*0.2*	*0.1*		*0.1*	*0.6*			
Marbled Godwit	-8	2	9	1	34	7			-0.2			0.2				
	15	*15*	*14*	*14*	*18*	*5*			*0.2*			*0.1*				
Wilson's Snipe	-4	2	1	2	3					0.0				1		
	2	*2*	*2*	*2*	*3*					*0.0*				*1*		
Willet	-5	-23	-22	-24	-10			1		0.1	-0.2	0.1			-14	3
	34	*6*	*5*	*5*	*7*			*1*		*0.0*	*0.2*	*0.0*			*8*	*2*
Wilson's Phalarope	17	-15	-15	-15	-32				0.1	0.0					-2	
	6	*5*	*5*	*5*	*7*				*0.1*	*0.0*					*1*	
Blackbirds																

Yellow-headed Blackbird	-148	168	154	183	309	46			-1.0	-0.8				67		-118	24
	100	*58*	*55*	*54*	*68*	*19*			*0.8*	*0.3*				*15*		*83*	*19*
Red-winged Blackbird	905	62	74	74	155			-21	-0.8	-0.3			-2.0				
	183	*32*	*31*	*31*	*38*			*4*	*0.4*	*0.2*			*1.6*				
Passerines																	
Willow Flycatcher	-5	-1	-1	-1	4	1			0.0	0.0			-0.1	1		4	-1
	2	*1*	*1*	*1*	*2*	*1*			*0.0*	*0.0*			*0.1*	*0*		*2*	*1*
Sedge Wren	-48	6	4	5	6		4	1	-0.1	-0.1		-0.1				-2	
	28	*5*	*5*	*4*	*6*		*2*	*1*	*0.1*	*0.0*		*0.0*				*1*	
Marsh Wren	-94	55	40	77	56	10	12			-0.3		-0.4		60	-11	-14	
	44	*25*	*24*	*24*	*30*	*9*	*9*			*0.2*		*0.2*		*37*	*9*	*7*	
LeConte's Sparrow	-9	-1	-1	-1	-2		1	0		0.0		0.0		-2	1	-1	
	8	*1*	*1*	*1*	*2*		*0*	*0*		*0.0*		*0.0*		*2*	*0*	*0*	
Common Yellowthroat	398	37	28	39	48		16	-10	-0.3	-0.5	0.7	-0.3	-1.0	17			
	91	*16*	*15*	*15*	*18*		*5*	*2*	*0.2*	*0.1*	*0.5*	*0.1*	*0.8*	*4*			

Other colonial waterbirds																	
Franklin's Gull	-4	3	2	2	0						0.1	0.0	0.3				
	3	*3*	*3*	*3*	*3*						*0.1*	*0.0*	*0.1*				
Ring-billed Gull	53	-46	-47	-48	-49	-6							0.6	-3			
	9	*8*	*8*	*8*	*10*	*3*							*0.4*	*2*			
Black Tern	-236	60	66	65	87	11	-12	4		-0.1				6		-15	
	132	*22*	*21*	*21*	*25*	*8*	*8*	*3*		*0.1*				*5*		*6*	
Double-crested Cormorant	0	-4	-4	-4	-6					0.0	0.1			4	-1		
	6	*3*	*3*	*3*	*4*					*0.0*	*0.1*			*5*	*1*		
American White Pelican	-9	4	3	5	3	-1				0.0			0.3			5	-1
	4	*2*	*2*	*2*	*3*	*1*				*0.0*			*0.1*			*3*	*1*

FIGURES

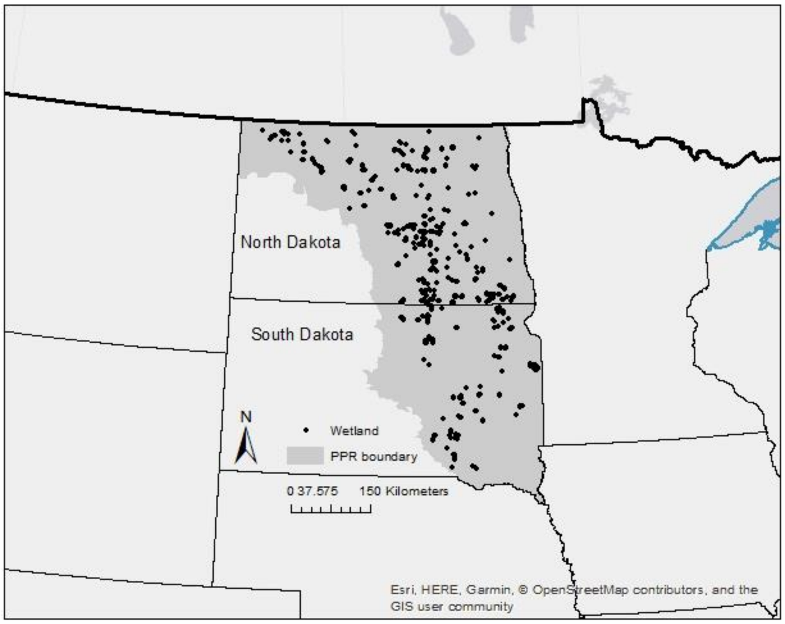

Figure 1-1. Distribution of 1,097 wetlands surveyed to evaluate the relationship of wetland bird diversity and abundances with wetland habitat in the Prairie Pothole Region (PPR) of North and South Dakota in 1995-1997.

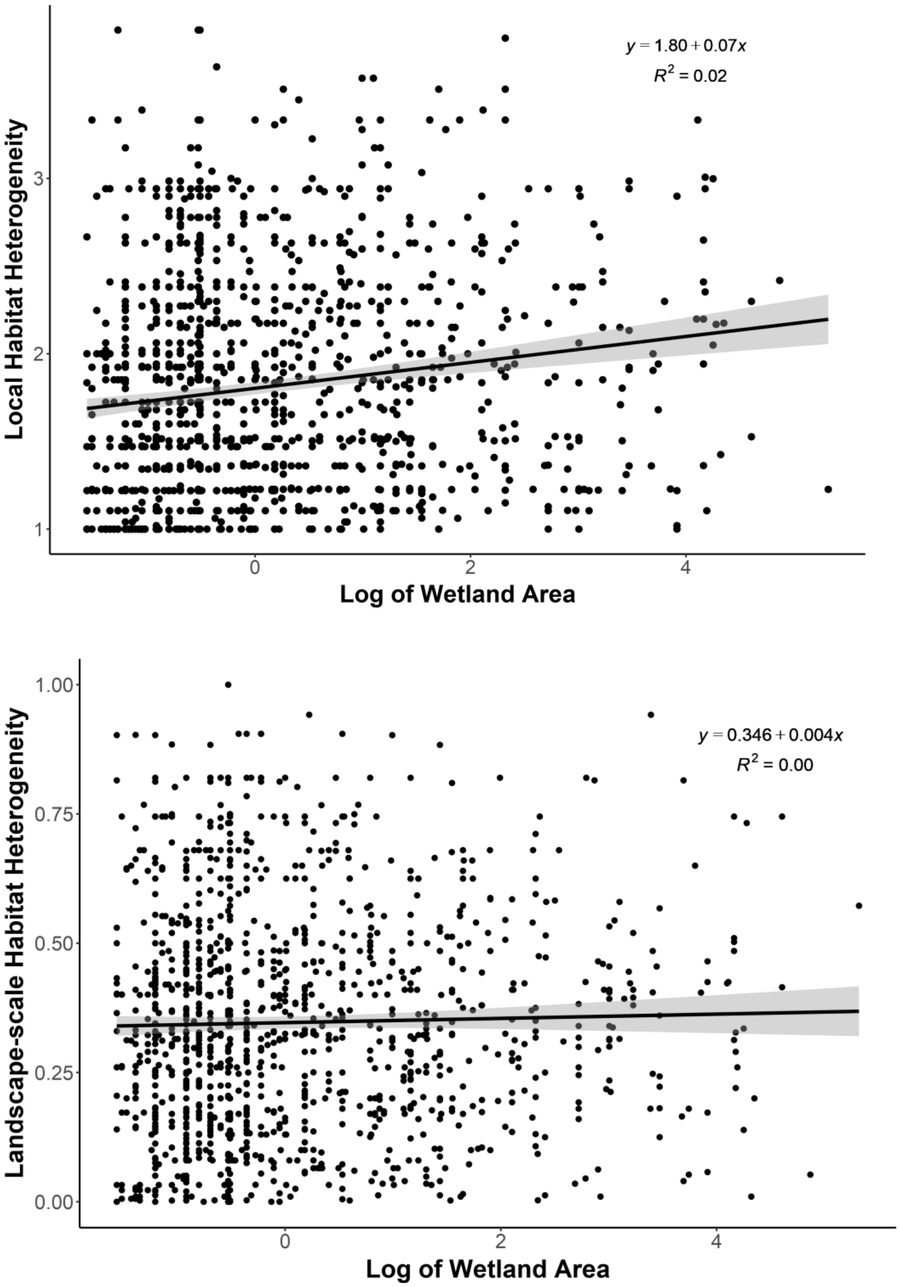

Figure 1-2. Relationship between habitat heterogeneity and log-transformed area for 1,097 wetlands in the Prairie Pothole Region of North and South Dakota. Habitat heterogeneity measures were calculated using Simpson's Diversity Index of either (A) local-scale habitat heterogeneity or (B) landscape-scale habitat heterogeneity.

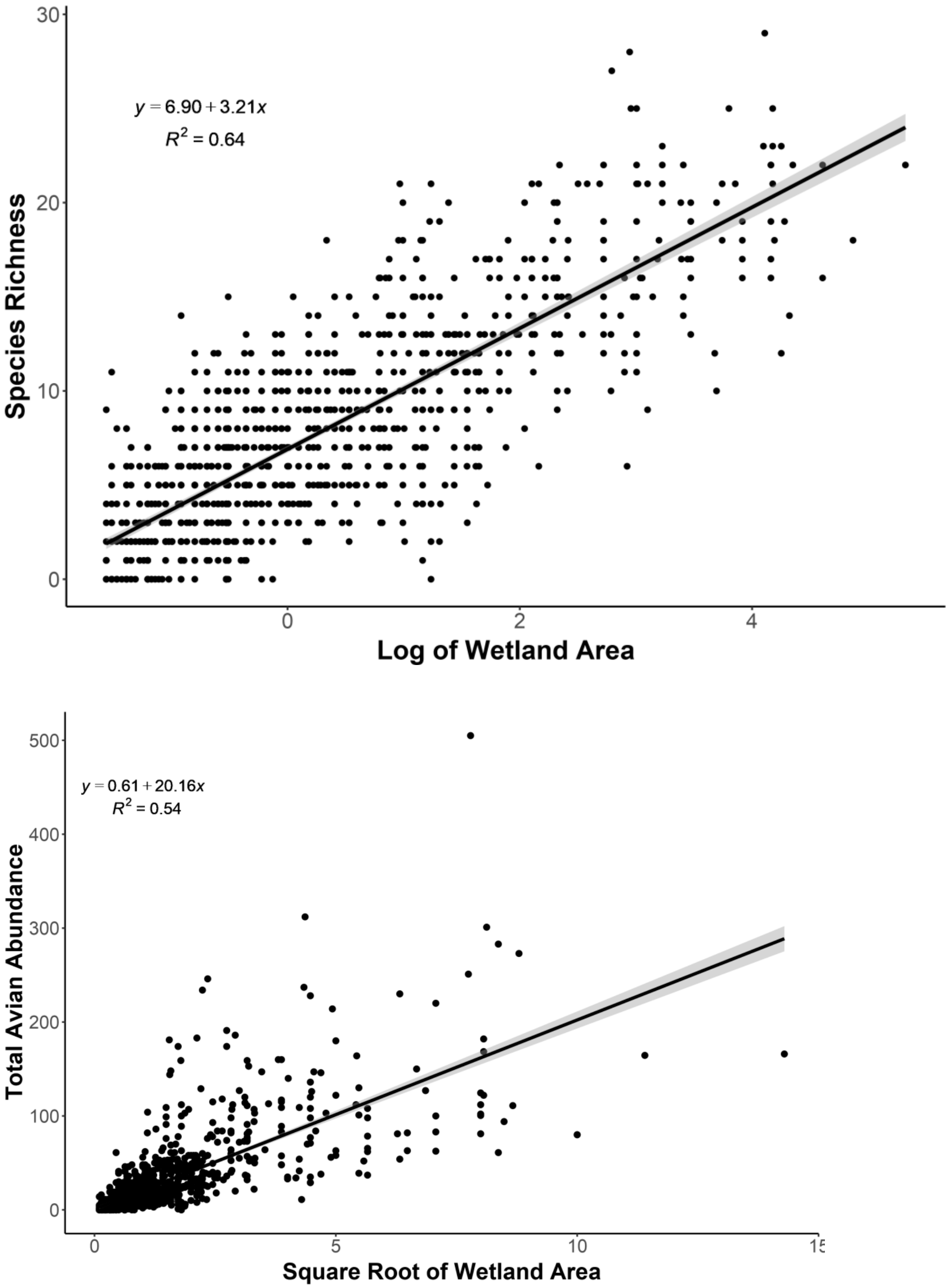

Figure 1-3. Relationship between (A) species richness or (B) total avian abundance and log-transformed area for 1,097 wetlands in the Prairie Pothole Region of North and South Dakota. Gray bands represent 95% confidence intervals. Note that reported R-squared values are slightly different from those reported in Table 3 because these values were created from all 1,097 wetlands, not just the 770 wetlands used for habitat model creation.

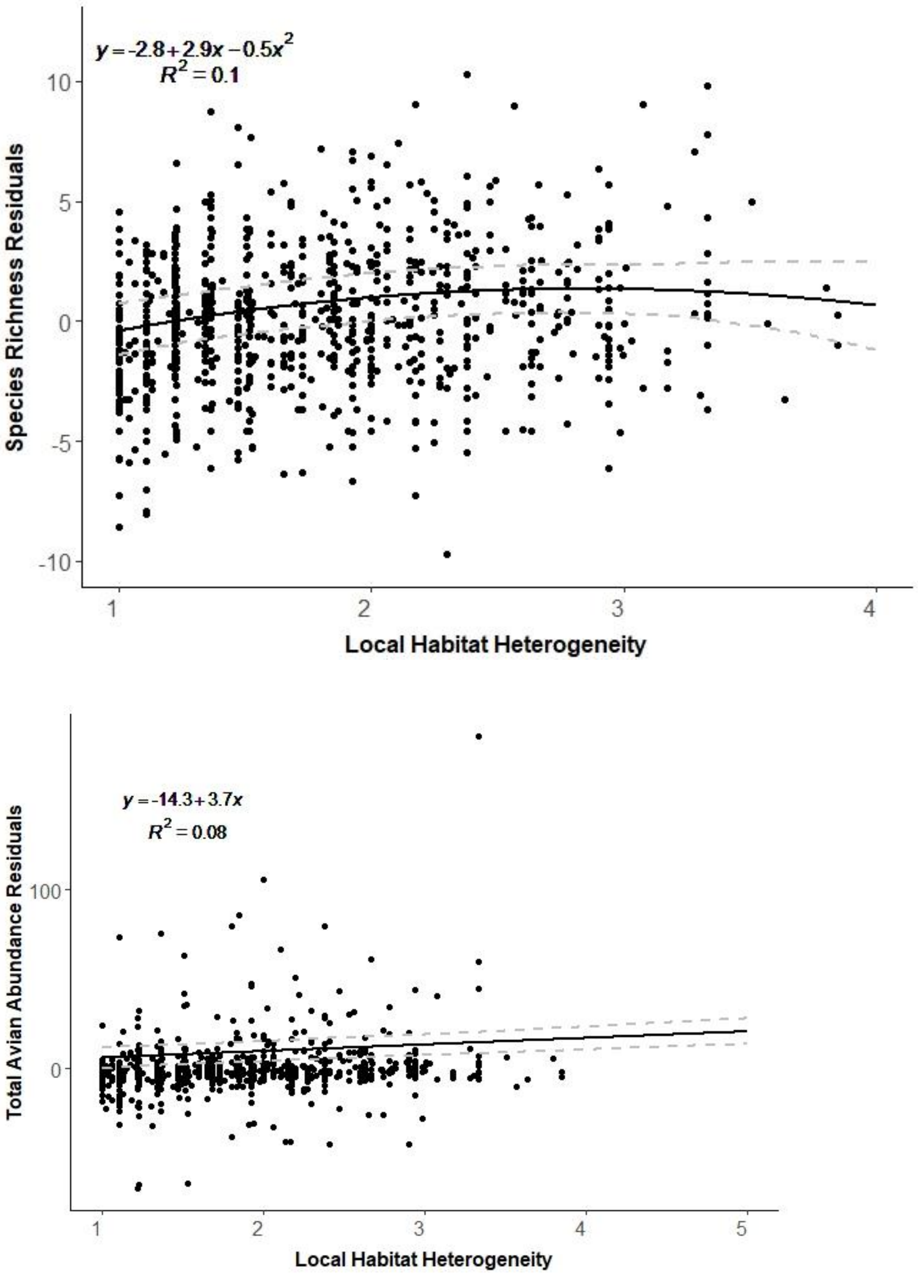

Figure 1-4. Relationship between (A) species richness or (B) total avian abundance and local habitat heterogeneity for the training dataset of 770 different wetlands (845 wetland-years) in the Prairie Pothole Region of North and South Dakota. Black line represents predicted values of species richness/abundance at different values of local habitat heterogeneity for permanent wetlands when all other variables are held at their mean or reference values. The intercept is influenced by the additional coefficient values of the other variables included in the models (see Tables 4 & 6). Gray lines represent upper and lower 95% prediction intervals.

Chapter 2: Hierarchical modeling to identify habitat associations of wetland-obligate birds in Great Lakes coastal wetlands

SYNOPSIS

To better understand the habitat associations of rare or declining wetland birds in the Great Lakes basin, I developed single-species multi-scale occupancy models for eight species of regional conservation concern using seven years (2011-2017) of bird survey data from the Great Lakes Coastal Wetland Monitoring Program and remotely sensed landscape data. These hierarchical models account for separate processes of occurrence and, given occurrence, detection, while simultaneously accounting for the spatial and temporal replication of the sampling methodology. Effective sample sizes for two declining tern species (Black Tern [*Chlidonias niger*] and Forster's Tern [*Sterna forsteri*]) were too low to reliably model multi-scale occupancy and detection patterns, and more targeted monitoring of these colonial-nesting species will be required to better understand their habitat associations. My results for the secretive marsh birds indicate that Pied-billed Grebe (*Podilymbus podiceps*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Common Gallinule (*Gallinula galeata*), Least Bittern (*Ixobrychus exilis*), and American Bittern (*Botaurus lentiginosus*) are primarily eurytopic species, with tolerance for a wide range of habitat characteristics. While these species were uncommonly encountered, my hierarchical models suggest that individual species occupied 35-68% of surveyed wetlands during at least one year of the study. Detection probabilities were consistently above 80% for all six of these species and were enhanced by active listening periods using broadcast calls for all but American Bitterns. Anthropogenic influences such as human population density, watershed-scale percentages of agriculture and development, and percentages of cropland and development within 200-m of a given point had surprisingly little effect on the site-level and point-level occupancy for these species. These results suggest that wetland loss is more detrimental to these species than habitat degradation, and

thus protection of any wetlands will be a valuable contribution towards conservation of these eurytopic species.

INTRODUCTION

Successful conservation of birds and other wildlife requires protection of large areas of appropriate habitat (Robbins 1979; Soule & Terborgh 1999; Winter & Faaborg 1999; Riffell et al. 2001; Brown et al. 2019). Determining what constitutes appropriate habitat requires an understanding of the environmental features birds use to select habitat (Wiens 1969). Previous work on habitat selection shows that birds make use of a variety of environmental cues at multiple spatial and temporal scales to select habitat (Johnson 1980; Wiens 1989; Levin & Levin 1992; Brennan & Schnell 2005; Meyer & Thuiller 2006; Conway & Gibbs 2011; Chave 2013; McGarigal et al. 2016). Furthermore, environmental stressors may make certain habitats less suitable by reducing the useable area of a site (e.g., Fletcher 2005), degrading the habitat quality (e.g., Crosbie & Chow-Fraser 1999), or by directly impacting reproductive success or health of the adult birds themselves (e.g., Barham et al. 2007). Given all these complicating factors, understanding the habitat associations of at-risk species is critical to developing specific and effective conservation plans.

Birds that use coastal wetlands in the Great Lakes region need targeted conservation efforts because of continuing loss and degradation of coastal habitat (USFWS 1985; SOLEC 2009). Great Lakes coastal wetlands are a valuable resource because of the critical habitat they provide birds and other wildlife, as well as their functional role in ecosystem dynamics (Sierszen et al. 2012; Luisetti et al. 2014). These wetlands are sites of nutrient storage and cycling, interfaces between aquatic and terrestrial systems, and moderating influences on the effects of waves on coastal regions (Luisetti et al. 2014). They also support important commercial and recreational fisheries (Trebitz and Hoffman 2015). Despite the important ecosystem services provided by these coastal habitats, over half of coastal wetlands in the Great Lakes basin have been converted to human uses such as agriculture, industry, and urban development since European settlement (SOLEC 2009, 2017). Human development in the Great Lakes basin has been primarily concentrated within one kilometer of the shoreline (Wolter et al.

2006), and increasing coastal development has been concurrent with increased intensity of recreational use of shorelines (Stynes et al. 1997; Johnson et al. 2002).

As a result of these conflicts between critical avian breeding habitat and human land use, populations of many species of coastal birds have shown concerning declines in this region (SOLEC 2009, 2017). Over half of the 19 obligate wetland-breeding species that use Great Lakes coastal wetland habitat have declined significantly within the Great Lakes basin (Tozer 2013). For some of these species, declines have been severe or widespread enough to merit attention beyond the Great Lakes basin. For example, the King Rail (*Rallus elegans*) has been placed on the State of the Birds Yellow Watchlist of species with troubling declines and high threats (Rosenberg et al. 2014), with an average decline of 5.1% per year across its range between 1993 and 2015 (Sauer et al. 2017). The Black Tern (*Chlidonias niger*) has been identified as a Species in Steep Decline by the State of the Birds Report (North American Bird Conservation Initiative U.S. Committee 2014), and the Forster's Tern (*Sterna forsteri*) has been listed as a species of special concern in several Midwestern states (Wires et al. 2010; Pfannmuller et al. 2017).

Because of these population declines, it is especially important that I understand the habitat associations of these species. Previous studies have shown that wetland-level environmental conditions influence patterns of avian occupancy and distribution. For example, bird abundances respond to wetland size (Tozer et al. 2010; Uzarski et al. 2017; Elliott et al. 2019) and hydrology (Jobin et al. 2009; Tozer et al. 2010; Chin et al. 2014). Some studies have found an effect of wetland hydrogeomorphic class on species richness (Elliott et al. 2019) or community composition (Hanowski et al. 2007)—both measures that derive from occupancy patterns. Birds have also been documented responding in abundance or occupancy to local-scale wetland features including vegetation structure (Riffell et al. 2001), plant cover such as emergent vegetation (Bolenbaugh et al. 2011; Tozer 2016; Elliott et al. 2019), plant species composition (Glisson et al. 2015), and open water cover (Tozer 2016; Elliott et al. 2019).

In addition to these wetland- or local-scale characteristics, birds are often affected by features beyond the immediate wetland. For instance, surrounding land cover (Fairbairn & Dinsmore 2001; Riffell et al. 2003; Tozer et al. 2010; Forcey et al. 2014; Tozer 2016; Panci et al. 2017) and anthropogenic stressors such as human land use, human population density, atmospheric deposition, and point source pollution also affect the suitability and use of particular habitats (see reviews in Brazner et al. 2007 and Danz et al. 2007), especially in the Great Lakes region (Howe et al. 2007b, 2007a). In the Great Lakes basin, wetland bird occupancy varies among the five lakes (SOLEC 2017), with occupancy probability of wetlands associated with each lake varying possibly as a result of water quality, anthropogenic influence, or species-specific geographic distribution patterns.

At temporal scales, bird distributions may show annual variation driven by climatic variables. Occupancy patterns of wetland birds in the Great Lakes region are affected by water levels (Craigie et al. 2003; Jobin et al. 2009; Gnass et al. 2018), as are wetland bird abundance (Timmermans et al. 2008; Gnass et al. 2018), density (DesGranges et al. 2006), and overall species diversity (Chin et al. 2014; Gnass et al. 2018). Furthermore, limited evidence shows that spring precipitation may affect the occurrence or abundance of wetland-obligate species such as Black Terns and Pied-billed Grebes among others (Forcey et al. 2007, 2011, 2014; Panci et al. 2017). Similarly, spring temperatures influence the occurrence or abundance of many of the same species (Forcey et al. 2007, 2011, 2014). These annual differences in wetland use are especially important to account for in occupancy studies because they violate the basic assumption of population closure between repeated sampling periods (i.e. birds are not moving into or out of the study area between surveys; MacKenzie et al. 2018).

In addition, availability of wetland birds and detection probabilities are often affected by temporal variables such as timing of sampling within the day and within the season (Conway & Gibbs 2011; Harms & Dinsmore 2014; Wiest & Shriver 2015). Within individual surveys, vocalizations and the ability of observers to detect vocalizations can be strongly influenced by wind conditions (Conway & Gibbs 2011;

Tozer 2016). Similarly, effects of traffic and ambient noise have been documented on vocalizations and occupancy patterns of forest birds (Pacifici 2007; Goodwin & Shriver 2010) and on the ability of observers to estimate distances to detected individuals in grasslands (Pacifici 2007; Koper et al. 2016; Rigby 2016). These impacts of ambient noise are also expected to affect the occupancy and detection probability of marsh birds (Conway & Gibbs 2001; Conway 2011). Noise is an especially important confounding variable to consider for roadside surveys or surveys conducted in urbanized areas, where anthropogenic noise may be particularly high.

These multiple spatial and temporal scales of occupancy can be structured within a hierarchy of nested levels (Johnson 1980; Meyer & Thuiller 2006; Kery & Royle 2016; McGarigal et al. 2016; MacKenzie et al. 2018). For example, at a wetland level, occupancy patterns may be influenced by characteristics of the wetland itself, or by surrounding landscape features such as land use and land cover or anthropogenic stressors. At an annual level, occupancy of a given wetland may change from year to year based on climatic variables such as water levels and temperature or precipitation. Within the wetland, a given location may be occupied or not based on the proximate composition of the habitat within a small buffer distance around the occupied location. At a visit, or survey level, I could assume within-season closure of the population, but possible changes in availability could occur due to temporal patterns in vocalization probabilities, or influences of confounding noise or weather conditions. This nested structure pairs nicely with many avian point count protocols (Bird Studies Canada 2008; Conway 2011; Uzarski et al. 2017), in which repeated visits are made within breeding seasons and across multiple years to multiple point count locations within the same wetlands.

Considerable research has been done on the variables that affect habitat use by wetland birds in general. However, no basin-wide effort has attempted to identify the landscape and proximate habitat features that influence habitat selection of Great Lakes coastal wetland birds while accounting for the spatial and temporal replication of bird surveys and the coinciding hierarchy of spatial and temporal occupancy levels (Riffell et al. 2001; Tozer et al. 2010). Therefore, the primary objective of this study is to identify variables that influence the occupancy of eight species of obligate wetland-breeding birds within a nested hierarchy of spatial and temporal levels.

I expected that probability of occurrence of obligate wetland birds would be highest in coastal wetlands with little landscape-scale human disturbance (as measured by proximity to agriculture, human development, and human populations; Danz et al. 2007) and a species-specific combination of climate and proximate vegetation and land cover characteristics. To test this hypothesis I developed species-specific multi-scale occupancy models of habitat association based on spatial and temporal covariates.

I selected eight species of obligate wetland-breeding birds that use coastal wetlands during the breeding season in the Great Lakes basin and show evidence of declining populations (Cooper 2008; Tozer 2013). The focal species are Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Common Gallinule (*Gallinula galeata*), Black Tern (*Chlidonias niger*), and Forster's Tern (*Sterna forsteri*). Of these species, the first six have been especially under-studied because of their cryptic coloration and inconspicuous behavior, thus they are designated as "secretive marshbirds" (Johnson 2009; Bolenbaugh et al. 2010; Conway 2011) The two remaining species of terns have experienced some of the most severe population declines of any wetland-obligate birds in the Great Lakes basin (Tozer 2013). With detailed habitat association information for all eight of these focal species, it will be possible to provide basin-wide predictive models of the distribution of Great Lakes coastal species that can then be used to develop species-specific management guidelines.

METHODS

Sampling Points

Bird surveys were conducted by the Great Lakes Coastal Wetland Monitoring Program (CWMP). The CWMP is a Great Lakes Basin-scale monitoring program that began in 2011 to assess conditions in Great Lakes coastal wetlands and is the largest ongoing Great Lakes coastal wetland monitoring effort. The CWMP includes basin-wide monitoring of a stratified, random sample of coastal wetlands in the U.S. and Canada (Uzarski et al. 2017). Coastal wetlands (hereafter "wetlands") were defined as wetlands >4 ha with a surface-water connection to one of the Great Lakes. Selected wetlands are re-sampled at least every five years and a rotating subset of 10% of the wetlands was resampled in consecutive years. See Uzarski et al. (2017) for additional details of sampling design and protocols.

Between 2011 and 2017, 641 individual wetlands were surveyed for birds as part of the CWMP random sample. Survey points are located at least 250-m apart and the number of points sampled per wetland is proportional to the size of the wetland, with 1-6 points per wetland—though in some cases up to 15 points were added opportunistically to especially large wetlands. A total of 1,392 points have been surveyed, with a mean of 321 points surveyed per year.

Bird Surveys

The CWMP bird survey methodology (outlined in Uzarski et al. 2017 and Panci et al. 2017) uses 100-m radius point counts and simultaneous unlimited-distance counts. Point counts last for 15 minutes. During minutes 6-10 (inclusive), broadcast calls of Pied-billed Grebe, Least Bittern, Virginia Rail, Sora, Common Gallinule, and American Coot (*Fulica americana*) are played at 80 decibels. Calls of Common Gallinule and American Coot are combined during the playback period. The broadcast calls include a 30-second recording of the vocalizations of the focal species and a 30-second period of silence between calls. During the survey period, birds are identified to species using visual and aural cues. Focal species are recorded in every 60 second bin in which they vocalize or are observed. Non-focal species are recorded only during the initial 60 second bin in which an individual is first observed. Data quality is ensured with extensive annual training, certification of field personnel, and mid-season quality control checks (Uzarski et al. 2017). Surveys are conducted from late May through mid-July, with dates differing slightly across the basin to reflect differences in the peak breeding season of birds across the latitudinal gradient. Observers also recorded data related to factors that may have affected detection probabilities during the survey, including standardized measures of noise and wind.

Environmental variables

Landscape-scale variables were quantified within 200-, 400-, 500-, 1000-, and 2000-m buffers of each sampling point using ArcGIS 10.2 (ESRI 2013; Table 1). In subsequent analysis I used the 200-m buffer because this distance ensured that individual points could largely be considered independent of one another based on a minimum distance apart of 250-m (and a more typical distance of 500-m). Lorenzón et al. (2016b) also found that a 200-m buffer was an informative scale for measuring landscape composition.

Land cover and stressor variables were obtained from remotely sensed data to facilitate the development of habitat association models across large spatial scales. One of the major challenges I faced was finding appropriate remotely sensed data that were comparable between the U.S. and Canada. I obtained measures of land use and land cover data from the 2010 North American Land Cover 30m dataset, produced as part of the North American Land Change Monitoring System (NALCMS). This spatially explicit dataset reflects 2010 land cover information for Canada and 2011 information for the U.S. I obtained remotely sensed roads from ESRI 2010 North American StreetMaps (ESRI 2010). Only information on primary and secondary roads was available for Canada, so I limited my subsequent analysis to primary and secondary roads in the U.S.

Site-level stressor data were obtained from the GLEI 2 Watershed-based Stressors for the Great Lakes Basin (Host et al. 2015) and are based on a set of 5,971 watersheds that cover the U.S. and Canadian Great Lakes basin (Hollenhorst et al. 2007). Where wetlands spanned multiple watersheds (e.g. a continuous wetland with two or more inputs), I calculated the site-level stressor variable value as the mean of the variable values for the individual points. This ensured that the stressor value was weighted more heavily towards the watershed that contained more points.

Temperature and precipitation data were obtained from North American Regional Reanalysis data set (Mesinger et al. 2005). These values represent the average spring precipitation and temperature values, which were calculated by taking the mean monthly values for March through June and are specific to the year in which a survey was conducted. Similarly, water level data are specific to the year in which a survey was conducted. The data were obtained from the Coordinated Monthly Mean Lake-wide Average Water Levels 1918-2017, which calculates a lake-wide mean using the coordinated gage network (Fry 2018). I averaged the monthly means for each lake and year from March through June and scaled them over the 100-year mean spring water level for that lake.

I also included geographic variables such as the latitude of the wetland, the lake on which the wetland is located, and the wetland hydrogeomorphic class (barrier, lacustrine, and riverine; see Uzarski et al. 2017).

In some parts of the Great Lakes basin, coastal wetlands are essentially contiguous, making wetland area difficult to quantify. I used pre-determined wetland boundaries for wetland site selection, but these boundaries do not necessarily reflect actual differences between wetlands (V. Brady, pers. comm). Therefore, I used the percentage of wetland area within the 2 km buffer of the wetland to represent the available area of wetland habitat. This measurement is reasonable because the mobility of birds allows them to fly between disconnected wetland patches, and a similar proxy for wetland area of total wetland land cover within a 3 km buffer was used by Fairbairn and Dinsmore (2001).

Analysis

I used hierarchical multi-scale occupancy models for each focal species to separately account for processes influencing probability of occurrence and, given presence, probability of detection (Kéry & Royle 2016; MacKenzie et al. 2018). Multi-scale occupancy models are especially useful when data exhibit spatial or temporal nestedness or clustering that fails the traditional occupancy model assumption of independence in the data (MacKenzie et al. 2018). My model structure followed the hierarchical structure of spatial and temporal dependencies in the sampling design of the CWMP field data collection protocols.

I defined the following model parameters:

- Site-level presence/absence z_i:

$$z_i \sim Bernoulli(\psi_i)$$

- Year-level presence/absence $a1_{ij}$:

$$a1_{ij}|z_i \sim Bernoulli\left(z_i * \ \theta_{ij}\right)$$

- Point-level presence/absence $a2_{ijk}$:

$$a2_{ijk}\middle|a1_{ij} \sim Bernoulli\left(a1_{ij} * \ \gamma_{ijk}\right)$$

- Visit-level presence/absence $a3_{ijkl}$:

$$a3_{ijkl}\middle|a2_{ijk} \sim Bernoulli\left(a2_{ijk} * \ \omega_{ijkl}\right)$$

- Replicated presence/absence measurements y_{ijkl}:

$$y_{ijkl}\middle|a3_{ijk} \sim Bernoulli\left(a3_{ijkl} * \ p\right)$$

where ψ_i represents latent site-level occupancy (over the entire 7-year survey period), θ_{ij} represents latent year-level availability, γ_{ijk} represents latent point-level availability conditional on site-level occupancy, ω_{ijkl} represents latent visit-level availability conditional on point-level availability, and p represents detection probability associated with the replicated detection/non-detection measurement y taken at site *i*, in year *j*, at point *k*, during visit *l*.

Our five-level multi-scale model is an extension of the three-level multi-scale occupancy models described by Kery and Royle (2016). Other models have demonstrated combining spatial and temporal levels of information (Pavlacky Jr. et al. 2012; McGarigal et al. 2016) and in multi-scale models the temporal levels of information are modelled as presence or absence of the focal species at the sample unit (MacKenzie et al. 2018). Few studies have used more than three levels in multi-scale models (but see McClintock et al. 2010), although additional levels may often be appropriate in ecology and management (Kery & Royle 2016).

The detection/nondetection measurements in my model were replicated within each visit by dividing the 15-minute point count period into three separate detection periods. These included two passive listening periods (minutes 0 to 4 and minutes 10 to 14, inclusive) and the one active listening period (minutes 5 to 9, inclusive) when broadcast calls of the focal species were played. The detection probabilities of the two passive listening periods were constrained to be the same, while the detection probability during the middle active listening period was allowed to differ, given that detection probabilities for secretive marsh birds are typically higher during call-back surveys than passive surveys (Conway & Gibbs 2005). Such subdivision of point counts has been previously demonstrated to provide temporal replication of detection/non-detection measures in multi-scale occupancy models (Mordecai et al. 2011; Pavlacky Jr. et al. 2012). I then used these listening period-specific detection probabilities to calculate the detection probability for the entire survey.

The probabilities defined above were modelled as functions of level-specific covariates that potentially vary across spatial and/or temporal units via logit link functions. Any missing covariate values were imputed in the modelling process using the observed covariate mean as a model and assuming a normal distribution (Kery & Royle 2016). Due to the random sampling design employed in data collection, missing responses were missing at random (e.g., a site not selected for sampling in a given year), and were therefore estimated by JAGS based on the regression relationship between the counts and the covariates and the known covariate values (Kery & Royle 2016).

I implemented my models with JAGS v.4.3.0 and the jagsUI package (Kellner 2018) in program R v.3.4.3 (R Core Team 2018). I fit the resulting multi-scale models to the species-specific data using a Markov chain Monte Carlo (MCMC) algorithm for parameter estimation. I ran three independent MCMC chains and assigned priors for all coefficients using $\beta \sim N(0, 1.75)$. This distribution gives a uniform prior on the real scale (T. Arnold, pers. comm.).

To identify appropriate combinations of variables to include in the final model, I screened the remainder of my environmental variables of interest for each species. For this screening process, I considered simplified hierarchical models that contained only a single covariate (or a covariate and its quadratic term) at one of the levels of the hierarchy. All covariates were centered and scaled to have a mean of zero and a standard deviation of 1. I ran these single-variable models using k-fold cross-validation, dividing the dataset into 10 equal and randomly selected groups. I then ran a model for each combination of species, variable, and excluded 10% of data for 20,000 iterations after an initial burn-in of 4,000 iterations. If MCMC chains had not yet converged based on Gelman–Rubin statistic (Rhat) values < 1.1 (Brooks & Gelman 1998; Kery 2010), I ran additional iterations in batches of 20,000 iterations until convergence was achieved or 120,000 iterations were run. I retained only those variables for which the coefficient value's 95% credible interval did not include zero for > 50% of groups that converged.

I made an exception if no variables at a given level were retained and selected the variable at that level for which the greatest number of groups had credible intervals not including zero. For the Virginia Rail, no groups for any of the year-level variables had credible intervals that excluded zero. I chose to include water level instead, based on relations reported in the literature (e.g., Gnass et al. 2018).

I also included Julian date and time of day at the visit level for all species because estimates of occupancy of marsh birds has been shown to be affected by the timing of sampling within the season and within the day (Conway & Gibbs 2011; Harms & Dinsmore 2014; Wiest & Shriver 2015)—presumably due to effects on availability or other components of detection (Nichols et al. 2009). Similarly, I included a term for the passive versus the active listening period because I expected that detection probabilities would be higher during the broadcast of calls (Conway & Gibbs 2005, 2011; Tozer et al. 2017), and this might be true even for non-broadcast species because some species will respond to playback calls of other species (Allen et al. 2004).

I then used the selected variables to construct the final, more complex model for each species (Table 2). I used a threshold-based pre-selection of $|r| \geq 0.60$ to avoid collinearity among similar landcover covariates. When I encountered highly correlated variables, I based my decisions of which variable to include in the final model first on the biological rationale, and then on nestedness or the strength of correlations with other variables in the model. For example, I had no strong reason to believe that birds would distinguish between inland open water and Great Lakes open water. Therefore, I used total open water (which included both Great Lakes and inland open water components) if multiple of these covariates were identified as significantly different from zero when tested independently.

I ran the final species models for 100,000 iterations after an initial burn-in of 10,000 iterations. If the model did not converge after 100,000 iterations based on Rhat < 1.1, I ran the model for additional iterations in groups of 100,000 iterations until convergence was achieved or I reached 1 million iterations.

The main assumptions that I make in my model are as follows:

1. I assumed closure across detection periods within a survey, and across surveys within a single season (Nichols et al. 2008; MacKenzie et al. 2018). Wetlands surveyed in more than one year, however, could not satisfy the closure assumption over the entire course of the study. I modified occupancy across years by year-specific biological covariates to explain possible non-random lack of closure. For example, Gnass et al. (2018) have shown that habitat use by secretive marsh birds in the Great Lakes varies across years in relation to water level. I assumed that the probability of detecting the species in a survey, given presence, is equal across all sites unless modified by covariates (Mackenzie et al. 2003; Aing et al. 2011).
2. I assumed that the detection of the species in each survey of a site is independent of detections during other surveys of the site (MacKenzie et al. 2018).
3. I assumed that there were no false positives, based on the stringent testing requirements for observers (Uzarski et al. 2017).
4. I assumed that the degree of similarity across all points and surveys within a site is identical and no further spatial autocorrelation exists between points within a site (Kery & Royle 2016).

I based my inferences about effect sizes and direction of relationships on the posterior means and 95% Bayesian Credible Intervals (CIs). I report the regression coefficient and parameter estimates as the mean followed by the 95% CI. I considered these estimates statistically significant if the CI did not include zero (Kery 2010; Mordecai et al. 2011).

RESULTS

Our sample included 641 wetlands surveyed for birds by the CWMP between 2011 and 2017 (Fig. 2-1). Of these wetlands, 203 were located on Lake Huron, 186 on Lake Ontario, 108 on Lake Michigan, 75 on Lake Erie, and 69 on Lake Superior. Of these wetlands, 299 were riverine, 240 were lacustrine, and 102 were barrier wetlands. Out of the 641 wetland sites, 407 were surveyed in one year, 203 were surveyed in 2 years, and 31 were surveyed in 3 years for a total of 906 wetland-year combinations. Wetlands were surveyed at a mean of 2.2 (sd = 1.8, range = 1-15, median = 1.0) points, totaling 1394 points or 1,927 point-year combinations. Points were visited twice each year with only a few exceptions (such as when a point became inaccessible due to changes in water level) giving us a total of 3,729 visits. Point counts were conducted during each of these visits and were broken into 3 detection periods each for a total of 11,187 detection periods.

Water levels were calculated for each lake in each year, using mean spring (March-June) lake water level scaled over the 100-year average (1918-2017). Water levels across most of the Great Lakes basin were low in 2011-2013 and high in 2016 and 2017 (Table 3).

Occupancy and Detection

As expected, my focal species were rarely encountered during the surveys. My effective sample sizes for the different levels of my multi-scale occupancy model were lowest for the tern species and highest for the Virginia Rail (Table 4). I detected focal species at between 18 and 125 of the 641 wetland sites, on between 21 and 144 of the wetland-year combinations, on between 27 and 184 point-year combinations, at between 30 and 230 visits, and during 38 to 348 survey segments. The low number of detections resulted in naïve site-level occupancy estimates ranging from 0.03 to 0.20.

When fit to these data, the hierarchical occupancy models converged after 100,000 MCMC iterations for all species except Common Gallinule and Least Bittern. Convergence required 200,000 iterations for Common Gallinule and 500,000 iterations for Least Bittern.

The parameter estimates provided by these models were substantially higher than the naïve estimates (Table 4). The estimates of ψ suggested that between roughly 1/5 (for Forster's Tern) and 2/3 (for Virginia Rail) of sites were occupied during at least one year of the study. The probability that an occupied wetland was occupied during at least one year of the study (θ), ranged from 38% (for Pied-billed Grebe) to 85% (for Virginia Rail). The probability a point was occupied, conditional on wetland-level occupancy during some monitored year of the study ($\psi \times \gamma$), ranged from 8% (for Forster's Tern) to 35% (for American Bittern). The probability that the point was occupied during both replicate surveys, conditional on being occupied in that year (ω), ranged from 16% (for both bittern species) to 58% (for Black Tern).

The hierarchical occupancy models suggested that detection probabilities were very high for the secretive marsh bird species, with an 80-98% probability of detecting the species, given that it was present at a site. The two tern species had substantially lower detection probabilities, with Forster's Terns being detected at an estimated 46% of sites where they occurred and Black Terns being detected at an estimated 22% of sites where they occurred. Detection probabilities were considerably higher during the active listening period than the passive listening period for most but not all species (Fig. 2-19).

Finally, the estimated number of occupied sites ranged from 107 (for Forster's Tern) to 453 (for Virginia Rail). The wide 95% Credible Intervals for these and many of the other parameter estimates suggest that there is considerable uncertainty in all the values reported here. The low end of the range of occupied sites could be 57% lower for Forster's Tern, and could be 20% lower for Virginia Rail.

Habitat Associations

While at least one covariate was included at each level in the hierarchical model for each species, the 95% Bayesian Credible Intervals (95% BCI) of the estimated coefficient values often included zero. I report inferences and effect sizes based on the posterior means and 95% BCIs in brackets.

Wetland class was included as a covariate in the models of three species (Pied-billed Grebe, Virginia Rail, and Black Tern). Based on the estimates from the hierarchical models, the coefficients for lacustrine wetlands for Pied-billed Grebes ($\beta_{\text{lacustrine}}$ = 2.14 [0.66, 4.26]) and Black Terns ($\beta_{\text{lacustrine}}$ = 1.57 [0.18, 3.46]) were significantly higher than for other wetland classes (Table 5). For these two species, occupancy probability of lacustrine wetlands was higher than that for wetlands of other classes (Fig. 2-2).

Lake was included as a covariate in the models of all species except Black Tern (Fig. 2-3). At least one lake had significant coefficient values for Pied-billed Grebe (β_{Superior} = -2.85 [-5.17, -0.82]), Virginia Rail (β_{Michigan} = 1.77 [0.09, 3.97], β_{Superior} = -1.48 [-3.01, -0.10]), Sora (β_{Michigan} = 1.99 [0.36, 4.05]), and American Bittern (β_{Huron} = 1.33 [0.04, 2.72], β_{Ontario} = 1.50 [0.12, 3.32], β_{Superior} = -1.75 [-3.71, -0.04]).

At the site level, percentage of agriculture in the watershed was included as a covariate in the models of Common Gallinule and Least Bittern occupancy (Fig. 2-4), but the effect was not significant (Table 5). Percentage of development in the watershed was included as a covariate in the models of Black Tern and Least Bittern site-level occupancy (Fig. 2-5) and the quadratic effect was significant for Least Bittern (β_{pcntdev} = -0.31[-1.99, 1.49], $\beta_{\text{pcntdev}}{}^{2}$ = 1.65 [0.39, 3.33]). Human population in the watershed was included as a covariate in the model for Common Gallinule site-level occupancy (Fig. 2-6), but the effect was not significant.

At the year level, spring temperature was included as a covariate in the models of Pied-billed Grebe, Sora, Common Gallinule, Forster’s Tern, American Bittern, and Least Bittern occupancy (Fig. 2-7). The linear effect was significantly positive for year-level occupancy of Pied-billed Grebes (β_{temp} = 0.65 [0.14, 1.20]), although the quadratic effect was not significant; significantly positive for year-level occupancy of Common Gallinules (β_{temp} = 2.83 [1.34, 4.82]); and significantly negative for year-level occupancy of American Bitterns (β_{temp} = -0.72[-1.64, -0.09]). Although water level is an important driver of wetland characteristics and was included as a covariate in the models of Virginia Rail, Common Gallinule, Black Tern, Forster’s Tern, and Least Bittern occupancy, the effect of water level was not significant for any species. (Fig. 2-8). Common Gallinule, Forster’s Tern, and Least Bittern showed negative quadratic relationships; Black Tern showed a positive quadratic relationship; and Virginia Rail showed a positive linear relationship.

At the point level, log-transformed wetland area within 2 km was included as a covariate for Pied-billed Grebe, Virginia Rail, Common Gallinule, Black Tern, and Forster's Tern occupancy (Fig. 2-9). The linear effect but not the quadratic effect was significantly positive for Pied-billed Grebe (β_{logWet} = 1.18 [0.33, 2.28], β_{logWet}^2 = 0.61 [-0.05, 1.54]). The quadratic effect was significant for Black Tern (β_{logWet} = -0.07 [-1.94, 1.71], β_{logWet}^2 = 2.19 [0.20, 4.77]). Percentage of open water within 200 m was included as a covariate for Forster's Tern and American Bittern occupancy (Fig. 2-10). The quadratic effect was significant for American Bittern ($\beta_{totwater}$ = -0.55 [-2.43, 1.27], $\beta_{totwater}^2$ = 1.72 [0.21, 4.00]). Percentage of total wetland within 200 m was included as a covariate for Virginia Rail occupancy (Fig. 2-11), but the effect was not significant. Percentage of emergent wetland within 200 m was included as a covariate for Common Gallinule, Forster's Tern, American Bittern, and Least Bittern occupancy (Fig. 2-12). The quadratic effect was significant for American Bittern ($\beta_{emergent}$ = 0.23 [-1.45, 2.13], $\beta_{emergent}^2$ = 2.15 [1.09, 4.51]). Percentage of woody wetland within 200 m was included as a covariate for Pied-billed Grebe, Virginia Rail, Common Gallinule, Forster's Tern, and Least Bittern occupancy (Fig. 2-13). The effect was significantly negative for Pied-billed Grebe ($\beta_{woodywetland}$ = -0.95 [-1.76, -0.18]) and Common Gallinule ($\beta_{woodywetland}$ = -0.47 [-0.92, -0.05]). The quadratic effect was significant for Least Bittern ($\beta_{woodywetland}$ = -1.32 [-2.72, -0.42], $\beta_{woodywetland}^2$ = 1.03 [0.13, 2.76]). Percentage of forest within 200 m was included as a covariate for Pied-billed Grebe, Virginia Rail, and Sora occupancy (Fig. 2-14). The effect was significantly positive for Pied-billed Grebe (β_{forest} = 1.45 [0.27, 3.19]), Virginia Rail (β_{forest} = 0.32 [0.08, 0.56]), and Sora (β_{forest} = 0.83 [0.25, 1.92]).

Among anthropogenic land uses, percentage of developed land within 200 m was included as a covariate for Pied-Billed Grebe and Least Bittern occupancy (Fig. 2-15), but these effects were not significant. Road length within 200 m was included as a covariate for Pied-billed Grebe and Common Gallinule occupancy (Fig. 2-16).

At the visit level, the effect of Julian day was significantly positive for Pied-billed Grebe (β_{Jdate} = 0.45 [0.03, 0.89]) and Common Gallinule (β_{Jdate} = 0.85 [0.03, 1.57]), but not for the other six species (Fig. 2-17). The effect of time of day was not significant for any of the eight focal species (Fig. 2-18).

At the survey segment level, noise was included as a covariate for the models of detection probability for Virginia Rail and Black Tern (Fig. 2-20). Only detection probability for Black Tern at noise level 3 was significantly lower than the reference value of noise level 0 ($\beta_{noise:3}$ = -2.14 [-4.58, -0.15]).

DISCUSSION

Occupancy and Detection

While my naïve estimates of occupancy suggested that all focal species were rare, occupying fewer than 30% of sites (Specht et al. 2017), my hierarchical models suggest that the wetland-obligate birds, particularly those considered secretive marshbirds, used a high proportion of coastal wetland sites during the seven years of the study. The secretive marshbirds ranged from occupying one third to over two thirds of sites during at least one year of the study, and annual occupancy probabilities of the individual species of secretive marshbirds ranged from 0.19 to 0.59. These values are similar to the range of single-season occupancy probabilities reported for Least Bittern (ψ = 0.14 – 0.17) in the Illinois and Upper Mississippi River Valleys in 2006 and 2007 (Darrah & Krementz 2010), in Manitoba in 2005 (ψ = 0.53) and Quebec in 2006-2009 (ψ = 0.6 – 0.7; Jobin et al. 2013), as well as for Pied-billed Grebes in the Illinois and Upper Mississippi River Valleys in 2007 (ψ = 0.31) and 2006 (ψ = 0.21; Darrah & Krementz 2010).

The hierarchical models for the two tern species suggest that these species were less common across the sites than the secretive marshbirds. However, my encounter rates for these species were extremely low and thus my parameter estimates are questionable (Mackenzie & Royle 2005; Wisz et al. 2008; Guillera-Arroita et al. 2010). These low encounter rates may be explained by the clustering behavior of colonial breeding birds (affecting occupancy) and the fact that my survey protocol does not employ broadcast calls for these species (affecting detection). In addition, declines for these two species have been among the most severe experienced by any species in the Great Lakes basin (Tozer 2013), and Black Tern colony sites have declined in number by almost 90% since 1991 (Wyman & Cuthbert 2017). Monitoring efforts targeted at these colonial species may be more appropriate to identify their habitat associations and population trends in the Great Lakes basin (e.g., the binational Great Lakes Colonial Waterbird Survey).

The detection probabilities for the secretive marshbird species were also extremely high, with 80-98% probability of detecting these species during the entire 15-minute point count survey. There was a noticeable increase in detection probability during the active listening period for Pied-billed Grebe, Common Gallinule, and both rail species. This was not the case for the two tern species or American Bittern, for which their calls were not broadcast. This indicates that the broadcast of a species' calls was especially useful for improving the detection probability of cryptic species. Only a small increase was found for detection probability of Least Bittern during the active listening period, as has previously been documented for this species (Conway & Gibbs 2005). The repetitive frequency, volume, and distinctiveness of American Bittern vocalizations are reflected in the especially high detection probability for this species, even without the use of broadcasts, and further justify excluding this species' calls in the broadcast recordings.

Habitat associations

Site-level Habitat Associations

I found several significant relationships between individual species and habitat variables. At the site level, Pied-billed Grebe and Black Tern showed significantly higher occupancy probabilities at lacustrine wetlands. Hanowski et al. (2007) similarly found Pied-billed Grebe had a significant indicator value for lacustrine wetlands in the Great Lakes basin. These lacustrine wetlands differ from other wetland hydrogeomorphic classes in physical characteristics such as sediment type, wave energy, water quality, and hydrology, which may contribute to differences in vegetation and associated invertebrate and fish communities (Great Lakes Coastal Wetlands Consortium 2008). Lacustrine wetlands are also subject to greater influence from the associated Great Lake and experience somewhat less influence from the immediate watershed. Welch's ANOVA and a Games-Howell post hoc test indicated that individual sampling points of lacustrine wetlands were surrounded by a significantly higher mean amount of Great Lakes open water than were points in riverine and barrier wetlands ($F_{2, 433.38} = 9.78$, $p < 0.001$). This difference in surrounding percentage of Great Lakes open water extended as far as 500 m ($F_{2, 413.18} = 4.74$, $p < 0.001$), but not as far as 1000 m ($F_{2, 421.45} = 0.69$, $p =0.50$). The Pied-billed Grebe is generally considered an open-water species and its abundance has been documented as increasing with increasing open-water coverage in the Great Lakes region (Bolenbaugh et al. 2011; Tozer 2016) and elsewhere (e.g. Lor & Malecki 2006; Harms & Dinsmore 2013; Niemuth 2017). Similarly, Black Terns are associated with marshes with at least partial open water (Chin et al. 2014; Niemuth 2017) because open water is their primary foraging habitat (Heath et al. 2009).

For most species, site-level occupancy probability varied by lake. Hanowski et al. (2007) found that bird communities were significantly different across the five lakes. Uzarski et al. (2017) found that, contrary to other indicators of ecological condition in the Great Lakes basin, wetland birds did not show a north to south gradient of ecological condition. Instead, birds favored larger and more productive coastal wetlands. Large coastal wetlands are particularly sparse in the northern portion of Lake Superior, and I found that Lake Superior wetland points had a significantly lower percentage of total wetland (our proxy for wetland area) within 2 km than points on all other lakes except Lake Huron ($F_{4, 562.13} = 12.89$, $p <0.001$). Indeed, Lake Superior had the lowest occupancy probabilities for all species that included lake (all focal species except Black Tern) and these low values at Lake Superior wetlands were significant based on Bayesian Credible Intervals for Pied-billed Grebe, Virginia Rail, and American Bittern. The differences in occupancy probabilities among lakes may also be the result of spatial variation in relative abundance across the Great Lakes basin (Crewe & Timmermans 2005; Wires et al. 2010).

Year-level Habitat Associations

At the year level, spring temperatures affected the year-level occupancy probabilities positively for Pied-billed Grebe and Common Gallinule but negatively for American Bittern. In years when spring temperatures are especially low, birds may delay departure from the wintering ground or extend the length of the migratory period (Norris et al. 2004). For both Pied-billed Grebe and Common Gallinule I also found significantly positive relationships with Julian day of the survey. Days later in the year also correspond to generally warmer temperatures. In contrast, American Bittern occupancy probability decreased with increasing spring temperatures and this species did not exhibit a significant relationship with Julian day. Spring temperatures in the Great Lakes basin are projected to increase by as much as 5°C by 2050 (Hall & Stuntz 2008), and thus climate change may be especially problematic for a species like American Bittern. Conservation planning efforts would benefit from considering the climate vulnerability of these species.

Although other studies have shown that many wetland-obligate species respond positively to water level (Timmermans et al. 2008; Chin et al. 2014; Gnass et al. 2018), none of my focal species showed significant relationships with this environmental covariate. Both Timmermans et al. (2008) and Chin et al. (2014) found some lake-to-lake variation in these patterns, and I did not allow for an interaction effect in my models.

Precipitation was not included in any of the focal species' year-level occupancy models. While Forcey et al. (2007, 2011, 2014) found that spring precipitation was important for abundances of some waterfowl species in the Prairie Pothole Region, total annual precipitation or previous year's precipitation were more likely to be important for wetland bird species including Pied-billed Grebe and Black Tern. However, I would expect that the hydrologic regimes of prairie pothole wetlands would be more susceptible to variation in precipitation than Great Lakes coastal wetlands because the large surface area of the latter increases the relative importance of evaporation in these systems' water level dynamics (Gronewold et al. 2013).

Point-level Habitat Associations

At the point level, I found a few significant relationships between occupancy probability and natural land cover types. American Bittern point-level occupancy showed a significantly positive quadratic relationship with emergent wetland, indicating that intermediate values of emergent wetland resulted in the lowest occupancy probabilities for this species. However, the Bayesian Credible Intervals are so wide that the nature of this relationship is questionable. The same is true for the relationship of this species with open water, and for the significantly positive quadratic relationship of Black Tern with log-transformed wetland area within 2 km. Like us, Bolenbaugh et al. (2011) found no significant relationship between American Bittern occupancy and emergent vegetation, although American Bitterns use emergent vegetation during the breeding season (Riffell et al. 2001; Lor & Malecki 2006), occupy sites adjacent to open water (Bolenbaugh et al. 2011), and are associated with greater amounts of wetland in the landscape (Hay 2006; Tozer 2016). A positive relationship has also been documented between Black Tern abundance and wetland area in the landscape (Forcey et al. 2014), and several other species of wetland birds (e.g., Willard 2011; Quesnelle et al. 2013). A primary difference between my results and those of other studies was the incorporation of a multi-scale occupancy probability to simultaneously account for multiple levels of spatial and temporal nestedness. While both Forcey et al. (2014) and Tozer (2016) accounted for single levels of spatial or temporal dependence, neither of their models adhered as closely to considerations of the survey design as my 5-level multi-scale model. Forcey et al. (2014), for example, used a spatial conditional autoregressive prior distribution on a route effect. However, the Forcey model accounted for temporal autocorrelation by incorporating a "nuisance" year effect. This latter technique fails to explain the biological relevance of year-to-year variation. In contrast, Tozer (2016) accounted for temporal autocorrelation with a multi-season occupancy model but ignored spatial autocorrelation—all point count locations were treated as spatially independent, whether they occurred within the same wetland or in different wetlands. I speculate that appropriately accounting for both of these sources of autocorrelation may result in decreases in significance of certain covariate relationships.

I found a convincing significantly positive relationship between point-level occupancy probability of Pied-billed Grebe and log-transformed wetland area. Willard (2011) reported higher occupancy in larger wetlands. This relationship is also supported by patterns of wetland bird occupancy responding positively to wetland size as reported by Uzarski et al. (2017).

I also found significant, negative linear relationships of point-level occupancy for Pied-billed Grebe and Common Gallinule with percentage of woody wetland. A positive quadratic relationship between Least Bittern point-level occupancy probability and percentage of woody wetland also indicated that at least at low percentages of woody wetland, occupancy probability for this species declined as percentage of woody wetland increased. Likewise, Bolenbaugh et al. (2011) found that occupancy probabilities of these species were negatively associated with percentage of woody wetland.

While woody wetland was negatively associated with point-level occupancy probabilities of several of my focal species, Pied-billed Grebe, Virginia Rail, and Sora occupancy probabilities responded positively to percentage of forest cover. Willard (2011) found a similar association for Virginia Rail but not Sora, and Tozer (2016) found that Pied-billed Grebe colonization probability decreased with a positive change in percentage of trees, and extinction probability increased with a positive change in percentage of trees. I speculate that forested land cover represents the least disturbed landscapes because, historically, forest was the dominant land cover type in the Great Lakes basin (Zhang & Guindon 2005). Indeed, Pearson's product-moment correlations indicate a significant negative association between the points surrounded by the greatest percentages of forest within 2 km and the watershed-level metrics of human population ($r = -0.18$, $p < 0.001$) and combined agriculture and development ($r = -0.27$, $p < 0.001$).

Anthropogenic Influence

One of my most unexpected findings was the lack of support for effects of anthropogenic disturbance on occupancy patterns of these wetland obligate species. Cropland was not included in the final model for any of my focal species, nor was there a significant effect of development in any of the final models. At the watershed level, Least Bittern showed a significant relationship with percent development. This relationship was a positive quadratic relationship, which would indicate that an intermediate amount of development supported the lowest occupancy probabilities of this species. Such a relationship is the opposite of what I would expect from the intermediate disturbance hypothesis (Blair 1996; Roxburgh et al. 2004; Marzluff & Rodewald 2008), but the Bayesian Credible Intervals are so wide that the actual nature of this relationship seems questionable. Therefore, I believe that the focal species were relatively resilient to anthropogenic influences at the levels encountered in my study areas. Wetlands with a high degree of anthropogenic disturbance had the same probability of being used by the focal species in at least one year of the study as relatively undisturbed wetlands. Likewise, Uzarski et al. (2017) showed that indicators of coastal wetland condition based on birds responded to wetland size and productivity, whereas a set of indicators based on chemical and physical properties, plants, invertebrates, and fish consistently showed wetland condition declining in the more heavily disturbed southern Great Lakes basin. Likewise, Brazner et al. (2007) found that the number of wetland obligates responded more strongly to lake and wetland type than to a human disturbance index. Quesnelle et al. (2013) found that occupancy of Marsh Wren, Virginia Rail, and Least Bittern responded less to amount of agricultural land than to amount of wetland in the landscape, and not at all to road density.

In contrast to my results, other studies have found negative impacts of anthropogenic disturbance on wetland birds. Hanowski et al. (2007) found that the proportion of wetland-obligate birds in a survey generally decreased with increasing anthropogenic land use within 1 km. Gagne et al. (2016) found bird species richness related negatively to human population size. Wyman and Cuthbert (2017) found that Black Tern colony abandonment probability was higher at colony sites with higher percentages of surrounding development within 500 m. Panci et al. (2017) found that occupancy of Sedge Wrens occurrence was negatively associated with roads and Marsh Wren occurrence was negatively associated with percent development within 500 m and percent cropland within 500- or 2000-m buffers. These negative associations of wetland birds with anthropogenic disturbance are expected because development is related to habitat degradation in coastal wetlands (Morrice et al. 2008), in particular changes in wetland structure that make wetlands less suitable for many birds (Lee et al. 2006; Ward et al. 2010). Both the dramatic loss of emergent vegetation and dramatically increased density of emergent vegetation—resulting in opposite extremes of highly homogeneous open water or highly homogeneous vegetation—are undesirable consequences of anthropogenic disturbance (Ward et al. 2010). In the Great Lakes basin, invasion by *Phragmites australis* and other non-native plants changes the structural components and heterogeneity of the habitat, reducing both species diversity and the abundance of rare and specialist species (Benoit & Askins 1999; Glisson et al. 2015; Whyte et al. 2015; Tozer 2016). Coastal development has been identified as a driver of *Phragmites* invasions. I was not able to consider structural changes in wetland characteristics because vegetation and invasive plant records are not yet available at a basin-wide scale. However, future studies should examine whether this structural degradation may influence habitat associations of these species more directly than the anthropogenic disturbances that drive degradation.

Conclusions

Indeed, overall my results indicate that these species are eurytopic—they tolerate a wide range of wetland habitats. These species are more typically considered specialists because they are wetland-obligates and thus require wetland habitat for the purposes of nesting and foraging (Chin et al. 2014). However, my models identified relatively few significant habitat associations for these species, and in most cases the significant effects of habitat characteristics were accompanied by wide Bayesian Credible Intervals that indicated a great degree of uncertainty in the coefficient estimates.

The relative insensitivity of these wetland birds to wetland quality and anthropogenic disturbance may pose a challenge to conservation actions such as the prioritization of wetlands for protection or the development of zoning guidelines to improve wetland conditions. However, it also presents an opportunity for wetland bird conservation because essentially any wetland may serve as potential breeding habitat for these eurytopic species in at least some years. Gnass et al. (2018) similarly found that annual variation in distribution of the avian community across available wetlands meant that a broad range of wetland types play important ecological roles, and that the relative importance of a given wetland may vary across years. Like Quesnelle et al. (2013) found, my results also suggest that wetland loss represents a bigger threat to populations of wetland-obligate birds than does habitat degradation. Therefore, conservation planning should focus on protecting as many coastal wetlands and as much area of coastal wetlands as possible. It is also a priority to reverse trends of wetland loss in the Great Lakes basin, and at a broader global scale, as this is critical to providing habitat for wetland obligate birds and other wetland-dependent taxa in the long term.

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TABLES

Table 1. Definitions, sources, and descriptive statistics (mean, standard deviation, minimum value, and maximum value) of variables considered in my models at each hierarchical level.

Level	Variable	Definition	Source	Mean	SD	Min	Max
Site	pcntag	Percent agriculture within the watershed	GLStress5971 - NRRI	28.1	27.5	0	97.3
	pcntdev	Percent development within the watershed	GLStress5971 - NRRI	13.7	16.6	0	96.9
	popn	Human population density within the water-shed	GLStress5971 - NRRI	87.0	246.3	0	3812.0
	agdevbsn	Watershed-wide combined agricultural and development stress	GLStress5971 - NRRI	0.4	0.3	0.0	1.0
	lake	Great Lake on which the site is located	CWMP				
	class	Wetland classification (riverine, lacustrine, barrier)	CWMP				
Year	temp	Mean spring (March-June) temperature in Celsius at the site for a given year	North American Regional Reanalysis - NOAA	8.0	3.2	-1.3	16.2
	precip	Mean spring (March-June) precipitation (inches/month) at the site for a given year	North American Regional Reanalysis - NOAA	0.7	0.4	0.1	1.9
	waterLevel	mean spring (March-June) lake water level (m) for a given year, scaled over 100-year average (1918-2017)	Coordinated Monthly Mean Lakewide Average Water Levels	-0.2	0.9	-2.0	1.9
Point	Inwater200	Percent cover of open inland water within 200 m	2010 North American Land Cover - NALCMS	17.8	22.2	0	97.1
	GLwater200	Percent cover of open Great Lakes water within 200 m	2010 North American Land Cover - NALCMS	2.4	7.3	0	69.1

	Totwater200	Combination of Inwater200 and GLwater200	2010 North American Land Cover - NALCMS	20.2	23.6	0	97.9
	Developed200	Percent cover of developed land within 200 m	2010 North American Land Cover - NALCMS	1.1	4.7	0	55
	Forest200	Percent cover of forested land within 200 m	2010 North American Land Cover - NALCMS	26.8	27.5	0	100
	Grass200	Percent cover of grass/pasture land within 200 m	2010 North American Land Cover - NALCMS	9.6	19.2	0	100
	Crop200	Percent cover of cropland within 200 m	2010 North American Land Cover - NALCMS	4.1	10.0	0	77.4
	Woodywetland 200	Percent cover of woody wetland within 200 m	2010 North American Land Cover - NALCMS	14.0	15.8	0	92.9
	Emergent200	Percent cover of emergent wetland within 200 m	2010 North American Land Cover - NALCMS	24.3	24.1	0	100
	Totwet200	Percent cover of combined Woodywetland200 and Emergent200 within 200 m	2010 North American Land Cover - NALCMS	38.3	25.3	0	100
	Road200	Meters of primary and secondary roads within 200m	2010 North American Street Maps - ESRI	78.5	164.6	0	803
	wetArea	Km^2 of wetland within a 2000 m buffer of the point	2010 North American Land Cover - NALCMS	5.7	2.4	0.3	12.0
	logWet	Log-transformed wetland area	2010 North American Land Cover - NALCMS	15.4	0.6	12.6	16.3
Visit	Jdate	Julian day of survey	CWMP	166.7	15.0	137	263
	AM	Time of day of survey (AM or PM)	CWMP				

Detection	noise	Noise level recorded during survey (ordinal)	CWMP	1.3	1.1	0	4
	wind	Wind level recorded during survey (ordinal)	CWMP	1.4	1.0	0	5

Table 2. Variables included in the multi-scale occupancy model for each species of wetland bird. WaterLev = water level; Dev200 = developed land, Ewet200 = emergent wetland, and Wwet = woody wetland within a 200-m buffer. Active = active vs. passive listening period.

Vars	PBGR	VIRA	SORA	COGA	BLTE	FOTE	AMBI	LEBI
Site-level	Class	Class	Lake	Lake	Lake	Lake	Lake	Lake
	Lake	Lake		Pcntag	Pcntdev			Pcntag
				Pcntag^2				Pcntdev
				Popn				Pcntdev^2
				Popn^2				Popn
								Popn^2
Year-level	Temp	WaterLev	Temp	Temp	WaterLev	Temp	Temp	Temp
	Temp^2			WaterLev	WaterLev^2	Temp^2		WaterLev
				WaterLev^2		WaterLev		WaterLev^2
						WaterLev^2		
Point-level	Dev200	Forest200	Forest200	Ewet200	logWet	Ewet200	Ewet200	Dev200
	Dev200^2	logWet		logWet	logWet^2	logWet	Ewet200^2	Dev200^2
	Forest200	logWet^2		Road200		logWet^2	Totwater200	Ewet200
	logWet	Totwet200		Wwet200		Totwater200	Totwater200^2	Wwet200
	logWet^2	Wwet200				Wwet200		Wwet200^2
	Road200					Wwet200^2		

	Wwet200							
Visit-level	Jdate AM	Jdate AM	Jdate AM	Jdate AM	Jdate AM	Jdate AM	Jdate AM	Jdate AM
Detection	Active	Active Noise	Active	Active	Active Noise	Active	Active	Active

Table 3. 100-year mean (sd) water levels for the Great Lakes, and annual water levels scaled over the 100-year mean by subtracting the 100-year mean and dividing by the sd of the 100-year water levels. Water level data were obtained from Coordinated Monthly Mean Lakewide Average Water Levels, which are calculated using the coordinated gage network. Lakes Michigan and Huron are hydrologically connected and therefore have the same water levels.

Year	Superior	Michigan & Huron	Erie	Ontario
1917-2017	183.3 (0.2)	176.4 (0.4)	174.2 (0.3)	74.9 (0.3)
2011	-2.0	-1.1	0.2	0.3
2012	-1.7	-1.0	0.2	0.1
2013	-1.7	-1.5	-0.5	-0.3
2014	0.4	-0.7	0.0	0.0
2015	1.1	0.4	0.1	-0.6
2016	1.1	0.9	1.0	0.5
2017	1.1	0.8	1.3	1.9

Table 4. Parameter estimates (SD) and 95% Credible Intervals (below, in brackets) and naive estimates (below, in italics) for wetland bird occupancy in Great Lakes coastal wetlands. Psi (ψ) is the estimate of site-level occupancy for Great Lakes coastal wetlands, theta (θ) is the estimate of year-level availability, gamma (γ) represents the estimate of point-level availability at point-count locations within wetlands, and omega (ω) represents the estimate of visit-level availability. The parameter p^* represents the estimate of detection probability across the entire 15-minute point count during a given survey. The parameters p_p and p_a represent the estimates of detection probability during the passive and active listening periods, respectively.

Parameter	PBGR	VIRA	SORA	COGA	BLTE	FOTE	AMBI	LEBI
ψ	0.51 (0.10)	0.68 (0.07)	0.35 (0.09)	0.37 (0.08)	0.35 (0.16)	0.17 (0.08)	0.43 (0.11)	0.58 (0.06)
	[0.32 - 0.70]	[0.54 - 0.82]	[0.23 - 0.55]	[0.24 - 0.56]	[0.13 - 0.78]	[0.07 - 0.38]	[0.26 - 0.67]	[0.46 - 0.72]
	0.09	*0.20*	*0.08*	*0.06*	*0.04*	*0.03*	*0.11*	*0.10*
θ	0.38 (0.09)	0.85 (0.08)	0.56 (0.15)	0.51 (0.08)	0.40 (0.17)	0.54 (0.16)	0.57 (0.13)	0.72 (0.11)
	[0.24 - 0.60]	[0.67 - 0.98]	[0.30 - 0.86]	[0.35 - 0.67]	[0.14 - 0.79]	[0.24 - 0.88]	[0.34 - 0.83]	[0.49 - 0.90]
	0.07	*0.16*	*0.07*	*0.05*	*0.03*	*0.02*	*0.08*	*0.08*
γ	0.55 (0.08)	0.29 (0.05)	0.42 (0.12)	0.30 (0.06)	0.68 (0.14)	0.48 (0.15)	0.81 (0.08)	0.53 (0.12)
	[0.39 - 0.70]	[0.21 - 0.40]	[0.23 - 0.68]	[0.20 - 0.43]	[0.42 - 0.95]	[0.23 - 0.80]	[0.65 - 0.96]	[0.29 - 0.75]
	0.05	*0.10*	*0.04*	*0.04*	*0.02*	*0.01*	*0.05*	*0.05*
ω	0.39 (0.08)	0.51 (0.06)	0.33 (0.8)	0.57 (0.07)	0.58 (0.18)	0.48 (0.16)	0.16 (0.03)	0.16 (0.05)
	[0.26 - 0.57]	[0.39 - 0.63]	[0.20 - 0.50]	[0.43 - 0.70]	[0.23 - 0.92]	[0.21 - 0.81]	[0.11 - 0.23]	[0.09 - 0.29]
	0.03	*0.06*	*0.02*	*0.03*	*0.01*	*0.01*	*0.03*	*0.03*
p^*	0.90 (0.02)	0.82 (0.03)	0.80 (0.05)	0.92 (0.02)	0.22 (0.07)	0.46 (0.11)	0.98 (0.01)	0.90 (0.02)
	[0.86 - 0.94]	[0.77 - 0.87]	[0.69 - 0.89]	[0.88 - 0.96]	[0.12 - 0.39]	[0.26 - 0.68]	[0.97 - 0.99]	[0.85 - 0.93]
p_p	0.48 (0.04)	0.24 (0.02)	0.24 (0.03)	0.43 (0.03)	0.08 (0.03)	0.22 (0.07)	0.75 (0.03)	0.50 (0.04)
	[0.42 - 0.55]	[0.21 - 0.29]	[0.18 - 0.31]	[0.36 - 0.49]	[0.04 - 0.15]	[0.11 - 0.36]	[0.69 - 0.80]	[0.43 - 0.57]
p_a	0.64 (0.05)	0.69 (0.04)	0.66 (0.07)	0.77 (0.05)	0.08 (0.03)	0.14 (0.06)	0.71 (0.04)	0.59 (0.05)
	[0.54 - 0.73]	[0.61 - 0.76]	[0.52 - 0.79]	[0.67 - 0.85]	[0.04 - 0.16]	[0.05 - 0.27]	[0.63 - 0.79]	[0.50 - 0.69]

No. of Occupied Sites	324 (65)	453 (47)	235 (57)	234 (53)	217 (105)	107 (54)	286 (71)	374 (41)
	[198 - 449]	[362 - 540]	[145 - 366]	[152 - 359]	[78 - 499]	[46 - 244]	[177 - 444]	[298 - 461]
	58	*125*	*52*	*41*	*25*	*18*	*68*	*65*

Table 5. Coefficients (sd) from hierarchical multiscale occupancy models for wetland bird occupancy in Great Lakes coastal wetlands. Estimates with a 95% credible interval that excludes zero are indicated in bold italics.

		PBGR	VIRA	SORA	COGA	BLTE	FOTE	AMBI	LEBI
Site-level									
	Intercept	-0.03 (0.54)	-0.06 (0.61)	-0.93 (0.66)	-0.46 (0.73)	-1.57 (1.01)	-0.88 (0.62)	-1.17 (0.68)	0.27 (0.91)
	Class: Riverine	reference	reference			reference			
	Class: Barrier	-0.10 (0.74)	-0.06 (0.70)			0.48 (0.99)			
	Class: Lacustrine	***2.14 (0.92)***	0.64 (0.73)			***1.57 (0.82)***			
	Lake: Erie	reference	reference	reference	reference		reference	reference	reference
	Lake: Huron	-0.04 (1.01)	1.48 (0.93)	0.79 (0.77)	0.50 (0.91)		-0.55 (0.80)	***1.33 (0.68)***	-1.49 (0.95)
	Lake: Michigan	-0.67 (0.87)	***1.77 (0.97)***	***1.99 (0.93)***	-0.43 (0.99)		-0.74 (0.90)	1.01 (0.79)	1.62 (1.27)
	Lake: Ontario	-0.78 (0.73)	1.44 (0.91)	-0.87 (0.70)	1.39 (0.84)		-2.33 (1.22)	***1.50 (0.80)***	1.60 (1.12)
	Lake: Superior	***-2.85 (1.11)***	***-1.48 (0.74)***	-0.60 (0.80)	-1.98 (1.28)		-2.01 (1.25)	***-1.75 (0.94)***	-1.97 (1.18)
	Pcntag				-0.06 (0.49)				0.38 (0.73)
	Pcntag^2				-0.24 (0.39)				
	Pcntdev					-0.98 (0.58)			-0.31 (0.87)
	Pcntdev^2								***1.65 (0.78)***
	Popn				1.24 (0.88)				
	Popn^2				-0.84 (0.52)				
Year-level									
	Intercept	-0.90 (0.44)	2.22 (0.93)	0.37 (0.86)	-1.08 (0.79)	0.50 (1.05)		0.38 (0.69)	0.43 (1.14)
	Precip								
	Precip^2								
	Temp	***0.65 (0.28)***		-0.39 (0.67)	***2.83 (0.90)***		0.74 (1.18)	***-0.72 (0.39)***	1.26 (1.03)

	Temp^2	0.40 (0.28)					1.33 (1.20)		
	Water Level		0.62 (0.69)		-0.72 (0.66)	0.07 (0.51)	-1.75 (1.09)		-0.08 (0.95)
	Water Level^2				1.09 (0.76)	-1.06 (0.63)	-1.65 (1.38)		1.33 (0.97)
Point-level									
	Intercept	-0.42 (0.77)	***-1.02 (0.22)***	-0.29 (0.65)	***-0.98 (0.32)***	0.02 (1.05)	-0.88 (1.30)	-0.40 (0.96)	-0.77 (0.66)
	logWet	***1.18 (0.50)***	-0.22 (1.28)		0.30 (0.21)	-0.07 (0.91)	1.02 (0.99)		
	logWet^2	0.61 (0.41)	-0.12 (0.07)			***2.19 (1.19)***	0.53 (0.82)		
	Totwater200						-0.82 (0.75)	-0.55 (0.92)	
	Totwater200^2							***1.72 (0.98)***	
	Totwet200		-0.09 (1.28)						
	Emergent200				0.29 (0.21)		1.27 (0.82)	0.23 (0.88)	0.65 (0.47)
	Emergent200^2							***2.15 (1.09)***	
	Woodywetland200	***-0.95 (0.40)***	-0.22 (0.13)		***-0.47 (0.22)***		-0.61 (1.03)		***-1.32 (0.59)***
	Woodywetland200^2						0.53 (0.74)		***1.03 (0.74)***
	Forest200	***1.45 (0.79)***	***0.32 (0.12)***	***0.83 (0.42)***					
	Grass200								
	Crop200								
	Developed200	-0.84 (1.34)							-0.31 (1.33)
	Developed200^2	1.09 (0.96)							1.20 (1.02)
	Road200	-0.18 (0.35)			0.09 (0.21)				
Visit-level									
	Intercept	-0.47 (0.36)	0.06 (0.26)	-0.77 (0.39)	0.39 (0.39)	0.67 (1.27)	0.03 (0.99)	***-1.69 (0.23)***	***-1.74 (0.34)***
	Jdate	***0.45 (0.22)***	0.18 (0.20)	-0.31 (0.37)	***0.85 (0.39)***	-0.86 (0.89)	0.50 (0.85)	0.06 (0.19)	0.24 (0.18)
	AM	0.07 (0.22)	-0.02 (0.15)	-0.25 (0.25)	0.06 (0.29)	0.61 (0.83)	-0.60 (0.81)	-0.06 (0.13)	0.06 (0.13)

Detection									
	Intercept	-0.06 (0.14)	***-1.05 (0.19)***	***-1.15 (0.19)***	***-0.30 (0.14)***	***-2.29 (0.44)***	***-1.33 (0.40)***	***1.08 (0.15)***	-0.01 (0.15)
	Active listening	***0.63 (0.22)***	**1.97 (0.18)**	***1.82 (0.29)***	***1.52 (0.27)***	-0.01 (0.32)	-0.60 (0.40)	-0.16 (0.25)	0.38 (0.23)
	Noise: 0		reference			reference			
	Noise: 1		-0.11 (0.23)			-0.10 (0.40)			
	Noise: 2		-0.22 (0.28)			-0.26 (0.47)			
	Noise: 3		0.33 (0.33)			***-2.14 (1.13)***			
	Noise: 4		-1.77 (0.89)			-1.03 (1.49)			

FIGURES

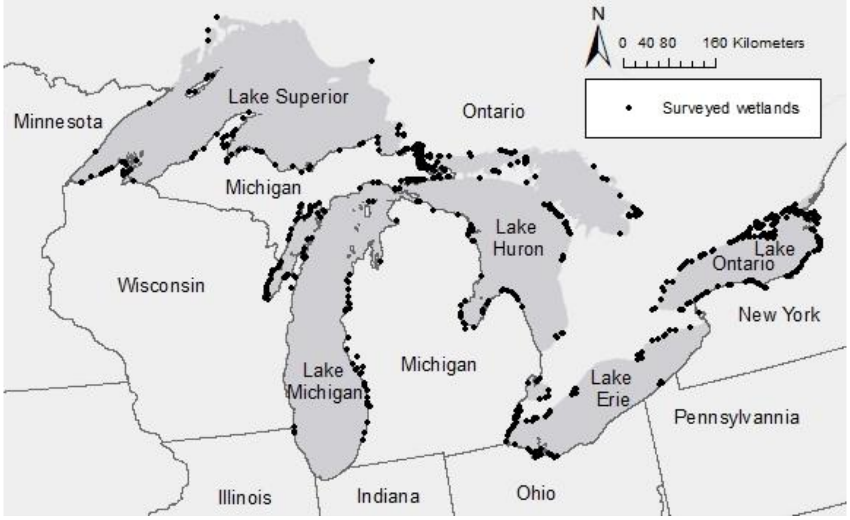

Figure 2-1. Distribution of 641 coastal wetlands in the Great Lakes basin that were sampled for birds in 2011-2017 as part of the random sample of wetlands in the Great Lakes Coastal Wetland Monitoring Program.

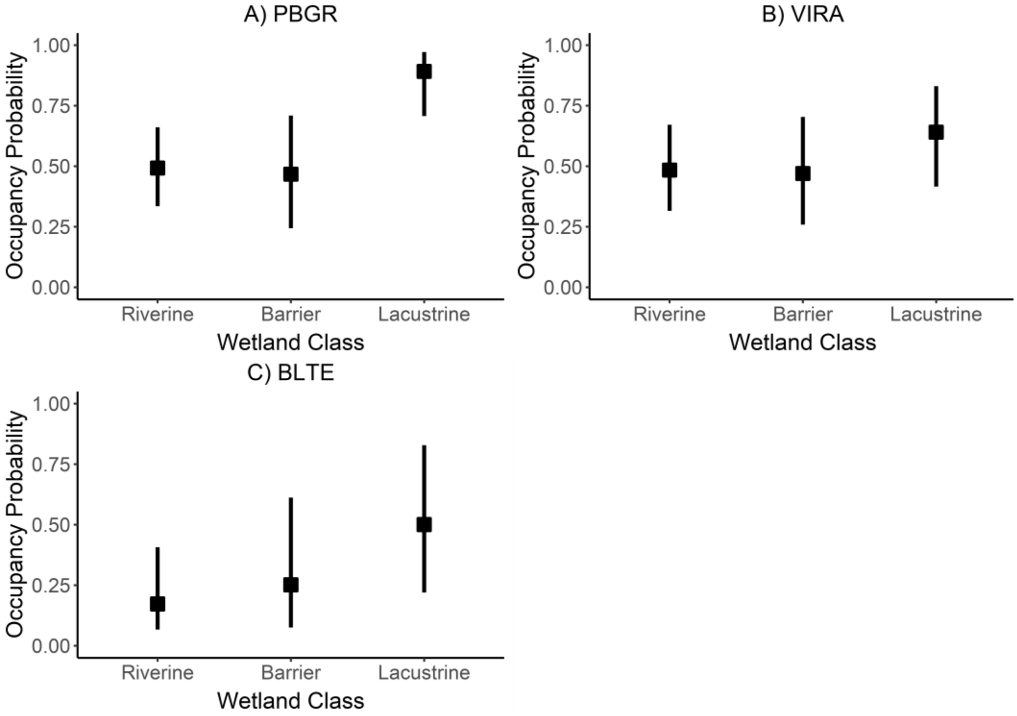

Figure 2-2. Wetland class was included as a covariate for the site-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, and C) Black Tern. Mean occupancy probability on each wetland class and associated 95% Credible Intervals are shown here.

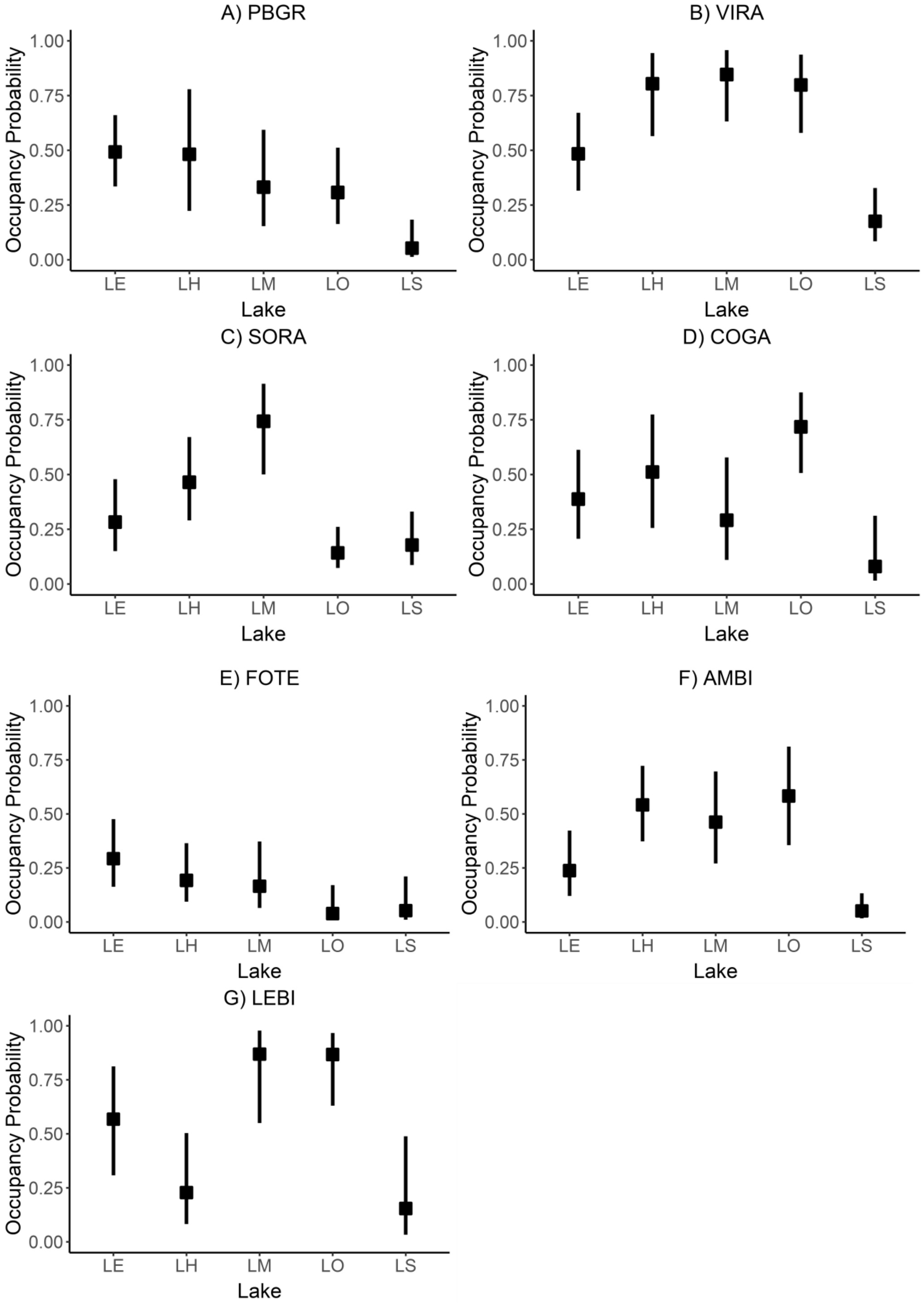

Figure 2-3. Lake was included as a covariate for the site-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, C) Sora, D) Common Gallinule, E) Forster's Tern, F) American Bittern, and G) Least Bittern. Mean occupancy probability on each lake and associated 95% Credible Intervals are shown here.

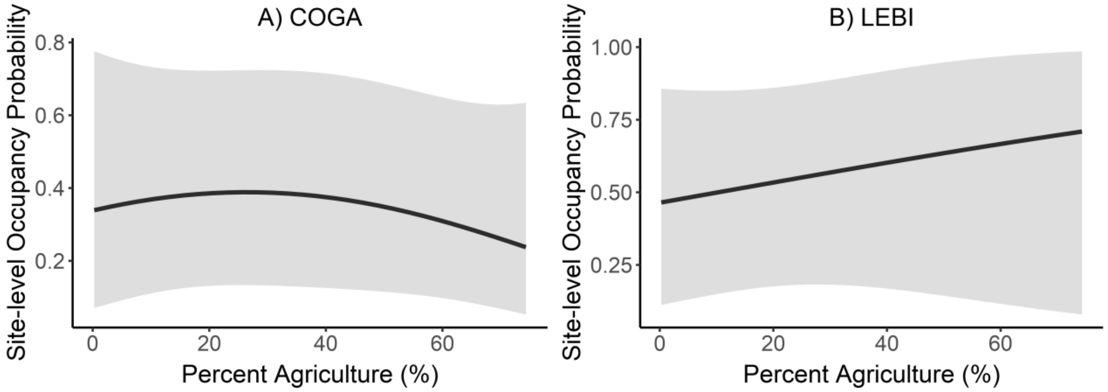

Figure 2-4. Effect of percent agriculture in the watershed on site-level occupancy probability for A) Common Gallinule and B) Least Bittern. Shaded area represents 95% BCIs.

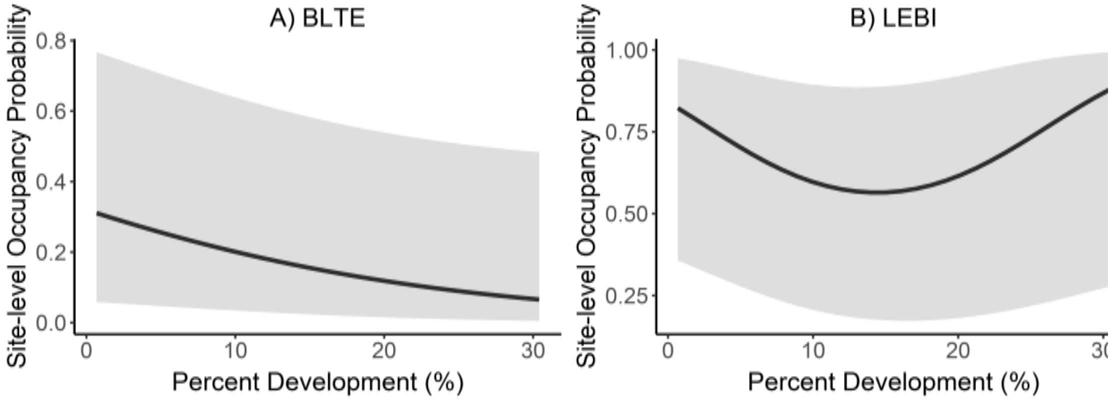

Figure 2-5. Effect of percent development in the watershed on site-level occupancy probability for A) Black Tern and B) Least Bittern. Shaded area represents 95% BCIs.

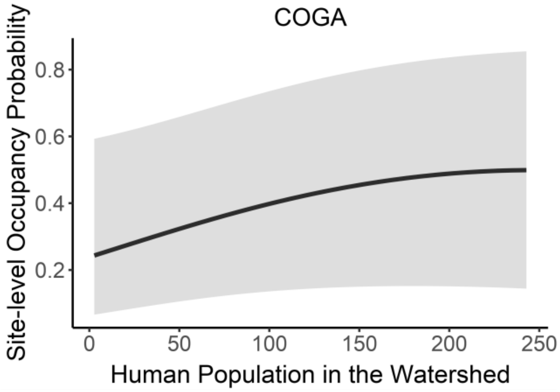

Figure 2-6. Effect of human population in the watershed on site-level occupancy probability for Common Gallinule. Shaded area represents 95% BCIs.

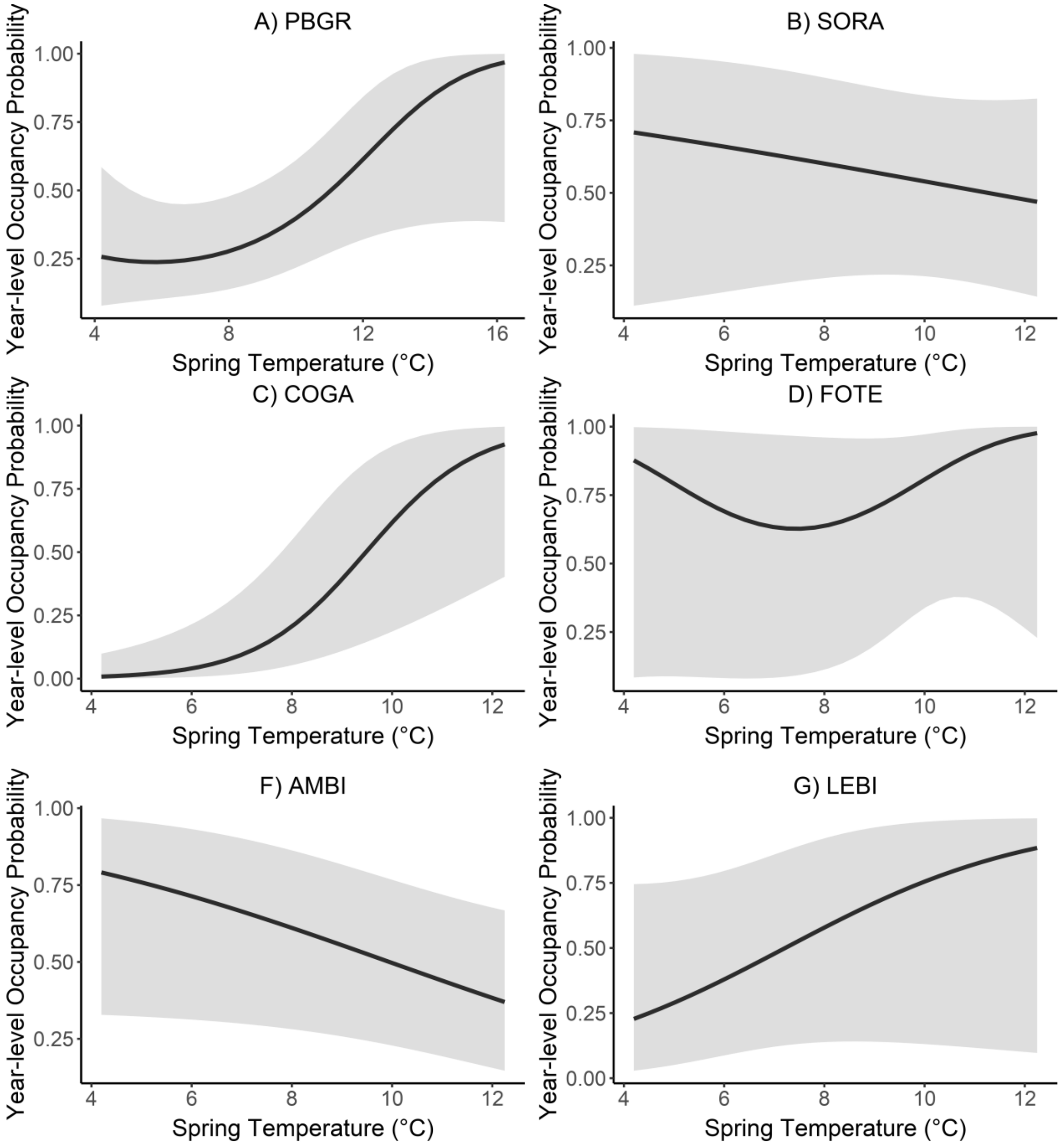

Figure 2-7. Effect of spring temperature on year-level occupancy probability of A) Pied-billed Grebe, B) Sora, C) Common Gallinule, D) Forster’s Tern, E) American Bittern, and F) Least Bittern. Shaded area represents 95% BCIs.

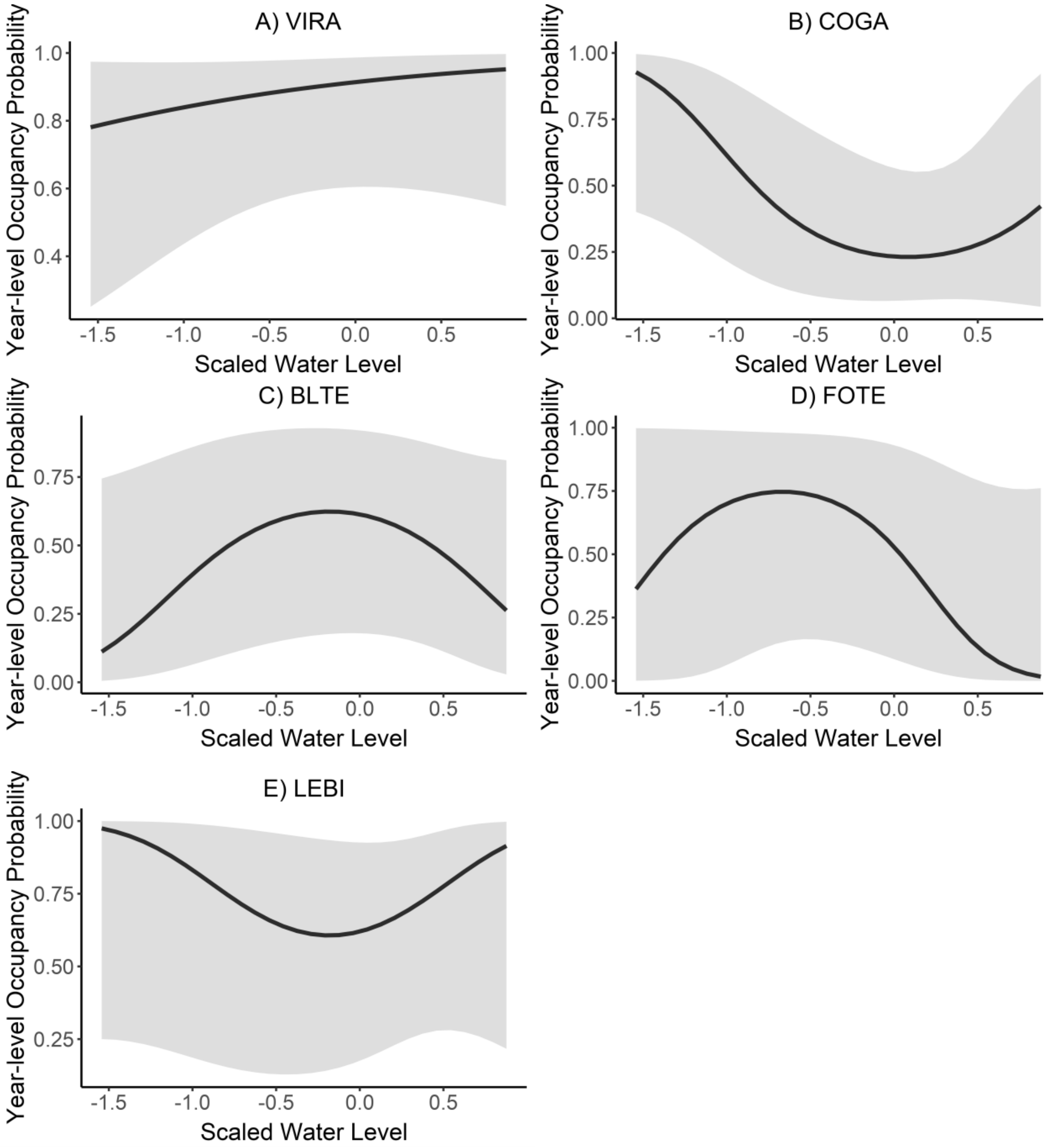

Figure 2-8. Effect of scaled water level on year-level occupancy probability of A) Virginia Rail, B) Common Gallinule, C) Black Tern, D) Forster's Tern, and E) Least Bittern. Shaded area represents 95% BCIs.

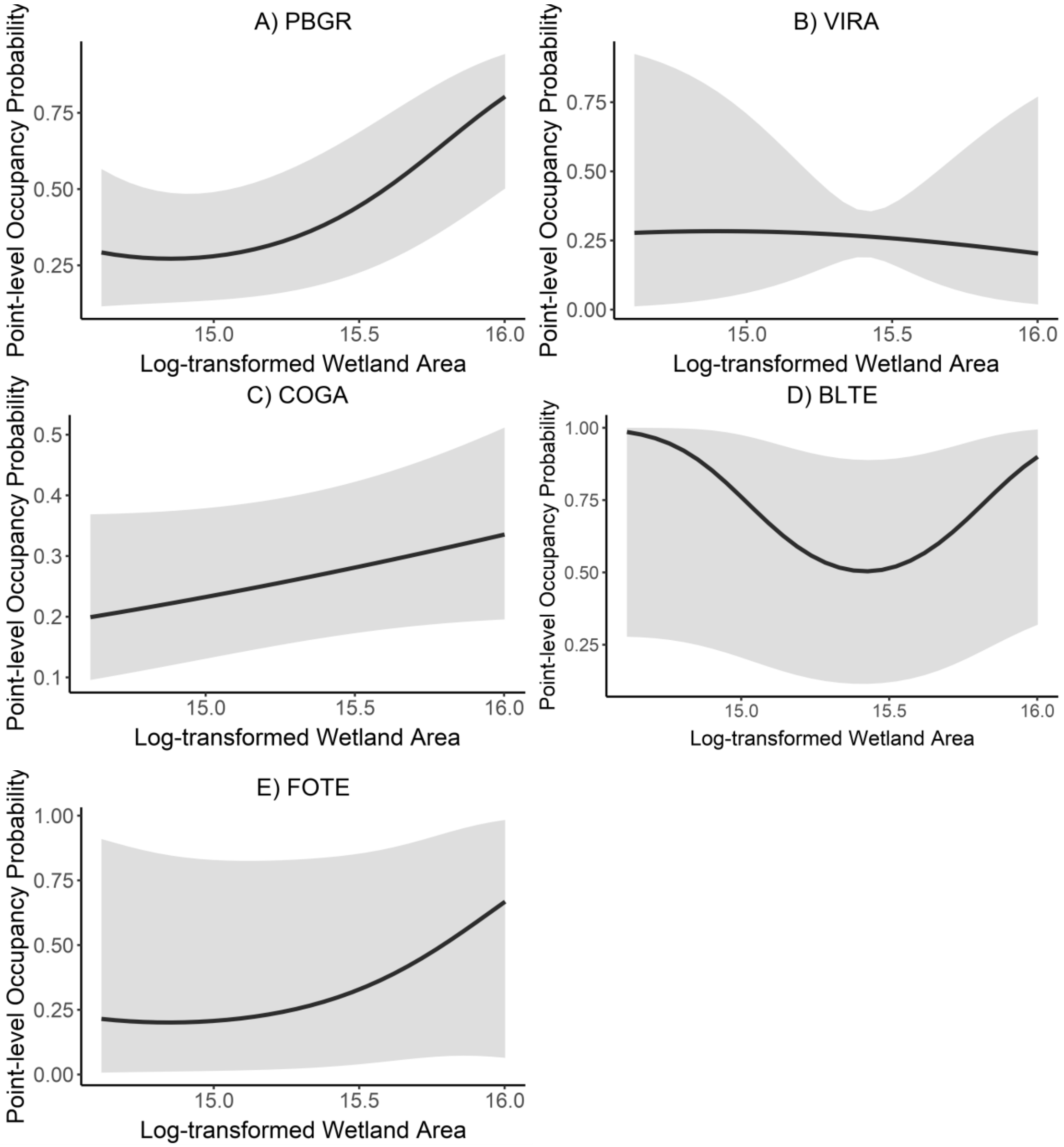

Figure 2-9. Effect of log-transformed wetland area within 2 km on point-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, C) Common Gallinule, D) Black Tern, and E) Forster's Tern. Shaded area represents 95% BCIs.

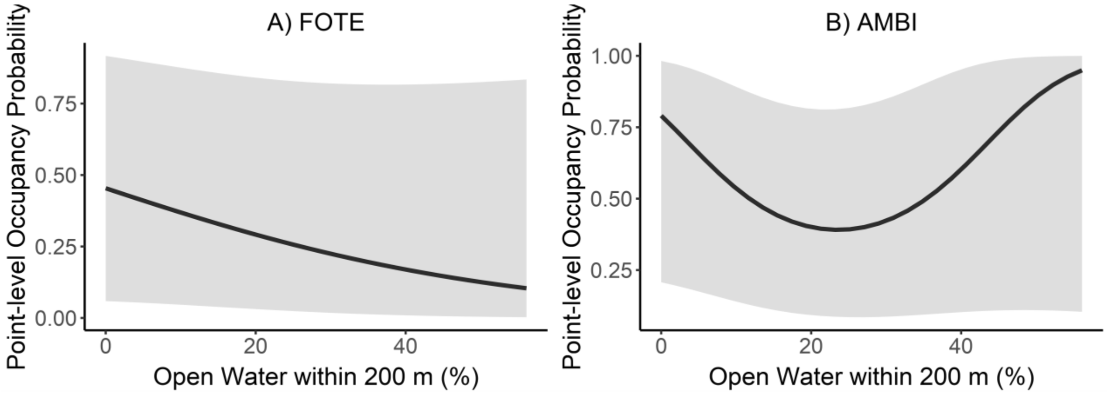

Figure 2-10. Effect of open water within 200-m on point-level occupancy probability of A) Forster's Tern and B) American Bittern. Shaded area represents 95% BCIs.

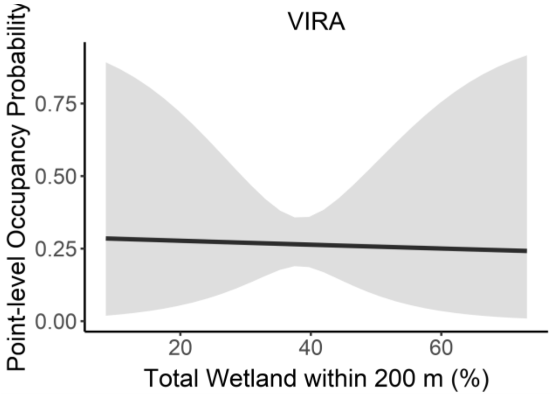

Figure 2-11. Effect of total wetland within 200-m on point-level occupancy probability of Virginia Rail. Shaded area represents 95% BCIs.

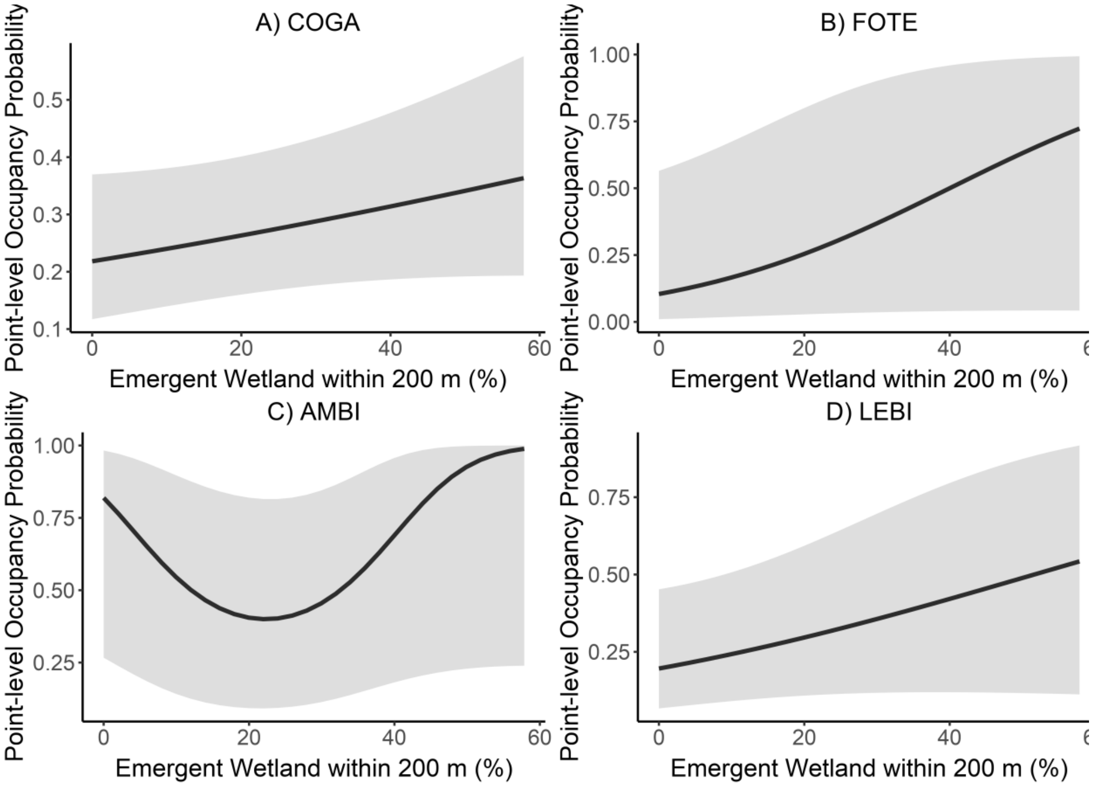

Figure 2-12. Effect of percentage of emergent wetland within 200-m on point-level occupancy probability of A) Common Gallinule, B) Forster’s Tern, C) American Bittern, and D) Least Bittern. Shaded area represents 95% BCIs.

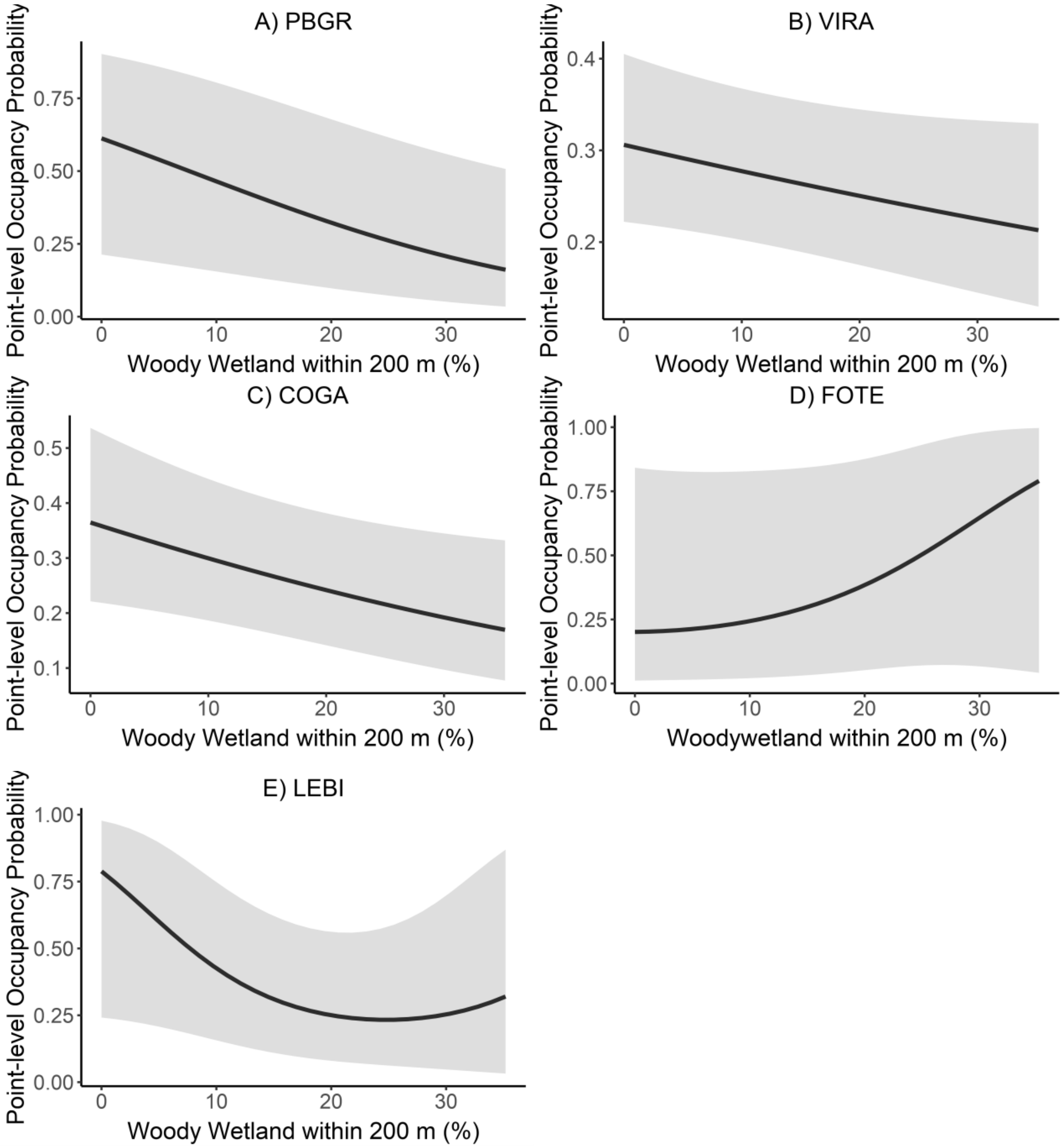

Figure 2-13. Effect of woody wetland within 200-m on point-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, C) Common Gallinule, D) Forster's Tern and E) Least Bittern. Shaded area represents 95% BCIs.

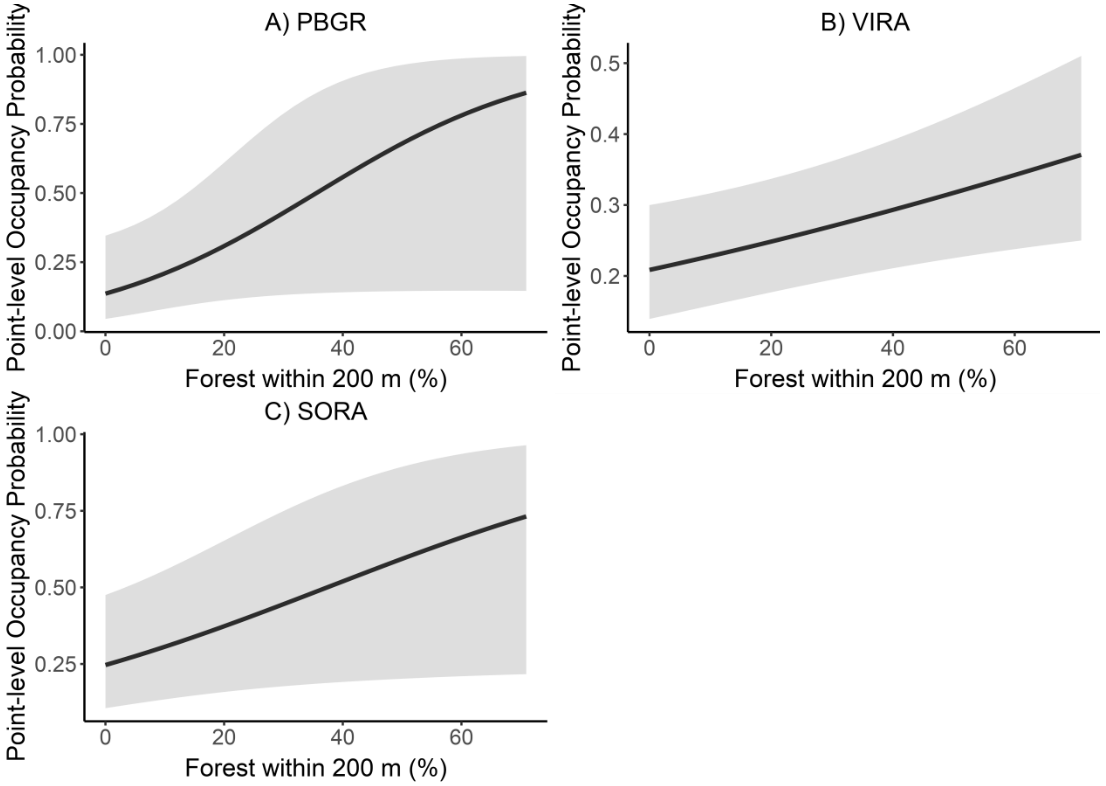

Figure 2-14. Effect of percentage of forest within 200-m on point-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, and C) Sora. Shaded area represents 95% BCIs.

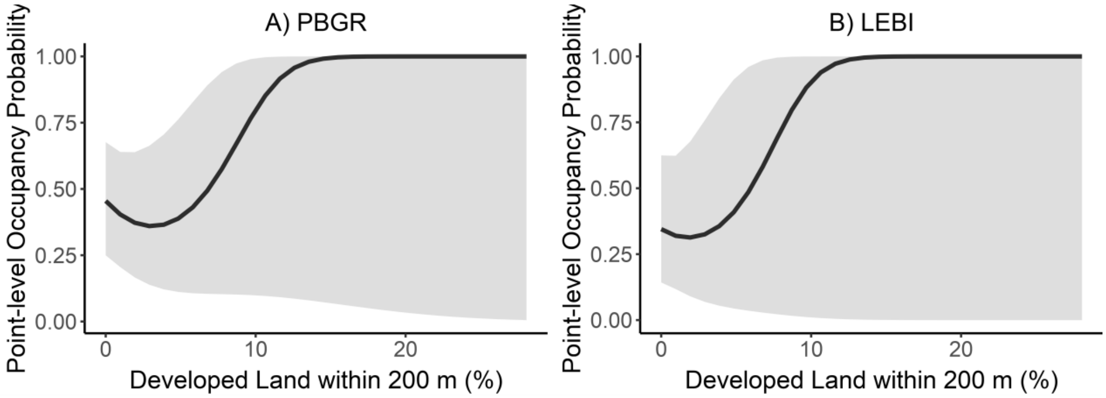

Figure 2-15. Effect of percentage of developed land within 200-m on point-level occupancy probability of A) Pied-billed Grebe and B) Least Bittern. Shaded area represents 95% BCIs.

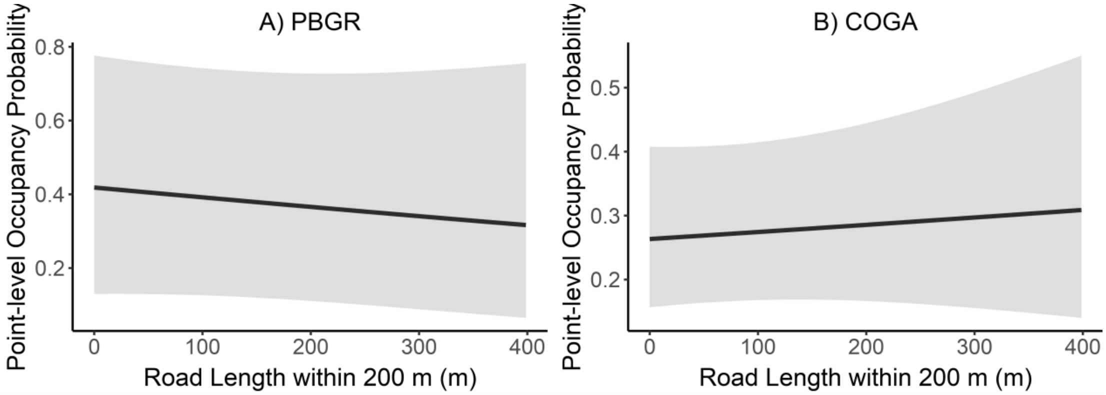

Figure 2-16. Effect of road length within 200-m on point-level occupancy probability of A) Pied-billed Grebe and B) Common Gallinule. Shaded area represents 95% BCIs.

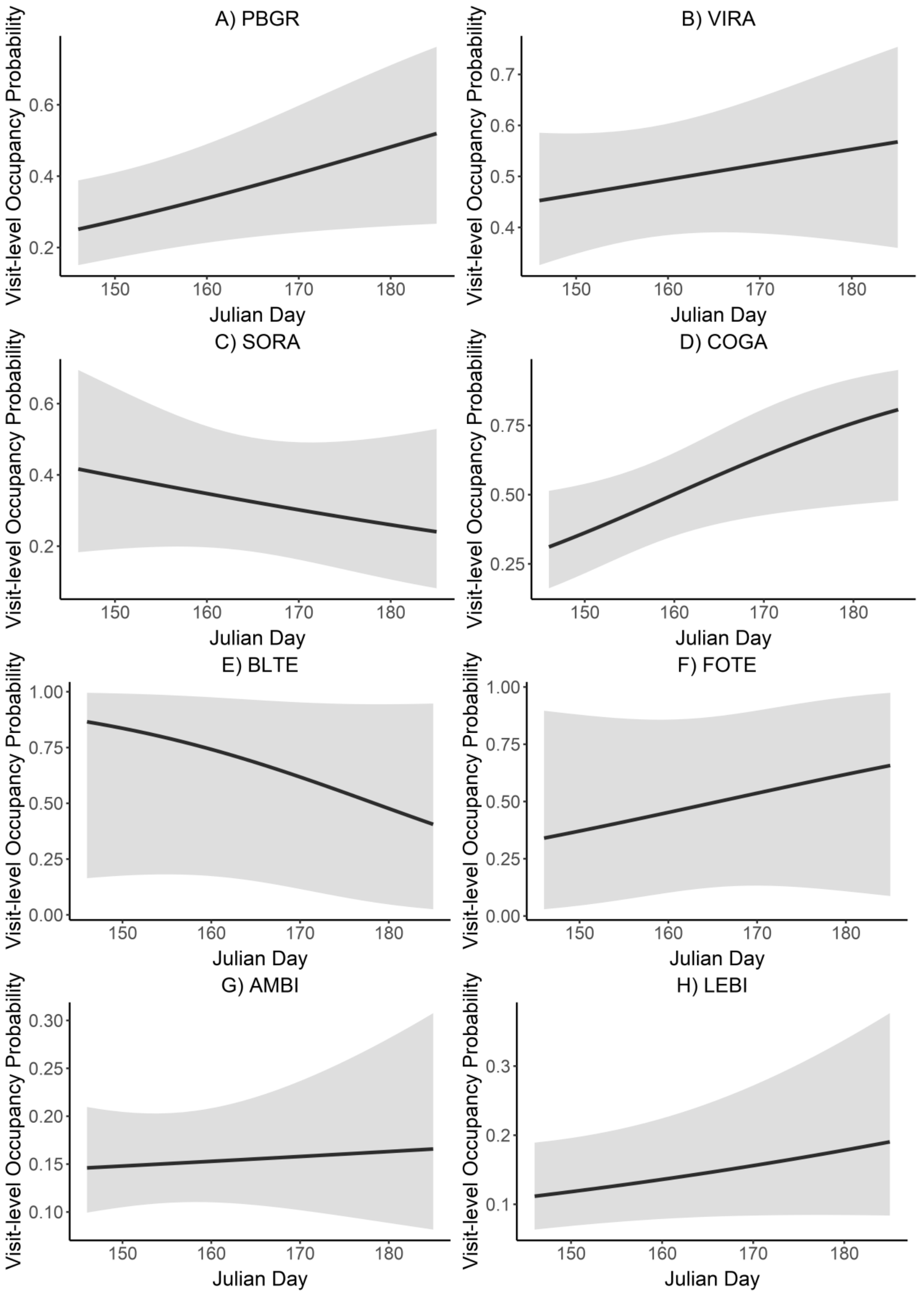

Figure 2-17. Effect of Julian day on visit-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, C) Sora, D) Common Gallinule, E) Black Tern, F) Forster's Tern, G) American Bittern, and H) Least Bittern. Shaded area represents 95% BCIs.

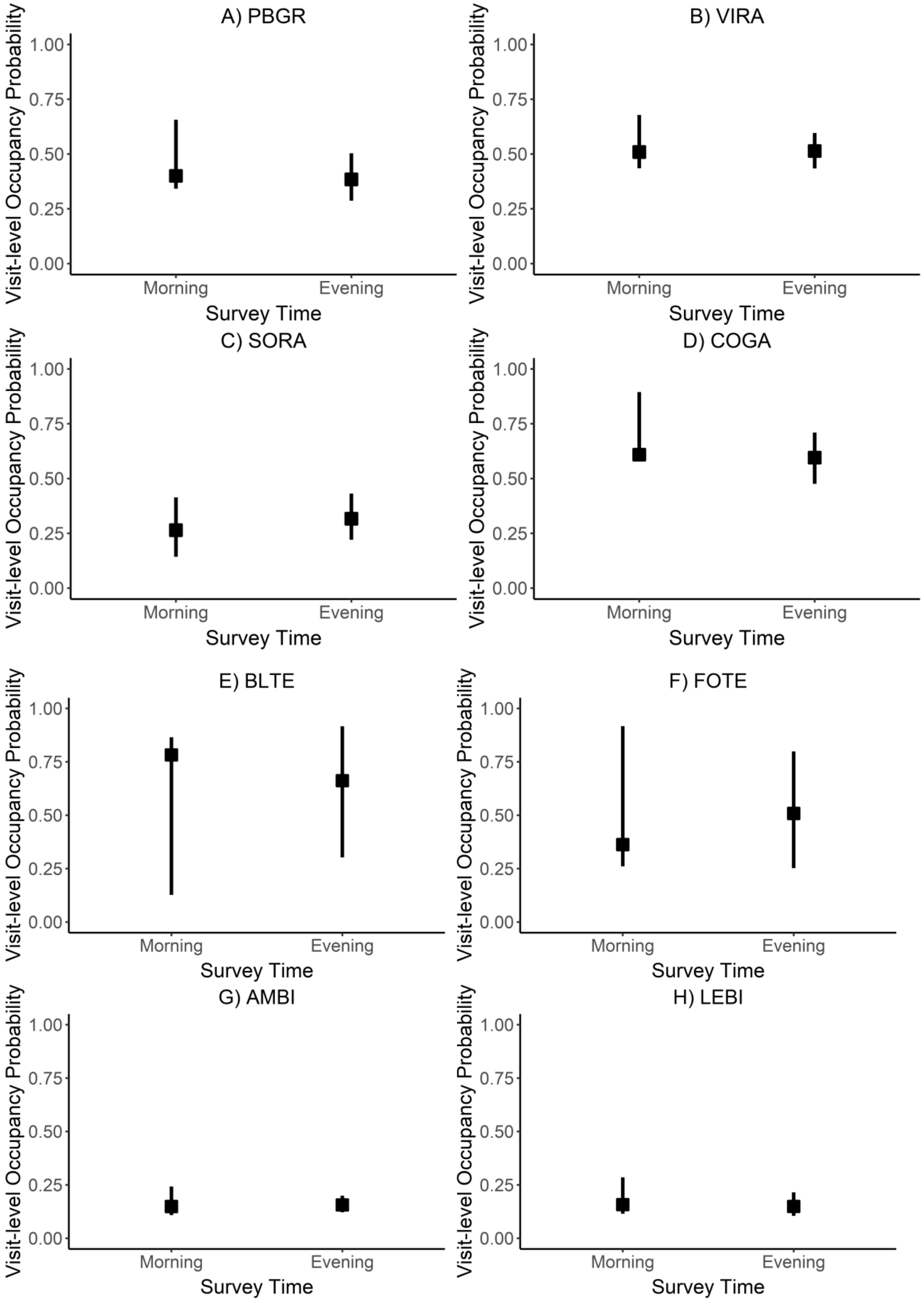

Figure 2-18. Effect of time of day on visit-level occupancy probability of A) Pied-billed Grebe, B) Virginia Rail, C) Sora, D) Common Gallinule, E) Black Tern, F) Forster's Tern, G) American Bittern, and H) Least Bittern. Error bars represent 95% BCIs.

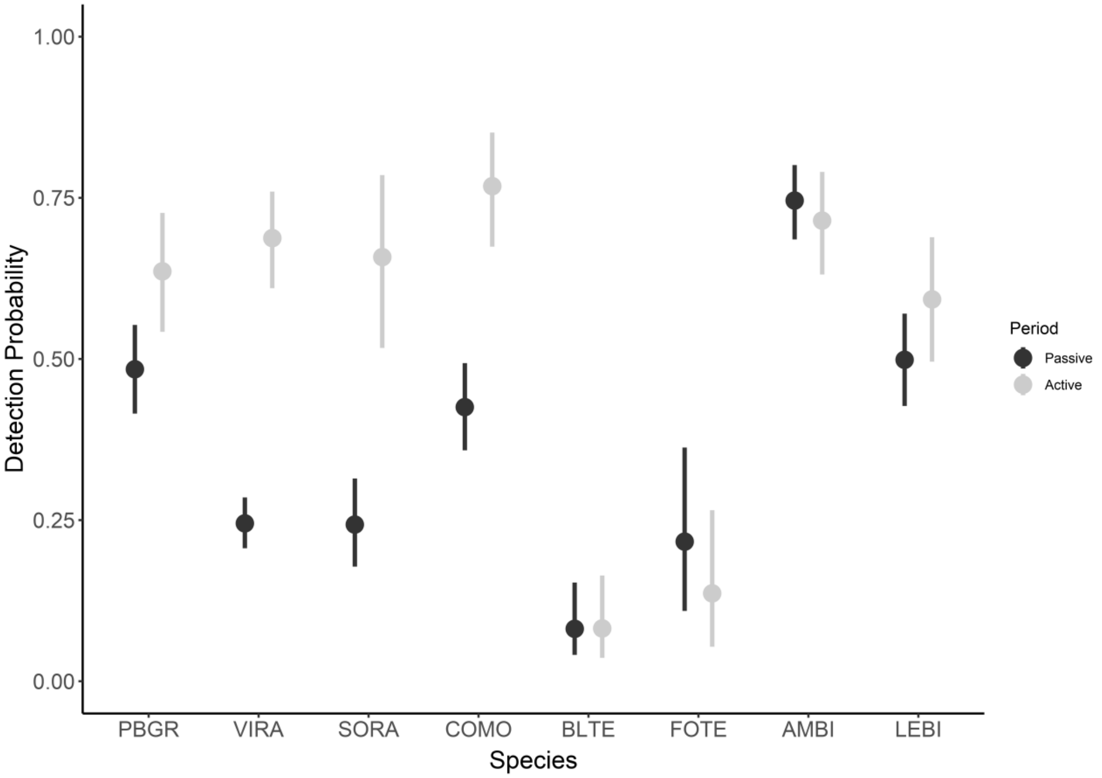

Figure 2-19. Detection probabilities and 95% Bayesian Credible Intervals during passive and active listening periods for eight coastal wetland bird species in the Great Lakes basin.

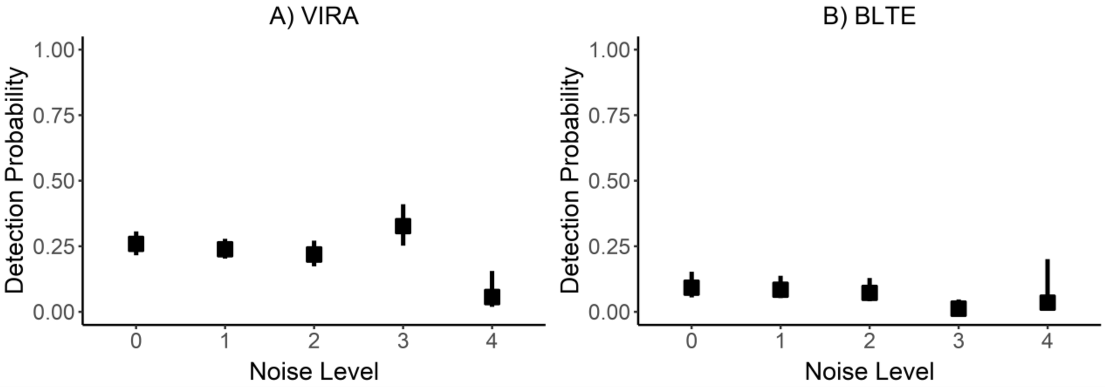

Figure 2-20. Detection probabilities and 95% Bayesian Credible Intervals at increasing observer-reported noise levels (0-4) for A) Virginia Rail and B) Black Tern.

Chapter 3: Regional modeling of habitat associations for wetland-obligate birds in the Upper Midwest

SYNOPSIS

Species exhibit regionally specific habitat associations. It remains unclear how well models of species density based on habitat associations developed in one region may predict the density of the same species elsewhere. Three existing marsh bird survey programs in 1) coastal Great Lakes wetlands, 2) inland Great Lakes wetlands, and 3) the Prairie Pothole Region offer an opportunity to identify general characteristics of species-specific habitat use by obligate wetland-breeding birds that are consistent across regions and to test whether models are transferrable across regions. I developed Poisson models of species density for four species of secretive marsh birds (Pied-billed Grebe [*Podilymbus podiceps*], Virginia Rail [*Rallus limicola*], Sora [*Porzana carolina*], and American Bittern [*Botaurus lentiginosus*]). I developed independent, species-specific models for each of the three study regions. I used adjusted pseudo-R^2 values to compare the amount of variation explained by each model when it was applied to data collected in its region and to data collected in the other regions. Species models differed by region, suggesting that habitat associations for these species are regionally specific. However, certain habitat characteristics were consistently important across regions, suggesting that some species-habitat relationships are consistent at larger scales. Habitat models consistently explained more variation in the density of a species in that respective region than did habitat models created elsewhere. When I applied a model developed in one region to data collected in another region, I found that most models still had a substantial amount of explanatory power, and models created from inland Great Lakes wetland data had the highest median levels of explanatory power when applied to other regions. Therefore, I suggest that conservation planning should emphasize the use of regionally specific habitat association models whenever possible; but, in the

absence of regional data, it is feasible to apply models of habitat associations developed in one region in another region. Additionally, I found that median explanatory power was higher when local-scale habitat characteristics were included in models, which suggests that, whenever possible, these region-specific models should be based on a combination of local and landscape-scale habitat characteristics.

INTRODUCTION

Much avian conservation and management activity happens at regional scales (Soule & Terborgh 1999; Pashley & Warhurst 2000; Regan et al. 2008; NAWMP 2018). This is often appropriate because habitat associations can differ from region to region (Noss 1983; Johnson & Igl 2001; Whittingham et al. 2007). Likewise, changes in population size over time can vary in magnitude and direction in different regions (Peterjohn et al. 1999), and regional changes in population size may be different from continent-level population dynamics (Herkert 1995). Population declines in some regions may reflect range shifts, possibly due to climate change (Bart 2005), or limiting factors in other regions used during the annual cycle of migratory species (Soule & Terborgh 1999; Rushing et al. 2016). Declining populations may also be a symptom of habitat loss (Rushing et al. 2016; Studds et al. 2017), habitat degradation (Studds et al. 2017), or a region-specific combination of habitat loss and climate (Rushing et al. 2016). Reasons for regional declines and their interactions with habitat associations often remain unclear; therefore, it is especially important that I understand the habitat associations of species both within and across regions (Ruth et al. 2003).

One example of regionally specific changes in population size is observed in obligate wetland bird species. Although as a whole wetland birds have been considered a relative conservation success story (North American Bird Conservation Initiative U.S. Committee 2014), regional changes in population sizes have been detected and these are concerning to conservation practitioners (e.g., Wires et al. 2010; Steen et al. 2014; Wyman et al. 2014; Harebottle & Underhill 2015; NAWMP 2018; Specht 2018). Many of these wetland bird species are extremely uncommon and cryptic, making it difficult to monitor their populations (e.g., King Rail (*Rallus elegans*; Conway 2011; Rosenberg et al. 2014). Thus, it is a challenge to identify regionally specific habitat associations, distributions, and population status for them.

The Great Lakes basin is one region where many species of wetland-obligate birds have shown concerning population declines (SOLEC 2009; Wires et al. 2010). Among the nineteen obligate wetland breeding species that use Great Lakes coastal wetland habitat, ten have declined significantly within the Great Lakes basin (Tozer 2013). In many cases, however, the same species that use these Great Lakes coastal wetlands are not declining in other parts of their breeding range. Even within the Great Lakes basin, declines in abundance tend to be more severe in coastal wetlands than in inland wetlands (Tozer 2013). Furthermore, limited evidence from the Breeding Bird Survey suggests that some of the same species have experienced significantly positive population growth over the last several decades in the Prairie Pothole Region (Sauer et al. 2017). These regional differences in population growth may result from differences in characteristics of available wetland habitat in these regions, differences in the anthropogenic influences in these regions, or differences in habitat associations of populations.

Covering over 217,000 ha along 15,000 km of U.S. and Canadian shoreline (Panci et al. 2017), Great Lakes coastal wetlands provide breeding and migratory habitat for a wide array of wetland birds (SOLEC 2009; Wires et al. 2010; Tozer 2013). Non-coastal wetlands in the Great Lakes basin represent 0-50% of the land cover of the various ecoregions (Detenbeck et al. 1999). These inland wetlands support a similar wetland bird assemblage to the coastal wetlands, and one study found that 18% of the globally significant species or community types that inhabit the Great Lakes basin rely on inland wetlands (Detenbeck et al. 1999). The Prairie Pothole Region contains greater than 2.5 million ha of wetlands in the United States, representing 2-9% of land cover of the prairie regions of five states (Dahl 2014). This region is acknowledged as a particularly important region for waterbird conservation due to the availability of wetland habitat, high wetland bird species richness, and high abundances of many wetland-obligate bird species (Niemuth et al. 2005; Niemuth 2017). Despite this region's high suitability for the majority of waterbirds, several species are of conservation concern because of declining populations (e.g., Black Tern [*Childonias niger*]) or limited knowledge about their populations (Niemuth et al. 2005).

The hydrology of wetlands in these three regions is highly divergent. Coastal wetlands are set apart by their proximity to the Great Lakes, which causes unique and variable combinations of physical, hydrological, biological, and chemical lake effects that result in biotic communities that are adapted to high levels of disturbance (Keough et al. 1999; Timmermans et al. 2008). Lake effects that influence the conditions in coastal wetlands include wind-driven seiches (periodic rises and falls in lake level that are somewhat analogous to daily tides), seasonal and inter-annual variations in water levels (Keough et al. 1999; Gathman et al. 2005), ice action, lake currents and waves, and variation in substrates that influence patterns of erosion and deposition (Keough et al. 1999). In contrast, the non-coastal Great Lakes wetlands have very different hydrological conditions, as they lack direct connections to the Great Lakes and are therefore not subject to the same lake influences. Similarly, absent lake effects, wetlands in the Prairie Pothole Region are shaped by different hydrogeology than Great Lakes coastal wetlands. The hydrology of Prairie Pothole wetlands is primarily determined by ground and surface water (Brannen et al. 2015), with snow accumulation playing a particularly important role in the dynamics of water levels in the subsequent year (Fang & Pomeroy 2009).

While the inland and coastal Great Lakes wetlands are subject to many of the same land cover and land use patterns, these patterns differ from those in the Prairie Pothole Region. The Great Lakes region was predominantly forested prior to European settlement (Zhang & Guindon 2005) and forest habitat remains the dominant cover type (Zhang & Guindon 2005; Wolter et al. 2006). While a significant land area in the Great Lakes basin was converted to agriculture, especially in the southern portion of the basin (Detenbeck et al. 1999; Zhang & Guindon 2005; Askins et al. 2007; Danz et al. 2007), the region has experienced a decline in agricultural land use in recent decades (Wolter et al. 2006; Pijanowski & Robinson 2011). In contrast, the primary pre-European land cover in the Prairie Pothole Region was mixed-grass prairie (Askins et al. 2007). There has been considerably more conversion to row-crop agriculture in the Prairie Pothole region (Wright & Wimberly 2013) and land use in the region is almost exclusively cropland and cattle ranching (Askins et al. 2007).

Human land use has resulted in wetland loss in all three regions, but the degree and causes of loss have varied. The Great Lakes coastal wetlands have experienced a high degree of wetland loss, with over half of coastal wetlands having been converted to human land use (SOLEC 2009). There has been a sizeable increase in human development in coastal areas (Wolter et al. 2006). Corresponding with increased development, intensity of recreational use in shoreline habitat has increased considerably in recent decades (Stynes et al. 1997; Johnson et al. 2002; Allan et al. 2013). This urban encroachment and accompanying increases in human activities disproportionately causes concerning degradation of associated coastal wetlands (Wires et al. 2010). Loss of inland wetlands has been highly variable across the basin, with the highest concentrations of wetland loss in the agricultural southern basin or the highly concentrated urban centers elsewhere (Detenbeck et al. 1999; Danz et al. 2007; Hollenhorst et al. 2007; Uzarski et al. 2019). As much as 99.6 % of wetland area was lost in the Great Lakes' Eastern Corn Belt Plains ecoregion, while the amount of inland wetland area in the forested northern Great Lakes basin has been limited to 0-30% of wetland area (Detenbeck et al. 1999). Inland wetlands in the Great Lakes region have also been spared some of the negative influences of human development, as the greatest concentration of human development has occurred within just one kilometer of the shoreline (Wolter et al. 2006). In the Prairie Pothole Region, wetland loss has been primarily the result of agricultural conversion rather than development; there has been considerable alteration of natural hydrologic conditions with human-caused drainage and consolidation (McCauley et al. 2015). Smaller wetlands have been drained preferentially into larger wetlands (Van Meter & Basu 2015) that have standing water for more of the year, and therefore more fish and fewer macroinvertebrates, resulting in lower productivity for many bird species (McCauley et al. 2015).

It remains unclear how these many regional differences in wetland hydrology, habitat composition, and degree of anthropogenic influences may affect habitat selection of obligate wetland breeding birds in coastal Great Lakes wetlands, inland Great Lakes wetlands, and Prairie Pothole wetlands. To better understand regional differences in habitat associations, I developed region-specific models of habitat association for four species of wetland obligate birds using data from three bird survey programs, each conducted in one of these regions. The primary objectives of this study were to determine how habitat associations vary across regions and then to determine if models developed in one region can be applied to other regions. I also summarized the relationship of habitat composition patterns to individual species abundances within regions to provide regionally specific guidance for conservation and management of these species.

For this study I selected four focal species: Pied-billed Grebe (*Podilymbus podiceps*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), and American Bittern (*Botaurus lentiginosus*). All four species are obligate wetland-breeding birds that occur in both the Great Lakes basin and the Prairie Pothole Region. The Pied-billed Grebe population is declining in the Great Lakes basin (Tozer 2013, 2016), with an average annual decline in the mean abundance per wetland of 4.2% between 1995 and 2012 (Tozer 2013). It is considered a high conservation priority species in the region under the Upper Mississippi Valley/Great Lakes Joint Venture (UMVGL) waterbird plan (Wires et al. 2010). While abundance was higher in inland Great Lakes wetlands than in coastal Great Lakes wetlands throughout 1995-2012, the differences were not statistically significant (Tozer 2013). The Pied-billed Grebe is a low-priority species for conservation in the Prairie Pothole Joint Venture (PPJV) Implementation Plan (Niemuth 2017), but is predicted to decline under future climate scenarios (Steen et al. 2014).

The Virginia Rail population is declining in the Great Lakes basin (Tozer 2013, 2016), with an average annual decline in mean abundance per wetland of 3.7% between 1995 and 2012 (Tozer 2013). It has been identified as a species of moderate conservation concern in the UMVGL waterbird plan (Wires et al. 2010). Abundance of this species is significantly higher in all years in inland wetlands than in coastal wetlands in the Great

Lakes basin (Tozer 2013). In the Prairie Pothole Region, the Virginia Rail is considered a moderate priority species in the PPJV Implementation Plan (Niemuth 2017).

The Sora population is declining in the Great Lakes basin (Tozer 2013, 2016), with an average annual decline in the mean abundance per wetland of 2.3% between 1995 and 2012 (Tozer 2013). This species is considered a high conservation priority species in the UMVGL waterbird plan (Wires et al. 2010). In most years, Sora abundance is significantly higher in inland Great Lakes wetlands than in coastal Great Lakes wetlands (Tozer 2013). In contrast, the Sora is a low-priority species in the PPJV Implementation Plan (Niemuth 2017), although it is predicted to decline in the Prairie Pothole Region as a result of future climate change (Steen et al. 2014).

The American Bittern population is declining in the Great Lakes basin (Tozer 2013, 2016), with an average annual decline in the mean abundance per wetland of 2.4% between 1995 and 2012 (Tozer 2013). It was identified as a high conservation priority species for the region in the UMVGL waterbird conservation plan (Wires et al. 2010). There is no statistically significant difference in the abundances of this species between inland Great Lakes wetlands and coastal Great Lakes wetlands (Tozer 2013). In the Prairie Pothole Region, the American Bittern is considered a high priority for conservation in the PPJV Implementation Plan (Niemuth 2017) and is listed as a Conservation Priority Level 1 species in the North Dakota list of Species of Greatest Conservation Need (Dyke et al. 2015; North Dakota PPJV Planning Team 2017). This species is also predicted to decline in the Prairie Pothole Region under future climate scenarios (Steen et al. 2014).

I expect that wetland birds breeding in Great Lakes coastal wetlands will differ in their habitat associations from conspecifics breeding in the Prairie Pothole Region due to the differences in the physical, hydrological, biological, chemical, and anthropogenic characteristics between the two regions. Similarly, I expect that birds using coastal Great Lakes wetlands will differ in their habitat associations from conspecifics using inland wetlands in the Great Lakes watershed, though I expect that the habitat associations between birds will be more similar within the Great Lakes basin regardless of coastal versus inland status than to the habitat associations of birds in the Prairie Pothole Region because there are more similarities between the habitat characteristics of these wetlands.

Despite these expected differences in habitat associations among regions, I also expect that there will be underlying habitat characteristics consistently associated with the occurrence of a particular wetland-dependent species. For instance, wetland area requirements may be consistent across regions if species are area-sensitive (Johnson 2001; Riffell et al. 2001; Ma et al. 2010)—though area sensitivity itself may be regionally specific (Johnson & Igl 2001; Riffell et al. 2001). Species with specialized niches may require certain combinations of emergent and open water habitat for foraging and nesting (Chin et al. 2015; Tozer 2016).

This comparison will improve our understanding of the different factors affecting avian communities in Great Lakes coastal wetlands, an ecosystem of particular conservation concern (Tozer 2013; Uzarski et al. 2017). This research will also provide species-specific models of wetland bird distribution in the Prairie Pothole Region, and basin-wide distribution in both Great Lakes coastal wetlands and inland wetlands. These models can provide the basis for policy recommendations to tailor species-specific management and conservation plans to particular regions. This outcome is important because many species occur across multiple regions or across entire continents, but regional management approaches may be more appropriate than range-wide management due to regional differences in habitat selection or habitat availability.

METHODS

Data Collection

Data for my analysis came from three monitoring programs (detailed below; Fig. 3-1).

Prairie Pothole Dakotas Wetland Surveys (DWS)

Bird surveys

The U.S. Geological Survey's Dakotas wetland surveys (DWS) was an extensive effort in the Prairie Pothole Region. Bird surveys were conducted between 3 May and 3 July at 1,281 wetlands in the Prairie Pothole Region of North and South Dakota in 1995-1997, with an average of 500 wetlands sampled in each year of the study. Wetlands were selected to maximize the diversity of wetland classes, ownership types, restoration statuses, and wetland sizes (Igl et al. 2017). The bird survey methodology aimed for a wetland-wide census and involved counting waterfowl with a spotting scope, broadcast calling to aurally identify secretive marsh birds, walking the perimeter of the wetland to obtain better views, and flushing birds if emergent vegetation obstructed the view (Igl et al. 2017). Data quality was ensured with careful training of field personnel.

Vegetation surveys and land cover data collection

For the DWS, environmental data were visually estimated in the field by the observers. These observer-generated variables included local habitat cover within the entire wetland basin and land use and land cover within a 400 m buffer of the wetland. Observers also estimated wetland area or used data from the National Wetlands Inventory and aerial imagery to quantify it. Comparison of the observer-generated landcover estimates to remotely sensed covariates calculated for many of the same wetlands by Igl et al. (2017) suggested that the observer-generated estimates were comparable to remotely sensed alternatives. Furthermore, observer-generated estimates were available for a larger sample of wetlands, and those that did not have remotely sensed data available were spatially and temporally biased. Therefore, I preferred to use the observer-generated estimates. See chapter 1 for complete details.

Great Lakes Coastal Wetland Monitoring Program (CWMP)

Bird surveys

The Great Lakes Coastal Wetland Monitoring Program (CWMP) is a Great Lakes Restoration Initiative-funded project that has monitored coastal wetlands across the entire Great Lakes basin annually since 2011 (Uzarski et al. 2017). Bird surveys are conducted at a stratified, rotating random sample of wetlands—each wetland in the random sample is revisited twice every five years, with a minimum of 15 days between visits. To account for latitudinal variation in avian phenology, wetlands in the southern portion of the Great Lakes basin are sampled between 20 May and 10 July whereas wetlands in the northern portion are sampled between 10 June and 10 July. Survey points are located at least 250m apart and the number of points sampled per wetland is proportional to the size of the wetland, with a cap of six points per wetland generally adhered to. Over 650 individual wetlands have been surveyed from 2011 to 2018, representing a total of over 1,500 individual survey points. Many wetlands were sampled in multiple years. The CWMP bird survey methodology (outlined in Uzarski et al. 2017, Panci et al. 2017, and Chapter 2) uses 100m radius point counts and simultaneous unlimited-distance counts for 15 minutes, including broadcast calling of focal species' vocalizations for minutes 6-10, inclusive. During this period, birds are identified to species using visual and aural cues. Data quality is ensured with extensive training and annual certification of field personnel and mid-season quality control checks.

Vegetation surveys

In 2016 and 2017, habitat data were also collected at the wetlands sampled for birds, resulting in a sample of 194 wetlands with both bird and habitat data available. Habitat monitoring followed the protocols outlined for the Marsh Monitoring Program (Bird Studies Canada 2009).

Land cover data collection

Remotely sensed land use and land cover data were used to supplement the vegetation surveys. I used the 2010 North American Land Cover 30m dataset from North American Land Change Monitoring System (NALCMS 2017) to obtain consistent data across the entire Great Lakes basin. Landscape-scale variables were quantified within 400 m buffers of each sampling point using ArcGIS 10.6.1 (ESRI, 2018). The percentage of land cover classifications within each buffer size was calculated using packages raster

(Hijmans & van Etten 2012) and rgdal (Bivand et al. 2019) in program R v. 3.4.3 (R Core Team 2018).

Great Lakes Marsh Monitoring Program (GLMMP)

Bird surveys

The Great Lakes Marsh Monitoring Program (GLMMP) is the largest volunteer-based wetland monitoring effort across the Great Lakes basin (Tozer 2016). The GLMMP began in 1995 and has run continuously since. Bird surveys are conducted along volunteer-selected routes that include between 1 and 8 points per route. Routes may include a single wetland or multiple wetlands. Participants conduct 100 m-radius semi-circular point counts at each point count location along the route between 20 May and 5 July, with each route sampled in a particular year visited 2-3 times with at least 10 days between surveys. Points are located at least 250 m apart to minimize double counting. From 1995 to 2007 counts lasted 10 minutes, and from 2008 to 2019 counts lasted 15 minutes. Research has shown that 10- and 15-minute counts are largely comparable, with only very modest gains in detections of a small number of species during the extra 5 minutes (Tozer et al. 2017). The point counts include broadcast calling of focal species' vocalizations during the first five minutes for 10-minute counts and during the middle five minutes for 15-minute counts.

For the purposes of this study, I limited the GLMMP dataset to only those points within the extent of the Great Lakes basin during the years 1995-97 and 2016-17 to temporally match the CWMP and DWS data. I also excluded any coastal wetlands by excluding any points that fell within the wetland boundaries used by the CWMP in ArcGIS 10.6 to avoid duplication of wetlands.

Vegetation surveys

GLMMP participants conduct basic habitat surveys for each point in each year in late May to mid-June, when flowering plants can most easily be identified (Bird Studies Canada 2008, 2009; Tozer 2016). Participants visually estimate the percent cover of open water, sand/mud/rock, and various plant species within the

100 m-radius point count semi-circle. These visual estimates are not significantly different from the estimates provided by more intense estimates in 20m x 20m subplots subplots (Crewe & Timmermans 2003).

Land cover data collection

Land cover data was collected using the same methods as described for the CWMP.

Analysis

Although some of these wetlands were sampled in multiple years, I considered each wetland in each year to be a unique wetland due to the potentially dramatic interannual variability in local vegetation in both Great Lakes wetlands and Prairie Pothole wetlands (Gathman et al. 2005; Igl et al. 2017). These differences in plant communities are often the result of differences in cumulative amounts or duration of precipitation (Igl et al. 2017) or water level (Gathman et al. 2005). Plant communities also respond differently to high water levels following a year of intermediate water levels as compared to after a year of similarly high water levels (Gathman et al. 2005), as was seen in the Great Lakes basin in 2016 versus 2017 (Gnass et al. 2018).

For each data set, I excluded woody wetlands by removing any wetlands where greater than 20 percent of surveyed habitat was trees or shrubs. I excluded these wetlands because they were intentionally excluded from the random sample of wetlands selected for the CWMP and do not exist in the Prairie Pothole Region. I also excluded wetlands where vegetation surveys were incomplete, with less than 50 percent of the local-scale habitat characteristics recorded by the observer, consistent with my approach in Chapter 1. For wetlands with more than one sample in a given year, I used only the count closest to the midpoint in the breeding season (June 11). If the surveys were equidistant from the midpoint, I used the earlier survey.

I then selected a random sample of two-thirds of each data set to use for model development. The remaining one-third of the data was reserved for model evaluation. Using each of the three data sets independently, I developed models of density for each focal species (American Bittern, Virginia Rail, Sora, and Pied-billed Grebe). I modeled counts of abundance using a Poisson regression with an offset for log-transformed wetland area with package dplyr (Wickham et al. 2019) and MuMIn (Barton version 3.4.3 (R Core Team 2018).

I restricted my explanatory variables to those that I considered comparable across all three data sets. I included local habitat characteristics, land use and land cover, heterogeneity measures, and hydroperiod. All variables were centered at their mean and scaled by their standard deviation. The local habitat characteristics included percentages of wet meadow, emergent vegetation, open water, and shoreline/mudflat cover. For GLMMP and CWMP, I calculated wet meadow and emergent vegetation percentages from the percentages of appropriate plant species (wet meadow = reeds, grasses and sedges, purple loosestrife [*Lythrum salicaria*], water willow [*Justicia americana*], and smartweed [*Persicaria amphibia*]; emergent = cattail, bulrushes [*Scripus* spp.], pickerel weed [*Pontederia cordata*], arrowhead [*Sagittaria podophyllum*], bur reed [*Sparganium natans*], and wild rice [*Zizania* spp.]). The land use and land cover variables included percentages of cropland, grassland, forest, and wetland cover within 400 m. The heterogeneity indices were based on Inverse Simpson Diversity Indices of either local-scale habitat characteristics or natural land uses (grass, forest, and wetland but not cropland; see Chapter 1).

Wetland classes were converted to estimated hydroperiod from existing definitions of wetland classes and related hydroperiods available in the scientific literature (Stewart & Kantrud 1971; Cowardin et al. 1979; Niemuth et al. 2010; Dahl 2014). The semipermanent category includes the growing season and fall months (Kantrud et al. 1989). Thus I defined hydroperiods of permanent wetlands as 365 days, semipermanent wetlands as 182 days, seasonal wetlands as 60 days, and temporary wetlands as 21 days. Alkali wetlands, found only in the Prairie Pothole Region, were assigned a hydroperiod of 365 days because most have standing water year-round (D. H. Johnson, *pers. comm.*). In models for the Prairie Pothole Region only, I included a binary variable for whether the wetland was classified as alkali to distinguish alkali wetlands from permanent wetlands, which also had a hydroperiod of 365 days.

Wetland area was included as a candidate variable in all species and dataset combinations given the importance of wetland area that I demonstrated in the Prairie Pothole Region (Elliott et al. 2019). However, actual area was not measured for the GLMMP and CWMP wetlands, and only observer-estimates of binned wetland area were available for these two regions. Thus, I based estimates of a representative wetland size for each bin on the DWS dataset. Wetlands from all three regions were first binned by size according to the GLMMP protocol. “Tiny” wetlands were defined as between 1.5 and 2.5 ha, “small” wetlands were between 2.5 and 5 ha, “medium” wetlands were between 5 and 25 ha, “large” wetlands were between 25 and 50 ha, and “huge” wetlands were greater than 50 ha. I then calculated the median value of Prairie Pothole wetlands that fell into each of these bins, and used this median value as the estimate for the representative area of the bin for modelling of all three regions. Thus, all “tiny” wetlands were assigned areas of 0.39 ha, “small” wetlands of 3.5 ha, “medium” wetlands of 10 ha, “large” wetlands of 32 ha, and “huge” wetlands of 65.5 ha.

I used Welch’s ANOVAs to compare wetland characteristics across regions. Welch’s ANOVA is not sensitive to unequal variances between groups but also can be applied in cases of equal variance (Rasch et al. 2009; Moder 2010). Given the differences in sample sizes (by an order of magnitude; Table 1) and in the expected land use and land cover compositions of the different regions, I expected that at least in some cases the three regions would have very different variances. For this reason, I did not combine the three datasets and use region as a categorical explanatory variable. However, heteroscedasticity was not a problem within the individual datasets. I made *post-hoc* comparisons using the Games-Howell test to identify which regions showed significantly different mean variable values at the $p < 0.05$ level.

I examined my variables for collinearity following Dormann et al. (2013) but found no pairs to be highly correlated (all $|r| < 0.60$) and so considered no pairs of variables as collinear. For all variables except area, I created density plots of the values for each variable at sites with and without the species of interest for each species, variable, and data set combination. Based on visual inspection of these plots, I determined which variables appeared to differ between occupied and unoccupied and included only these variables as candidates in my subsequent model selection step.

Finally, I compared these candidate models using adjusted pseudo- R^2 (Heinzl & Mittlbock 2003). I report here the model with the highest adjusted pseudo-R^2. This model explains the greatest amount of variation in the density of the species of interest while accounting for the number of covariates in the model. I then applied these models to the other datasets and identified the amount of explanatory power each model had in other regions by calculating the adjusted pseudo-R^2.

I considered the use of zero-inflated Poisson regression, but results of Vuong tests for each pair of species-specific combined models (Vuong 1989) showed either that the majority of models were indistinguishable or that the ordinary Poisson was superior to the zero-inflated version.

RESULTS

For the DWS, a total of 1262 wetlands were surveyed. Of these wetlands, 833 were included in the training dataset and 429 in the validation dataset. For the CWMP, 194 wetland points were surveyed for both birds and local vegetation and are used in these analyses. Of these wetlands, 128 wetlands were included in the training dataset and 66 wetlands were included in the validation dataset. For the GLMMP, 1250 wetlands are included and 825 were included in the training dataset and 425 were included in the validation dataset.

Wetlands in the three datasets showed distinct patterns of regionally specific wetland characteristics at the local scale (Table 1). There was a significant effect of region on percentage of open water ($F_{2, 557.74} = 26.26$, $p < 0.01$). *Post-hoc* comparisons using the Games-Howell test indicated that percentage of open water was higher in the DWS, but there was no significant difference between CWMP and GLMMP wetlands, as was the case for percentage of wet meadow ($F_{2, 548.05} = 84.93$, $p < 0.01$). There was also a significant effect of region on percentage of emergent vegetation ($F_{2, 529.98} = 115.6$, $p < 0.01$), with emergent vegetation significantly lower in the DWS than in either of the other two regions. Percentage of shoreline/mudflat differed significantly among regions ($F_{2, 521.25} = 8.10$, $p < 0.01$), being higher in the DWS than in the GLMMP, though neither of these regions was significantly different from the mean percentage of shoreline/mudflat in the CWMP.

Likewise, wetlands in the three regions showed regionally specific patterns of landscape-scale characteristics. There was a significant effect of region on percentage crop cover at 400 m ($F_{2, 552.71} = 307.19$, $p < 0.01$), with crop cover significantly higher in the DWS than in the other regions and significantly lower in the GLMMP than in the CWMP or DWS. There was a significant effect of region on percentage forest cover within 400 m ($F_{2, 449.62} = 600.92$, $p < 0.01$), with forest cover significantly lower in the DWS than the other two regions and significantly higher in the CWMP than in the other two regions, as was the case for percentage of wetland cover at 400 m ($F_{2, 498.33} = 250.50$, $p < 0.01$). There was a significant effect of region on percentage of grassland cover at 400 m ($F_{2, 616.88} = 42.97$, $p < 0.01$), with grassland cover significantly higher in the DWS than in the other two regions and significantly lower in the CWMP than in the other two regions.

In addition, local habitat heterogeneity was significantly different from zero ($F_{2, 544.60} = 3.18$, $p = 0.04$), but I found no significant differences among the three regions. There was a significant effect of region on landscape heterogeneity ($F_{2, 567.1} = 82.62$, $p < 0.01$), with heterogeneity significantly lower in DWS than in the other two regions and significantly higher in the CWMP than in the other two regions.

Wetland area also differed significantly among regions ($F_{2, 477.67} = 620.71$, $p < 0.01$), with wetlands in the DWS significantly smaller than those in the other regions. Most wetlands in the CWMP and GLMMP were permanent wetlands (91% and 80%, respectively), whereas most wetlands in the DWS were semipermanent (45%). These differences were statistically significant, χ^2 (4, N = 2702) = 1482.60, $p < 0.01$. Furthermore, more wetland classes were represented in the DWS, with temporary and alkali wetlands being surveyed only in this region.

Both numbers of positive observations of species presence and species composition of observations differed among regions (Table 2). The highest number of observations occurred in the DWS, with 1341 observations. Of these, 40% were Sora, 36% were Pied-billed Grebe, 15% were Virginia Rail, and 9% were American Bittern. In contrast, of the 494 observations of focal species in the GLMMP, Virginia Rails were the most common (52%), followed by Pied-billed Grebes (24%), Soras (16%), and American Bitterns (8%). Finally, in the CWMP there were 89 positive identifications of focal species and of these 33% were Pied-billed Grebes, 26% were Soras, 24% were Virginia Rails, and 18% were American Bitterns.

Our models consistently explained variation in species density. The three models had a median explanatory power of 20% for American Bitterns, 26% for Virginia Rails, 28% for Soras, and 17% for Pied-billed Grebes. Only one model appeared to be overfit; for the AMBI_CWMP model, the adjusted pseudo-R^2 value dropped from 0.61 to 0.28 when I evaluated the model with the validation dataset. This large drop suggests that the model is overfit, but because even the reduced version explains 28% of the variation in AMBI density, the model is still useful. Otherwise, average absolute value of difference between training and validation adjusted pseudo-R^2 is only 7.4%.

Within each region, my models also consistently explained variation in species densities (Table 3). Across species, the models created from the DWS data explained a median of 27% of variation across the focal species within the Prairie Pothole Region. The CWMP models explained a median of 23% of variation across the focal species within coastal Great Lakes wetlands. The GLMMP models explained the least amount of variation, with a median explanatory power of 16% of variation across the focal species within inland Great Lakes wetlands. (I report median values because of outliers among my adjusted pseudo-R^2 values that would unduly influence means).

There was some consistency in habitat associations for individual species independent of region. For American Bittern, wetland area, hydroperiod, and percentage of wet meadow were included in all three models. For Virginia Rail, wetland area and percentages of open water and wet meadow were included in all three models. For Sora and Pied-billed Grebe, only wetland area was included in all three models.

I also found that certain variables were included in my selected models more consistently than others. Wetland area was the most consistently selected variable and was included in all 12 models. The categorical variable for alkali wetlands was included in all models where it was considered (the 4 DWS models). Percentage of open water was included in nine models, percentage of wet meadow in eight models, hydroperiod in seven models, local habitat heterogeneity and percentage of emergent vegetation in six models. Percentage of wetlands was included in five models, percentages of cropland and forest were each included in four models, percentage of grassland was included in three models. The quadratic local habitat heterogeneity term was included in two models, and landscape scale habitat heterogeneity was included in one model. The quadratic term for landscape scale habitat heterogeneity and the percentage of shoreline/mudflat habitat were not included in any of my selected models.

When I applied a model developed in one region to data collected in another region, I found that most models still had a substantial amount of explanatory power, with a median adjusted pseudo-R^2 value of 16%, and a maximum of 35% (Table 3). The one exception was the Pied-billed Grebe model developed in the Prairie Pothole Region. This model had an adjusted pseudo-R^2 value of zero when applied to the CWMP dataset. The GLMMP models had the highest median adjusted pseudo-R^2 values when applied to the other regions (19%), with median adjusted pseudo-R^2 values of 18% for CWMP data, and 22% for DWS data. The CWMP models explained a mean of 17% of variation in other regions, including medians of 22% for DWS data and 12% for GLMMP data. The DWS models explained a median of 14% of variation in other regions, with medians of 14% for both the CWMP data and the GLMMP data.

The best model for American Bittern was developed in the DWS and explained a median of 20% of variation across training and validation datasets in the three regions. The model included wetland area; hydroperiod; percentages of emergent vegetation, open water, and wet meadow; percentage of cropland, local heterogeneity and the quadratic term for local heterogeneity; and a categorical variable for whether the wetland was alkali. The best model for Virginia Rail was developed in the CWMP and explained a median of 25% of variation across training and validation datasets in the three regions. The model included wetland area; hydroperiod; percentages of open water and wet meadow; and percentages of grassland and woodland. The best model for Sora was developed in the GLMMP and explained a median of 26% of variation across training and validation datasets in the three regions. The model included wetland area and percentage of open water. The best model for Pied-billed Grebe was developed in the DWS and explained a median of 15% of variation across training and validation datasets in the three regions. The model included wetland area; hydroperiod; percentages of emergent water, open water and wet meadow; percentage of cropland; and local scale habitat heterogeneity.

DISCUSSION

Our results support the hypothesis that wetland birds have different habitat associations in different regions. The top-performing habitat models for each species differed in which variables were included across the different regions (Table 3). I also found that, while some of the same variables were included in the different regions for a particular species, the directionality of the relationships was not necessarily consistent (Table 4). For example, American Bittern density was positively associated with percentage of wetland cover and negatively associated with local habitat heterogeneity in the CWMP, but negatively associated with percentage of wetland in the GLMMP and positively associated with local habitat heterogeneity in the DWS. Such differences in regional habitat associations have also been demonstrated for Black-capped Vireos (*Vireo atricapilla*) in Texas (Grzybowski et al. 1994), riparian birds in California (Nur et al. 2008), farmland birds in Switzerland (Schaub et al. 2011), *Calidris* shorebirds in the DWS and Rainwater Basin (Gillespie 2015), Little Owls (*Athene noctua*) in Central Europe (Šalek et al. 2016), and Canada Warblers (*Cardellina canadensis*) in Alberta, Canada (Ball et al. 2016) and in Minnesota (Grinde and Niemi 2016), among others.

Indeed, species-specific habitat models created from data collected a given region consistently explained more variation in the density of that species in that region than did habitat models created elsewhere. Despite this difference, models developed in one region still retained explanatory power in almost every instance. While Chamberlain et al. (2016) found that models can successfully be applied across other regions, several other studies have found that models developed in one region are completely inappropriate elsewhere (Grzybowski et al. 1994; McAlpine et al. 2008; Schaub et al. 2011). Whittingham et al. (2003) found that regression equations developed in one region did not perform well when used as a direct predictor of the number of territories of skylarks in other regions, but they did identify strongly positive correlations between the predictions and the observed value. This suggested that models developed in other regions were good predictors of relative abundance, even if they could not be used to make absolute quantitative predictions. I similarly would suggest that it is preferable to use models developed within a given region to estimate densities of wetland obligate birds, but that in the lack of adequate data for developing such models, it would be feasible to use models developed elsewhere as a substitute.

The habitat associations of birds in the inland Great Lakes wetlands, though explained to some extent by the models, were consistently the most poorly explained by any model. While generally speaking, the GLMMP citizen science data show similar results to data collected by professional observers and more rigorous data collection protocols, such as that employed by the CWMP, this is less true specifically for the inland wetlands, such as those selected for this study (Tozer & Stewart 2019). Tozer and Stewart (2019) suggested that this disparity between observer performance in inland versus coastal wetlands may be due to smaller sample sizes for inland wetlands, and that increased sample sizes would negate this difference. Interestingly, though, models created from this dataset performed best when applied to the data from other regions. In fact, models created from this dataset were better when applied across regions than models developed in other regions applied across regions, but the difference was small.

I also expected that the habitat associations would be more similar within the Great Lakes basin regardless of coastal versus inland status than to the habitat associations of birds in the Prairie Pothole region because there are more similarities between the habitat characteristics of these wetlands—and the Prairie Pothole region is more isolated and geographically distant from the others. Habitat variables themselves were more similar between CWMP and GLMMP than either was with DWS. There were six examples of habitat variables that were not significantly different between CWMP and GLMMP wetlands whereas DWS habitat variables were only not significantly different from CWMP in two cases and not significantly different from GLMMP in one instance. Differences in the habitat associations between regions therefore might reflect differences in the habitat composition of a region (Nur et al. 2008).

As expected, some habitat characteristics were consistently associated with the occurrence of a particular wetland-dependent species regardless of region and wetland type. When applied to other regions, the models still have some explanatory power due to these within-species similarities across regions. Indeed, some models developed in one region had higher explanatory power when applied to another region than to their own.

Across all species, I found that wetland area was consistently included in the models. This suggests that wetland birds may be area-limited. Uzarski et al. (2017) similarly found that wetland-associated birds in coastal Great Lakes wetlands responded strongly to wetland size: birds avoided small wetlands, even if water quality was high and there was little human influence on the system. Indeed, such area sensitivity has been previously documented for all four species (Pied-billed Grebe & American Bittern: Brown & Dinsmore 1986; American Bittern, Virginia Rail, & Sora: Riffell et al. 2001; American Bittern & Sora: Craig 2008), although both Sora and Virginia Rail have also been classified as area-independent (Brown & Dinsmore 1986; Tozer et al. 2010; Kahler 2013) in other studies. My results suggest that while wetland was always selected for inclusion in the models, at least in these three regions, these species were largely insensitive to wetland area (Fig. 3-2). This insensitivity to area has also previously been demonstrated for occupancy probability of Pied-billed Grebe and Virginia Rail

(Harms & Dinsmore 2013). I saw exceptions to this trend in the Prairie Pothole Region for Pied-billed Grebe and Sora. These exceptions were most likely influenced by the low availability of larger wetlands in this region, and several small wetlands with high densities of these species in the training dataset.

All but one of my models included local-scale habitat characteristics. Previous studies have found that Virginia Rail and Sora (Hay 2006; Glisson et al. 2015), as well as Pied-billed Grebe (Naugle et al. 1999), respond only to within-wetland habitat characteristics. However, ten of my models indicated that landscape-scale habitat features were also informative for these species. Given that collecting local-scale data require much greater investments of time and labor, whereas remotely gathered data are relatively easily acquired and can be applied across wide geographic ranges (Williams et al. 2002), models of density and distribution based on remotely sensed data may be more feasible to construct and apply across regions. I therefore experimented with models involving only the landscape variables. The landscape-only models explained a mean of 6% less variation (StDev = 4, range 0-16%) than the models that contained both local and landscape scale covariates. Given this range, it may be reasonable to construct models for these species that are based solely on landscape-scale data, at least in these three regions. However, whenever possible it is preferable to use local-scale habitat characteristics to inform models of density, especially for species such as Sora, which responded only to local-scale habitat characteristics in two of my three models. Similarly, Pickens and King (2014) found that models of wetland bird abundances containing multiple scales of habitat information outperformed models with only a single scale. Future advances in remote sensing may make the acquisition of local-scale habitat characteristics more feasible, as well.

I also identified species-specific habitat variables that were included in all models for a given species, detailed below. While I found a number of similar habitat characteristics that had been identified in the literature as potentially important for my focal species, I attribute the high number of discrepancies between my results and those of other studies to the regionally specific nature of these relationships.

In my study, Pied-billed Grebes consistently responded only to wetland area across all three regions. The best model for this species was developed in the DWS, and also included a negative relationship with alkali wetlands; a negative relationship with hydroperiod; positive relationships with percentages of emergent vegetation, open water, and wet meadow; a negative relationship with percentage of cropland within 400 m; and a positive relationship with local-scale habitat heterogeneity. Relationships between this species and many of these habitat variables have been identified elsewhere in the literature for the regions I examined, as well as other regions. For instance, in the glaciated region of Ohio, Pied-billed Grebe occurrence differed between wetlands of different water permanence levels (hydroperiod), though occurrence was higher in semi-permanent wetlands than in seasonally flooded wetlands (Kahler 2013). Variables related to emergent vegetation and open water cover have been associated with probabilities of occurrence, extinction, and colonization in the Great Lakes (Tozer 2016) and to open water in at least some years in the Illinois and Upper Mississippi River Valleys (Darrah & Krementz 2010). My previous work showed a quadratic relationship between area-corrected grebe abundance and local scale habitat heterogeneity, as well as variation among wetland classes (Elliott et al. 2019).

Several habitat characteristics that predicted Pied-billed Grebe habitat use in other studies were not important predictors of Pied-billed Grebe occupancy in this study. Research in the Great Lakes basin has identified urban land cover and trees and shrubs as predictors of Pied-billed grebe occupancy, local colonization, and local extinction (Tozer 2016). These differences may be attributable to the difference in the response measure (occupancy versus density). Percentage of woody vegetation has also been found to be negatively associated with Pied-billed Grebe occurrence in Iowa (Harms & Dinsmore 2013) and the Illinois and Upper Mississippi River Valleys (Darrah & Krementz 2010). In southern Manitoba, this species was associated with areas that had a higher proportion of *Typha* spp. and tall shrubs. In New York, Pied-billed Grebes nested in moderately dense vegetation with a higher percentage of horizontal cover (Lor & Malecki 2006). These differences may be attributable to regional differences in habitat associations. Water depth was also important for this species in Iowa (Harms & Dinsmore 2013), although I was unable to measure this variable in my study.

I found that Virginia Rail consistently responded to wetland area and percentages of open water and wet meadow habitat across all three regions. The best model for this species was developed in the CWMP, and also included a positive relationship with hydroperiod, a negative relationship with percentage of grassland, and a positive relationship with percentage of wetland within 400 m. As in my study, wet meadow and open water were associated with Virginia Rail density in the DWS of Iowa (Fairbairn & Dinsmore 2001). In Great Lakes coastal wet meadows, Virginia Rail were associated with dense, tall stands of emergent sedges and grasses that were representative of the most productive wet meadows (Riffell et al. 2001). However, other studies found contradictory trends such as no association with wetland permanence in Ohio (Kahler 2013) or with any landscape-scale metrics in southern Manitoba (Hay 2006). Tozer (2016) found a negative relationship between colonization probability and percentage of surrounding wetland in the Great Lakes basin. Several studies also found that percentages of certain species of emergent vegetation (some cases invasive species) were associated with occupancy (Willard 2011; Harms & Dinsmore 2013; Tozer 2016). Other studies also found occupancy increased with more surrounding woodland cover in Ohio (Willard 2011); and in the Great Lakes basin colonization probability decreased with increasing percentage of urban land use while extinction probability increased with increasing percentages of agriculture and wetland (Tozer 2016). In New York, nests associated with smaller wetlands with shallow water and lower vegetation height but moderately dense vegetation and a high percentage of horizontal cover (Lor & Malecki 2006).

I found that Sora consistently responded only to wetland area across all three regions. The best model for this species was developed in the GLMMP and also included a negative relationship with percentage of open water within the wetland. In other studies, as well, wetland area has been positively associated with this species (Kahler 2013; Tozer 2016). At a local habitat scale, this species has also been associated with emergent vegetation (Riffell et al. 2001; Willard 2011), changes in invasive purple loosestrife (Tozer 2016), and deeper water (Riffell et al. 2001). While Hay (2006) found no landscape-scale associations for this species in southern Manitoba, Willard (2011) found higher occupancy in sites with more surrounding wetland cover in Ohio. Wetland permanence was an important predictor for this species in Ohio (Kahler 2013). In New York, Sora nests were associated with shorter vegetation, lower water levels, and a higher percentage of horizontal cover (Lor & Malecki 2006).

Our models showed that American Bitterns consistently responded to wetland area, hydroperiod, and percentage of wet meadow habitat across all three regions. The best model for this species was developed in the DWS and also included a negative effect of alkali wetlands, a very slight relationship with hydroperiod, positive relationships with percentages of open water and emergent vegetation, a negative relationship with percentage of cropland within 400 m, and a quadratic relationship with local-scale habitat heterogeneity. In Ohio, wetland permanence was also an important predictor, as was wetland area (Kahler 2013). In the Great Lakes basin, probability of local extinction decreased with increasing log area (Tozer 2016). At the landscape scale, American Bittern were positively associated with the amount of wetland in the surrounding landscape in southern Manitoba (Hay 2006) and the Great Lakes basin (Tozer 2016). At the local scale, American Bitterns were associated with areas with higher shrubs in southern Manitoba (Hay 2006) and Minnesota (Hanowski and Niemi 1988). Breeding territories of American Bitterns in Minnesota were also associated with higher densities of cattails and lower densities of grasses and sedges (Hanowski and Niemi 1988). Riffell et al. (2001) found that American Bitterns in Great Lakes coastal wet meadows were associated with dense and tall stands of emergent vegetation typical of the most productive wet meadows and wet meadows with relatively taller, denser, more robust graminoid vegetation. In contrast, nest sites of American Bitterns in northwestern Minnesota were positively associated with dead vegetation cover and density and negatively associated with vegetation height, whereas foraging sites were negatively associated with distance to small water openings and vegetation height (Lor 2007). In New York, American Bittern nests were associated with higher percentage of emergent vegetation, higher percentage of horizontal cover, and greater water depth (Lor & Malecki 2006).

Our results suggest that densities of obligate wetland breeding birds are best modeled regionally because habitat associations of these species vary by region. Conservation planning, especially for species that are at risk in particular regions, can benefit from such regionally specific modeling approaches. These methods can help to identify habitats that support the highest densities of species of interest. This is especially valuable in situations where regional population trends are not reflective of continental population trends. Whenever possible, these models should be developed from data collected within the region of interest and should include local habitat variables as well as landscape-scale habitat characteristics. In the absence of region-specific models, I demonstrate that models from other areas still provide useful information on the density of wetland-obligate birds.

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Land use and land cover data were obtained for the Great Lakes basin from The North American Land Change Monitoring System, which is a collaborative effort by Natural Resources Canada, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional Forestal, Instituto Nacional de Estadística y Geografía, and the U.S. Geological Survey and is facilitated by the Commission for Environmental Cooperation.

Although the collection of these data has been partly funded by the U.S. Environmental Protection Agency and the U.S. Geological Survey, this research has not undergone governmental peer and policy review. Therefore, this research does not necessarily reflect the views of these agencies and any use of trade, firm,

or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

TABLES

Table 1. Means, standard deviations (in parentheses) and ranges (below) of wetland characteristics, and sample sizes of each wetland class for each of three datasets. Mean values with different letters are significantly different from the means of that variables for other datasets at the $p < 0.05$ level based on Welch's ANOVA and Games-Howell post hoc tests, while means with the same letters are not significantly different from one another.

Variable	CWMP	GLMMP	DWS
Sample size (no. of wetland-year combinations)	194	1250	1262
Wetland Area (ha)	25.7 (21.9)^{A}	29.1 (26.1)^{A}	3.2 (9.3)^{B}
	0.4-65.5	0.4-65.5	0.4 - 65.5
Local Characteristics			
Open Water (%)	27 (26)^{A}	30 (27)^{A}	37 (31)^{B}
	0-90	0-100	0-100
Shoreline/ Mudflat (%)	3 (11)^{AB}	2 (8)^{A}	4 (11)^{B}
	0-90	0-100	0-100
Emergent Vegetation (%)	37 (32)^{A}	41 (31)^{A}	23 (28)^{B}
	0-100	0-100	0-100
Wet Meadow (%)	22 (27)^{A}	20 (25)^{A}	35 (34)^{B}
	0-100	0-100	0-100
Landscape Characteristics			
Cropland (%)	5 (8)^{A}	2 (7)^{B}	20 (25)^{C}
	0-44	0-87	0 - 98
Forest (%)	36 (27)^{A}	25 (27)^{B}	2 (4)^{C}
	0-94	0-100	0-16
Grassland (%)	10 (17)^{A}	16 (24)^{B}	23 (28)^{C}
	0-90	0-100	0-95
Wetland (%)	50 (21)^{A}	26 (23)^{B}	18 (12)^{C}
	6-89	0-100	0-75
Heterogeneity Indices			
Local Heterogeneity	1.7 (0.6)^{A}	1.8 (0.5)^{A}	1.8 (0.6)^{A}

	1.0-3.7	1.0-3.6	1.0-3.8
Landscape Heterogeneity	1.9 (0.4)^{A}	1.7 (0.5)^{B}	1.5 (0.5)^{C}
	1.0-2.9	1.0-3.0	1.0 -2.9
Wetland Class			
Temporary	0	0	177
Seasonal	4	46	422
Semipermanent	13	197	570
Permanent	176	1004	49
Alkali	0	0	44
NA	1	3	0

Table 2. Numbers of observations of the focal species in each of three datasets used in these analyses. All datasets were divided into training and validation datasets.

Species	CWMP	GLMMP	DWS
PBGR			
training	16	77	354
validation	13	40	124
total	**29**	**117**	**478**
VIRA			
training	14	171	122
validation	7	87	83
total	**21**	**258**	**205**
SORA			
training	13	55	365
validation	10	25	173
total	**23**	**80**	**538**
AMBI			
training	10	26	89
validation	6	13	31
total	**16**	**39**	**120**

Table 3. The amount of variation in density explained by the best performing models. Explanatory variables include alkali wetland class (Alkali); wetland area (Area); hydroperiod (Hydroperiod); percentages of emergent vegetation (EV), open water (OW), shoreline/mudflat (SM), wet meadow (WM); percentages of cropland (Crop%), forest (Forest%), grassland (Grassland%), wetland (Wetland %) within a 400-m buffer of the wetland; and Inverse Simpson diversity indices of proximate cover (Local Het), landscape-scale habitat heterogeneity (Landscape Het), and the quadratic form of each (Local Het2, Landscape Het2). Sites were randomly assigned to model or validation data sets. After best-performing models were generated using training data sets, each best-performing habitat model was evaluated using the validation dataset. Differences in the amount of variation in species richness explained did not differ substantially when models were applied to the validation dataset for almost all models, indicating that models were not overfit.

Species	Dataset	Best Model	Sample	Null Deviance (df)	Residual Deviance (df)	Adjusted pseudo-R^2	CWMP Adjusted pseudo-R^2	GLMMP Adjusted pseudo-R^2	DWS Adjusted pseudo-R2
PBGR	CWMP	Area + EV + Forest% + Wetland% + Local Het + Landscape Het	Training	76.8 (127)	55.0 (121)	16	16	6	17
			Validation	66.4 (65)	45.3 (59)	15	15	6	17
	GLMMP	Area + Forest% + OW + WM	Training	449.3 (838)	388.7 (834)	12	9	12	14
			Validation	288.3 (433)	227.8 (429)	18	14	18	16
	DWS	Alkali + Area + Hydroperiod + EV + OW + WM + Crop% + Local Het	Training	853.4 (832)	665.8 (824)	20	0	12	20
			Validation	415.1 (428)	318.6 (420)	20	15	23	20
VIRA	CWMP	Area + Hydroperiod + OW + WM + Grass% + Wetland%	Training	62.6 (127)	51.8 (121)	9	9	14	33
			Validation	31.7 (65)	21.3 (59)	23	23	26	31
	GLMMP	Area + EV + OW + WM + Wetland%	Training	923.4 (838)	737.2 (833)	17	5	17	35
			Validation	519.6 (433)	362.1 (428)	28	12	28	31
	DWS	Alkali + Area + Hydroperiod + EV + OW + WM + Crop% + Local Het	Training	796.2 (832)	482.2 (824)	38	3	14	38
			Validation	380.9 (428)	211.2 (420)	42	14	28	42
SORA	CWMP	Area + Crop% + Forest% + Wetland%	Training	70.9 (127)	39.3 (123)	37	37	13	20

			Validation	54.7 (65)	35.5 (61)	22	22	26	23
	GLMMP	Area + OW	Training	419.3 (838)	355.1 (836)	14	26	14	28
			Validation	147.4 (433)	105.5 (431)	27	22	27	31
	DWS	Alkali + Area + Hydroperiod + EV + OW +	Training	1516.2 (832)	1053.0 (826)	29	22	14	29
		Local Het	Validation	827.8 (428)	533.5 (422)	34	9	26	34
AMBI	CWMP	Area + Hydroperiod + OW + WM + Grass% +	Training	52.8 (127)	18.3 (118)	61	61	7	12
		Forest% + Wetland% + Local Het + Local Het^2	Validation	32.0 (65)	17.6 (56)	28	28	12	24
	GLMMP	Area + Hydroperiod + WM + Grass%	Training	178.0 (838)	164.9 (834)	5	22	5	8
			Validation	103.8 (433)	93.7 (429)	5	23	5	10
	DWS	Alkali + Area + Hydroperiod + EV + OW +	Training	324.8 (832)	266.8 (823)	15	35	9	15
		WM + Crop% + Local Het + Local Het^2	Validation	225.4 (428)	157.1 (419)	25	35	3	25

Table 4. Coefficient values and SE below in italics for top-performing Poisson models of species density. Explanatory variables include alkali wetland class (Alk); wetland area (Area); hydroperiod (Hydroperiod); percentages of emergent vegetation (EV), open water (OW), shoreline/mudflat (SM), wet meadow (WM); percentages of cropland (Crop), forest (Forest), grassland (Grass), wetland (Wetl) within a 400-m buffer of the wetland; and Inverse Simpson diversity indices of proximate cover (Local Het), landscape-scale habitat heterogeneity (Land Het), and the quadratic form of each (Local Het^2, Land Het^2). Coefficients for area, hydroperiod, and percentage of cropland are reported to the thousandths place due to the small coefficient values. The remaining coefficients are reported to the tenths place.

Species	Dataset	Int	Alk	Area	Hydroperiod	EV	OW	SM	WM	Crop	Forest	Grass	Wetl	Local Het	Local Het^2	Land Het	Land Het^2
		-4.2		-0.045		-0.6					0.6		0.6	-0.04		0.6	
	CWMP	*0.5*		*0.015*		*0.3*					*0.3*		*0.4*	*0.27*		*0.3*	
		-4.6		-0.033			0.5		-0.3		0.2						
	GLMMP	*0.2*		*0.006*			*0.1*		*0.2*		*0.1*						
		-1.8	-0.3	-0.026	-0.026	1.5	1.8		1.6	-0.042				0.41			
PBGR	DWS	*0.1*	*0.2*	*0.003*	*0.059*	*0.3*	*0.4*		*0.4*	*0.065*				*0.07*			
		-6.1		-0.030	4.958		-0.1		-0.2			-0.4	0.5				
	CWMP	*190.4*		*0.014*	*604.064*		*0.3*		*0.4*			*0.4*	*0.3*				
		-3.5		-0.042		1.5	0.8		0.9				-0.4				
	GLMMP	*0.1*		*0.003*		*0.3*	*0.3*		*0.3*				*0.1*				
		-2.4	-0.3	-0.078	0.193	3.2	2.6		3.2	-0.084				0.39			
VIRA	DWS	*0.2*	*0.6*	*0.011*	*0.103*	*0.7*	*0.9*		*0.9*	*0.096*				*0.10*			
		-3.8		-0.074						0.644	0.8		0.9				
	CWMP	*0.6*		*0.022*						*0.254*	*0.4*		*0.4*				
		-4.2		-0.044			-0.3										
SORA	GLMMP	*0.2*		*0.006*			*0.2*										

		-1.2	-0.7	-0.042	-0.013	0.2	-0.5						0.09	
	DWS	*0.1*	*0.3*	*0.004*	*0.062*	*0.1*	*0.1*						*0.06*	
		-6.7		-0.054	-0.697		-0.5	0.2		2.1	-0.6	1.3	-0.80	0.3
	CWMP	*1.5*		*0.026*	*0.280*		*0.5*	*0.4*		*0.7*	*1.0*	*0.6*	*0.57*	*0.4*
		-5.5		-0.032	0.130			0.1			-0.1			
	GLMMP	*0.4*		*0.009*	*0.232*			*0.2*			*0.2*			
		-3.0	-0.2	-0.026	0.005	0.7	0.3	0.8	-0.444				0.34	-0.2
AMBI	DWS	*0.2*	*0.5*	*0.007*	*0.139*	*0.6*	*0.8*	*0.8*	*0.178*				*0.19*	*0.1*

FIGURES

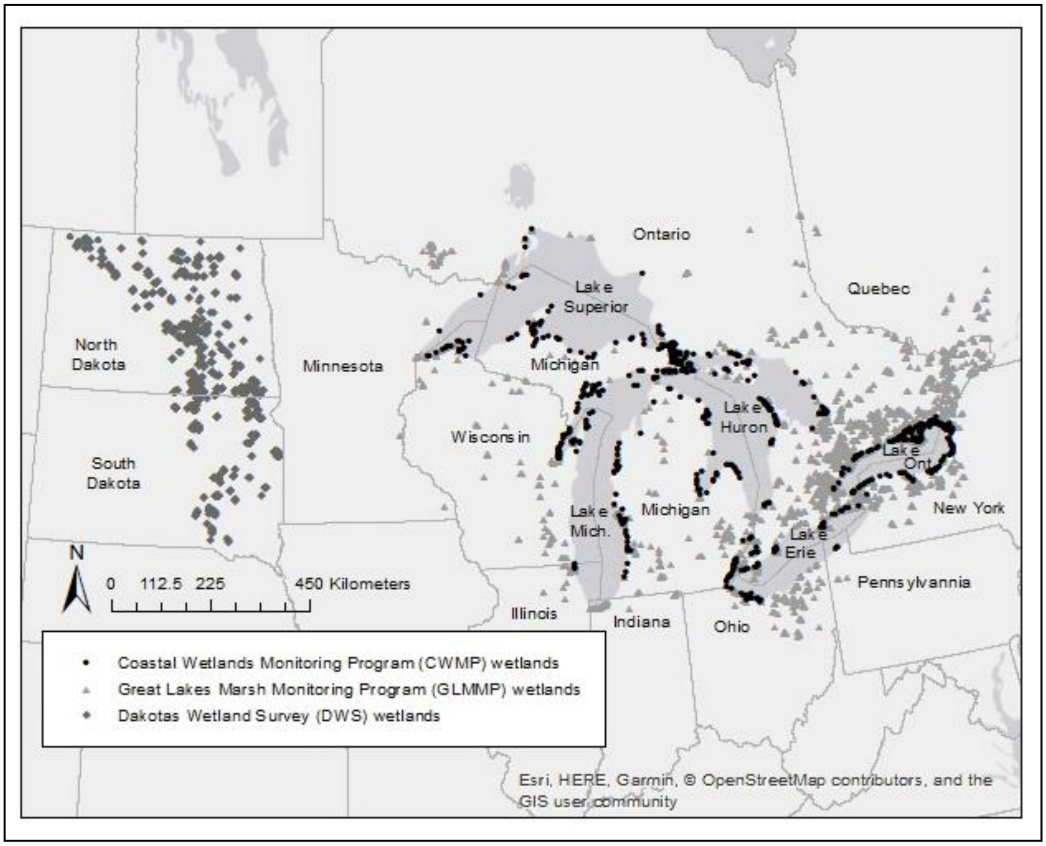

Figure 3-1. Distribution of wetlands surveyed as part of three monitoring programs: the Coastal Wetlands Monitoring Program (CWMP) and the Great Lakes Marsh Monitoring Program (GLMMP) in the Great Lakes basin, and the Dakotas Wetland Survey (DWS) dataset in the Prairie Pothole Region of North and South Dakota.

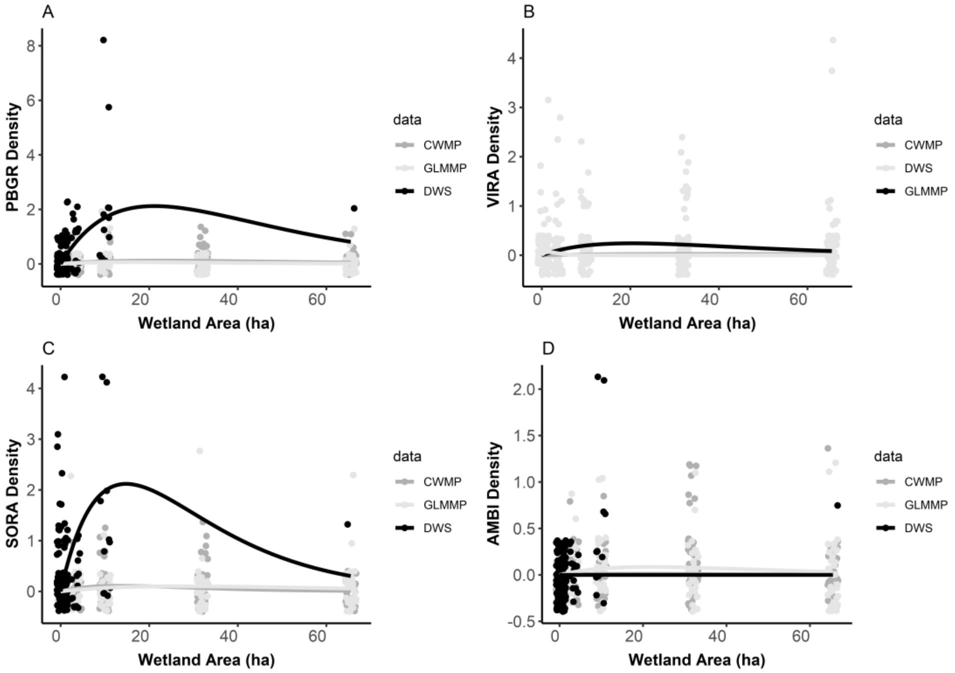

Figure 3-2. Observed and predicted densities of A) Pied-billed Grebe (PBGR), B) Virginia Rail (VIRA), C) Sora (SORA), and D) American Bittern (AMBI) across wetland size bins for wetlands surveyed as part of the Coastal Wetland Monitoring Program (CWMP), Great Lakes Marsh Monitoring Program (GLMMP) and Dakotas Wetland Survey (DWS). Points represent observed densities (jittered) from the training datasets (a randomly selected sample of two thirds of wetlands from each monitoring program). Lines represent predicted density values based on species- and region-specific Poisson models reported in Table 3, with all covariate values except area held at the mean or reference value.

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