Habitat Associations of Migratory Waterbirds Using Restored Shallow Lakes in Iowa

Authors: Vanausdall, Rachel A., and Dinsmore, Stephen J.

Source: Waterbirds, 42(2) : 135-153

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.042.0201

WATERBIRDS

JOURNAL OF THE WATERBIRD SOCIETY

VOL. 42, NO. 2 2019 PAGES 135-249

Habitat Associations of Migratory Waterbirds Using Restored Shallow Lakes in Iowa

RACHEL A. VANAUSDALL[1,*] AND STEPHEN J. DINSMORE[1]

[1]Department of Natural Resource Ecology and Management, Iowa State University, 2310 Pammel Dr., Ames, Iowa, 50011, USA

[*]Corresponding author; E-mail: rvanausd@iastate.edu

Abstract.—Wetlands in the Prairie Pothole Region (PPR) have experienced declines in areal cover, and many remaining wetlands are degraded. Recently, restoration of wetlands has been a key management strategy for waterbirds. In Iowa, the Department of Natural Resources and Ducks Unlimited, Inc. have restored 38 shallow lakes, which are large, mostly permanent wetlands. To assess the impact of habitat variables on migrant waterbird use (waterfowl, shorebirds, and secretive marsh birds), surveys were conducted at 19 shallow lakes restored 1 to 12 years prior to this study and at 11 soon-to-be-restored shallow lakes in Iowa during the spring of 2016-2018. A total of 713,338 waterbirds were identified in 82 species, and more waterbirds and species were detected at restored shallow lakes (582,148 waterbirds and 78 species) than at non-restored shallow lakes (130,895 waterbirds and 70 species). Greatest numbers of diving ducks and waterbird species occurred around 40-50% emergent cover. Water level negatively influenced dabbling ducks and shorebirds and positively influenced diving ducks and total waterbird abundance. Years-since-restoration positively influenced goose/swan abundance and secretive marsh bird abundance, and total wetland area had a positive effect on all groups. These findings emphasize how management strategies for restored shallow lakes should mimic the natural wet-dry cycle of prairie wetlands to provide benefits for all waterbirds. *Received 5 February 2019, accepted 14 April 2019.*

Key words.— migration, Prairie Pothole Region, restoration, shallow lake, waterbird, wetland.

Waterbirds 42(2): 135-153, 2019

Wetlands in the Prairie Pothole Region (PPR) of North America are important resources for birds throughout the year. They are critical to the foraging, nesting, and shelter requirements for migrant waterbirds, including waterfowl, wading birds, shorebirds, rails, and other wetland-associated species (Tiner 1984; Johnson *et al.* 1994; Anteau and Afton 2004). The PPR was once comprised of a vast network of poorly drained potholes and larger shallow lakes, interconnected and interspersed with grasslands that supported a variety of migrating birds (Bishop 1981; Tiner 1984; Van Meter and Basu 2015). Today, this area still provides habitat for more than 100 species of birds. During migration, wetlands in the PPR provide foraging habitat and allow migrants to gain energy and build nutrient reserves in between flights of up to several thousand kilometers (Skagen and Knopf 1993; Naugle *et al.* 2001; Murphy and Dinsmore 2014). For some species, the energy gained from seeds, plants, and macroinvertebates may have an important influence on their reproductive success (Krapu *et al.* 1981; Ankney *et al.* 1991; Jenni and Jenni-Eiermann 1998; Anteau and Afton 2004). Thus, adequate habitat available for migrating birds in this region is a key management concern, and may be a limiting factor for several species (Stafford *et al.* 2014).

Abundance of wetland and grassland areas across the PPR has declined dramatically since European settlement, and many of the wetlands that remain are highly degraded (Anteau and Afton 2008; Dahl 2014). Draining wetlands and converting grasslands for agriculture were widespread in the 19th and 20th Centuries, resulting in a nearly 50% reduction in wetland area throughout the PPR in the USA (Dahl 2014). Furthermore, many of the wetlands that remain have been dramatically altered due to watershed changes, increased benthivorous and planktivorous fish abundance (Hanson *et al.* 2005), increased sedimentation (Martin and Harman 1986; Euliss and Mushet 1999; Gleason *et al.* 2003), and excess nutrient loading (Neely and Baker 1989) and chemical drift (Main *et al.* 2014). Such factors can lead to wetlands lacking hydrological fluctuations, which may further lead to persistently turbid water and a loss of vegetation (Scheffer *et al.* 1993; Hanson and Riggs 1995; Zimmer *et al.* 2002). Wildlife species, including birds, rely on emergent and submersed aquatic plants for nesting and foraging, so the severe decline in quality wetland habitat has likely led to a decline in many species (Igl and Johnson 1997; Anteau and Afton 2008; Anteau *et al.* 2011).

To try to combat these issues, several management agencies are restoring wetlands and protecting existing wetlands (e.g., Brinson and Eckles 2011), and one restoration project is targeting Iowa shallow lakes, which generally describes a semi-permanent or permanent wetland with a mean water depth < 1.5 m (Cowardin *et al.* 1979; Geisthardt *et al.* 2013). Through a partnership between the Iowa Department of Natural Resources and Ducks Unlimited, Inc., the Shallow Lakes Restoration Project (SLRP) aims to restore degraded shallow lakes throughout the Des Moines Lobe region, which is the southernmost portion of the PPR and located in Iowa (Miller *et al.* 2009). Approximately 90% of Iowa's historical wetland area has been lost due to agriculture and other anthropogenic land uses (Dahl 1990; Miller *et al.* 2009; Van Meter and Basu 2015). The overall goal of the SLRP is to restore the hydrology of shallow lakes to improve water quality and provide habitat for wildlife. This involves mimicking the wet-dry cycle that characterizes wetlands in the PPR by managing water levels. As part of the natural process, during periods of drought and low water levels wetland plant seeds can germinate (Harris and Marshall 1963), and more nutrients become available as plant litter decomposes (Bärlocher *et al.* 1978). As water depth increases, emergent and submersed aquatic vegetation replace mudflat annuals, and if the basin is inundated long enough, vegetation may eventually die off (Harris and Marshall 1963; van der Valk and Davis 1976; van der Valk and Davis 1978). For the SLRP, managers install infrastructure, such as water control and fish exclusion structures, to control water levels, improve water quality, and mimic the wet-dry cycle. Ideally, complete drawdowns occur every 5 to 10 years, but the timing varies among individual shallow lakes and based on logistical factors. About 38 sites have been restored using this method since the implementation of the SLRP in 2006, and these shallow lakes have shown improvements in water quality and vegetation structure (Geisthardt *et al.* 2013).

When implementing these restoration techniques it is important to understand the habitat variables that may influence wildlife or limit populations and how those variables may change over the course of the restoration. The important factors that influence habitat selection by migrant waterbirds include foraging habitat availability, roost availability and safety, and disturbance (Myers *et al.* 1987; Sprague *et al.* 2008). Additionally, these factors can vary by species, within a species' annual life cycle, and based on changing environmental conditions (Beerens *et al.* 2011). Different phases of wetland vegetation and inundation can provide optimal habitat for a variety of avian species. As such, the migrating birds using these wetlands change as resources in the wetlands fluctuate. For example, the amount and density of emergent vegetation can be an important predictor of use by several species (Weller and Spatcher 1965; Fairbairn and Dinsmore 2001). During the initial drawdown period and for a couple of years following, exposure of the basin bottom and lower water levels will not be optimal habitat for species such as rails or diving ducks. On the other hand, shorebirds may forage on the mudflats during spring and fall migration, and dabbling ducks will utilize areas with shallow water and emergent vegetation as the basin gradually refills (Taft *et al.* 2002; Skagen *et al.* 2008). Other important variables that affect waterbird use include water depth (Colwell and Taft 2000; Taft *et al.* 2002), water level fluctuations (Dimalexis and Pyrovetsi 1997;

Ntiamoa-Baidu *et al.* 1998; Taft *et al.* 2002), disturbances (Webb *et al.* 2010), and the surrounding landscape (Naugle *et al.* 1999; Froneman *et al.* 2001; Pearse *et al.* 2012). Thus, monitoring restored wetlands over time or wetlands in different stages of vegetation development will help yield a more accurate picture of bird use.

The SLRP has not formally monitored wetland bird communities on these restored shallow lakes in Iowa. Geisthardt *et al.* (2013) recorded birds at several restored and degraded shallow lakes, but these were not systematic surveys. Furthermore, there has not been an assessment on the habitat variables that influence waterbird use at these shallow lakes. Our objectives were to monitor waterbird use of shallow lakes restored and soon-to-be restored by the SLRP and determine habitat characteristics that influence use by migrating waterbirds. We conducted weekly surveys of both non-restored and restored shallow lakes for waterbirds. We hypothesized that restoration would positively improve waterbird use and that this would be reflected in a positive relationship between abundance or species richness and percent emergent vegetation cover. Additionally, we expected water level management to provide habitat for a variety of waterbirds at both low and high water levels. Results from our study will help inform future decisions for managing restored shallow lakes for waterbirds and should be particularly informative for regular monitoring of migrant waterbirds and managing drawdowns for a variety of species.

Methods

Study Area

The PPR covers about 700,000 km^2 in the United States and Canada and is characterized by palustrine wetlands, often known as potholes, and lacustrine wetlands (Bishop 1981; Kantrud *et al.* 1989; IAN 2001; Dahl 2014). Emergent wetlands still cover about 20,000 km^2 in the United States, and in the Des Moines Lobe region about 800 km^2 is emergent wetland area (Dahl 2014). This area represents the southernmost extent of the PPR and the Wisconsin glacial advance, which retreated from Iowa about 14,000 years ago (IAN 2001; Miller *et al.* 2009).

In this study, the term “shallow lakes” refers to both palustrine and lacustrine wetlands (Cowardin *et al.* 1979) that are relatively large (>20 ha) and on average < 1 m deep. The term “restored” refers to palustrine wetlands that were severely degraded and subsequently restored by manipulating the hydrology to improve water quality and vegetation. These shallow lakes were passively restored (i.e., no seed additions), and they were drained using an existing outlet structure to begin the restoration process. Infrastructure, such as water control structures, water channels, pipelines, and fish exclusion structures, were installed in nearly all shallow lakes to manage water levels and exclude rough fish. Once the restoration process began, sites were refilled gradually over (ideally) a 2-year period to allow vegetation to reestablish. Likewise, the term “non-restored” refers to lacustrine wetlands that were not manipulated. Most of these shallow lakes were void of emergent vegetation and contained turbid water; some may be restored within the next few years. We considered the date of restoration to be the start of the drawdown, even if it was before completion of the water control structure.

Site Selection

To examine how shallow lakes in different restoration states influence migrant waterbird use, we randomly chose 19 restored sites based on age and their relatively large size (>20 ha) spanning the period from less than 1 to 12 years post restoration. We also chose 11 non-restored shallow lakes to examine pre-restoration bird use of shallow lakes. Wetlands were in 12 Iowa counties (Fig. 1; Appendix 1), and all wetlands were surveyed in the spring of 2016, 2017, and 2018.

Bird Surveys

In Iowa, spring migration of waterbirds generally begins around early to mid-March and continues through May (Kent and Dinsmore 1996), and we initiated surveys in conjunction with spring thaw. We focused on waterbirds including waterfowl (Anseriformes), loons (Gaviiformes), grebes (Podicipediformes), cormorants (Suliformes), pelicans (Pelicanformes), cranes and rails (Gruiformes), and shorebirds (Charadriiformes: Recurvirostridae, Charadriidae, Scolopacidae).

Surveys were organized based on the “standardized search” approach described by Watson (2003) and utilized by Hopps (2012), where unit effort is measured in terms of the survey, rather than a fixed number of samples (e.g., point counts). Migrating birds can be more difficult to survey than breeding birds and often aggregate in large numbers that may be difficult to accurately count. Birds are also generally not as vocal during the migration season when compared to the breeding season (Wilson *et al.* 2000). The surveyor moved around the entire site in order to count all individuals and species present (Watson 2003; Aagard *et al.* 2015; Loges *et al.* 2015). Specifically, we utilized vantage points around the perimeter of each shallow lake to count waterbirds. These points were fixed throughout the season and were chosen to provide maximum visibility of each shallow lake. The maximum amount of time spent at each shallow lake depended on the size of the shallow lake basin. For sites ≤ 50 ha we surveyed

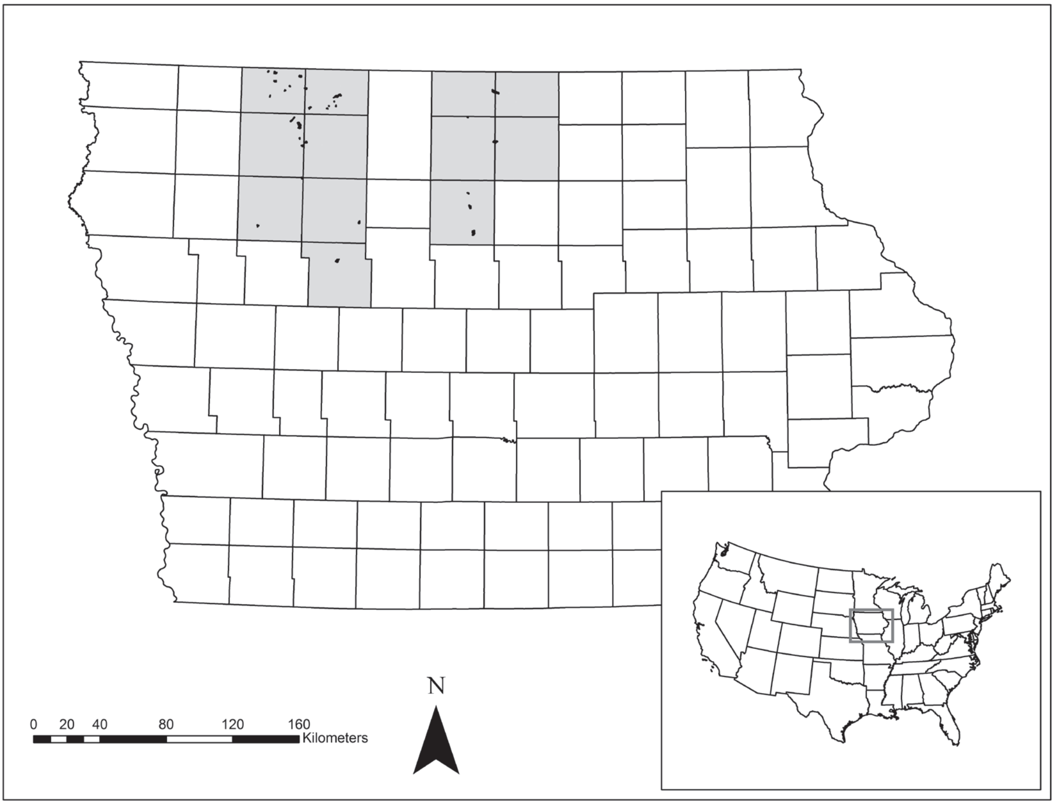

Figure 1. Location of shallow lakes in the Iowa Prairie Pothole Region (gray outline) for waterbird surveys conducted in the spring, 2016-2018. Each black dot represents a site, and the 12 shaded counties are those that include the surveyed wetlands.

for up to one hour and for sites > 50 ha we surveyed for up to two hours (Hopps 2012). This time included the time spent counting birds and not the time it took to drive from one point to another. Individuals were identified to species by sight and/or sound. Several secretive marsh birds (i.e., rails, bitterns, grebes) were primarily detected aurally. Although playback recordings are appropriate for estimating secretive marsh birds (Gibbs and Melvin 1993; Lor and Malecki 2002), we did not use this method due to logistical constraints and the fact that we did not do in-wetlands surveys. We counted waterbirds such as Wood Ducks (*Aix sponsa*), Great Blue Herons (*Ardea herodias*), and Double-crested Cormorants (*Phalacrocorax auritus*) that were perched in trees immediately adjacent to the shallow lake. We attempted to get complete counts for flocks of < 100 birds, but for larger flocks a "blocking" technique was used (Webb *et al.* 2010; Loges *et al.* 2015). We also included birds that left or entered the site during the duration of the survey. Surveys were conducted weekly, and the average time between surveys was 7.14 days. Surveys were conducted during daylight hours (sunrise to sunset), so three to four sites were generally surveyed in a single day. We maintained a consistent daily schedule for which sites were surveyed each day of the week, but we varied the time of day each site was surveyed each week to account for any intraday variation (O'Neal *et al.* 2008). Surveys were conducted on days with no precipitation and when winds were consistently < 20 km/hr (Loges *et al.* 2015).

We acknowledge that emergent vegetation negatively influenced our ability to see the entire wetland and, as a result, record all birds at some sites. As such, our estimates of abundance may be biased low, particularly at restored sites. However, we visually estimated the percent visibility of each site during every survey and all sites had at least 80% visibility. Furthermore, while most non-restored sites had 100% visibility, and we were confident we recorded all birds at those sites, we still detected a greater number of birds and species at restored sites than at non-restored sites. Thus, diversity and abundances recorded in this study are conservative estimates and improvements in visibility would likely increase the magnitude of these differences.

Habitat Variables

Several habitat variables at the site scale were measured and hypothesized to influence waterbird use, and we measured six variables at this scale. After each vantage point had been visited and the survey completed, we obtained a single estimate of the percent cover of the entire shallow lake that was emergent vegetation, open water, bare ground, or "other" vegetation. These were visually estimated to the nearest 5% and summed to 100%, and all observers received training on this method prior to the start of the seasons to ensure consistency. Both live and senesced vegetation were recorded, and emergent vegetation included vegetation between 2.5 cm and 6 m in height (Loges *et al.* 2015). Percent other included shrub-scrub and forested habitat (Cowardin *et al.* 1979), and these were included in a single category because they were uncommon.

Due to logistical constraints, we were not able to estimate the actual basin elevation of each shallow lake. Instead, we measured the weekly change in water level for each shallow lake. Water depth was monitored using water level gauges installed in the shallow lakes. For sites that did not have a gauge, we used other installed structures, such as concrete weirs and culverts, or installed metal posts to monitor weekly change. We defined water level as the weekly deviance (in cm) from the initial water level measurement.

We measured wetland area (ha) using ArcMap 10.3 (Environmental Systems Research Institute 2014). The border of each shallow lake's area was defined using both management area maps from the Iowa Department of Natural Resources and shapefiles from the National Wetlands Inventory (USFWS 2009). We delineated a fixed area that contained semi-permanent to permanent wetland types within the management property, which resulted in an area that represented the shallow lake basin. We acknowledge that this is not the total area inundated, which might be considered true wetland size. However, due to their large size and the intense practices used to manage the water levels, we were confident that the shallow lake basin was very similar to the total area inundated in most cases. This was not true during the drainage process, but drained shallow lakes still have a basin area that is relevant to waterbird use because instead of ponded water they have mudflats used by shorebirds (Murphy and Dinsmore 2013) and avoided by other groups such as diving ducks.

Statistical Approach

We assessed the relationship of six habitat variables, years-since-restoration, and survey week with total waterbird abundance, species richness, and waterbird abundance grouped by foraging strategy and migration chronology (Kent and Dinsmore 1996; Webb *et al.* 2010). Because we did not conduct in-wetland surveys for waterbirds, and there was some concern about seeing all birds from the shallow lake perimeter, we chose to model abundance rather than density. The waterbird groups included geese/swans, dabbling ducks, diving ducks, and shorebirds. Additionally, we were interested in secretive marsh birds, a group identified as wetland quality indicators (Conway *et al.* 2009, 2011). This group included the following species: Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), and Common Gallinule (*Gallinula galeata*). American Coot (*Fulica americana*) are also considered to be secretive marsh birds and use wetlands and bodies of water in a wide range of conditions (Brisbin and Mowbray 2002). We excluded coots from the secretive marsh bird group for analysis because of differences in behavior (e.g., flocking), their frequent use of open water, and due to their lower conservation priority. We were also most interested in the use of these wetlands by species more sensitive to wetland quality changes. Based on a literature review, we made predictions concerning the effects of habitat and survey week on these groups, and these directional hypotheses are shown in Table 1.

We used a linear mixed modeling approach to examine the relationship between the explanatory variables and either goose/swan abundance, dabbling duck abundance, diving duck abundance, secretive marsh bird abundance, shorebird abundance, waterbird abundance, or species richness. We used a square root transformation for groups that did not meet assumptions of normality (Zar 2010), which we assessed by visually inspecting plots of the residuals. However, models for three groups (goose/swan abundance, secretive marsh bird abundance, and shorebird abundance) did not improve with this transformation, so they were transformed with $\log_{10}(x + 0.5)$ (Zar 2010). To avoid using highly correlated variables, we only used variables that had a variance inflation factor (VIF) < 2 (Zuur *et al.* 2010). When we encountered variables with a VIF > 2, we used the most biologically relevant variable. We scaled and centered all variables to improve model convergence (Gelman 2008). Due to missing data for water level, we used only 604 wetland surveys in the final models for all groups except shorebirds. Birds in the order Charadriiformes primarily migrate through the PPR beginning around mid-April (Skagen *et al.* 2008), so we only included surveys conducted after the third week of April for shorebirds to capture the main migratory period. We used site and year as random effects (Pinheiro and Bates 2000; Schabenberger and Pierce 2002; Zuur *et al.* 2009). Additionally, to address issues with heterogeneity, we incorporated a variance structure for the abundance models that allowed for a different variance for each survey week (Zuur *et al.* 2009).

We used program R (ver. 3.4.4.; R Core Team 2018) to initially examine, build, and select models using the "nlme" package (Pinheiro *et al.* 2017). We used a two-step approach for model selection. We were particularly interested in the effect of the amount of emergent vegetation and its interaction with survey week on abundance and species richness, but we first wanted to determine whether it should be included in the subsequent model selection step. We compared a model with all covariates, including a quadratic effect of emergent vegetation and its interaction with survey week, to subsets of this model that included 1) no emergent vegetation, 2) a linear effect of emergent vegetation, 3) a quadratic effect of emergent vegetation, 4) an interaction between a linear effect of emergent vegetation and survey week, and 5) an interaction between a quadratic effect of emergent vegetation and survey week. Using Akaike's Information Criterion (AIC; Akaiki 1973), we compared the most competitive model with models that included all possible combinations of the covari-

Table 1. Hypothesized responses of local-scale habitat variables to waterbird abundance by taxonomic group and three community-level measurements for waterbird surveys conducted in the Prairie Pothole Region of Iowa, spring 2016 and 2017. An "L" represents a linear trend and "Q" represents a quadratic trend. In parentheses, "+" indicates a positive trend and "-" indicates a negative trend, and both symbols in parentheses indicate the direction of the relationship for a quadratic trend. A "0" means we did not expect the covariate to influence the response variable. Some of the sources used to justify the relationships are given.

Response variable	Percent emergent vegetation	Water level change	Wetland area	Wetland age	Sources
Goose/Swan	L(+)	L(-)	L(+)	L(+)	Webb *et al.* (2010)
Dabbling ducks	Q(+ -)	L(-)	L(+)	L(+)	Colwell and Taft 2000, Fairbairn and Dinsmore 2001, Webb *et al.* 2010
Diving ducks	L(-)	L(+)	L(+)	L(-)	Murkin *et al.* 1997, Anteau and Afton 2009, Webb *et al.* 2010, Baschuk *et al.* 2012
Secretive marsh birds	L(+)	L(+)	L(+)	L(+)	Naugle *et al.* 1999, Baschuk *et al.* 2012,
Shorebirds	L(-)	L(+)	0	L(-)	Weber and Haig 1996, Taft *et al.* 2002, Webb *et al.* 2010
Total waterbird abundance	Q(+ -)	L(-)	L(+)	L(+)	Murkin *et al.* 1997
Species richness	L(+)	L(-)	L(+)	L(+)	Colwell and Taft 2000, Fairbairn and Dinsmore 2001, Webb *et al.* 2010

ates in that top model. Similar to Devries *et al.* (2008), we only considered models to be competitive if they had a ΔAIC < 2, and if they were not more complex versions of the top model (Burnham and Anderson 2002). We did not report or make inferences from models in such cases (Arnold 2010). After initial model selection, we used program SAS (PROC MIXED; SAS Institute, Inc. 2008) to determine coefficients, *F*-statistics, and significance of covariates (P. Dixon, pers. commun.). We used program SAS in order to obtain *P*-values using the Satterthwaite approximation, which is not available in the "nlme" package in program R (Luke 2017). For reporting purposes we used the highest ranking models and the back-transformed values of the response variables and their 95% confidence intervals.

RESULTS

We conducted surveys from 20 March to 26 May 2016, 17 February to 25 May 2017, and 12 March to 31 May 2018. The earlier start in 2017 was due to the unusually early onset of spring migration. We completed a total of 35 surveys per shallow lake throughout the three years: 10 surveys in 2016, 13 surveys in 2017, and 12 surveys in 2018. Shallow lake area ranged from 19.52 ha to 470.13 ha, with a mean area of 121.00 ha. Percent emergent cover was variable across non-restored and restored shallow lakes (Table 2), with restored shallow lakes having greater emergent cover than non-restored sites. In 2016 and 2017, weekly water level remained relatively consistent but showed an increase on average in 2018 (Fig. 2).

We counted a total of 713,338 waterbirds and identified 82 species. More waterbirds and species were detected at restored shallow lakes, with 582,148 waterbirds and 78 species, than at non-restored shallow lakes, which had 130,895 waterbirds and 70 species. Of the restored shallow lakes, those that were restored six years prior to this study had the greatest number of waterbirds overall with 101,764 waterbirds. Shallow lakes restored five years prior to this study had the greatest number of waterbird species with 67 overall. Of the taxonomic groups of interest, geese and swans were the most frequently encountered (25.87%), followed by dabbling ducks (22.94%), and diving ducks (20.42%). Secretive marsh birds (0.54%) and shorebirds (0.25%) made up a small proportion

Table 2. Mean (SE) percent emergent vegetation cover and the total number of surveys conducted (*n*) in spring 2016-2018 at non-restored shallow lakes (19 lakes) and restored shallow lakes (11 lakes) in the Prairie Pothole Region of Iowa.

	Percent emergent cover					
	2016		2017		2018	
Years since restoration	*n*	x̄ (SE)	*n*	x̄ (SE)	*n*	x̄ (SE)
Not restored	110	22.18 (0.82)	143	15.90 (0.64)	120	5.98 (0.27)
1	0	—	0	—	12	10.00 (0.00)
2	10	28.00 (1.53)	0	—	0	—
3	20	25.75 (0.91)	13	31.92 (1.06)	0	—
4	50	48.50 (2.50)	26	25.38 (0.38)	12	5.00 (0.00)
5	30	66.33 (3.14)	65	40.08 (1.20)	36	14.87 (0.73)
6	20	51.75 (0.83)	39	56.41 (1.95)	48	40.21 (2.84)
7	10	65.50 (0.50)	26	37.50 (0.50)	60	42.00 (2.42)
8	20	36.82 (4.14)	13	75.00 (0.00)	0	—
9	10	27.00 (0.82)	26	41.26 (2.99)	12	60.00 (0.00)
10	20	80.25 (1.12)	13	21.15 (0.83)	24	30.00 (3.13)
11	0	—	26	60.19 (1.56)	24	42.50 (7.82)
12	0	—	0	—	12	33.75 (0.90)

of encounters. Waterfowl numbers tended to be highest early in the season, while secretive marsh birds and shorebirds gradually increased in numbers later in the season. Total waterbird abundance was mostly driven by waterfowl numbers and was greatest early in the season. Species richness peaked around late April and early May in 2016 and 2018, but peaked in late March in 2017.

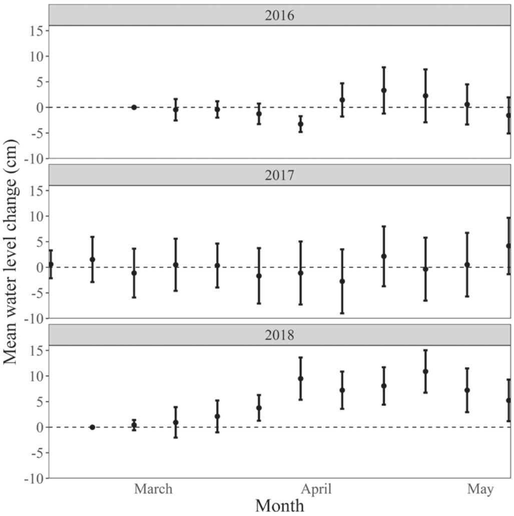

Figure 2. Mean water level change (with 95% confidence intervals) for each year throughout the survey period at shallow lakes in the Iowa Prairie Pothole Region, 2016-2018. The dashed line represents the first measurement and reference point from which subsequent measurements were compared.

The highest-ranking model for goose and swan abundance included years-since-restoration and wetland area (Table 3). Percent emergent vegetation, a quadratic effect of percent emergent vegetation, and water level were also included in competitive models. Years-since-restoration ($F_{1,\,32} = 15.99$, $P < 0.01$; Table 4; Fig. 3A) and wetland area ($F_{1,\,26.8} = 10.03$, $P < 0.01$; Table 4) had significant positive effects on goose and swan abundance in the top model, but the other covariates did not influence abundance in competing models.

The highest-ranking models for dabbling ducks included years-since-restoration, wetland area, water level, and an interaction between survey week and percent emergent vegetation (Table 3). In the top model, water level ($F_{1,\,155} = 5.11$, $P = 0.03$; Table 4) had a negative effect (Fig. 4A) and wetland area had a positive effect on dabbling duck abundance ($F_{1,\,26.7} = 4.83$, $P = 0.04$; Table 4). The interaction between survey week and percent emergent vegetation cover was significant ($F_{1,\,48.8} = 2.42$, $P = 0.01$). Percent emergent vegetation had a negative influence on abundance early and late in the season, but the effect was positive during most of the weeks in the middle of the season. Survey

Table 3. Model selection results for linear mixed models of habitat effects on spring migrant waterbirds surveyed in the Iowa Prairie Pothole Region, 2016-2018. The covariates considered included years since restoration (YSR), shallow lake area (area), water level change (water change), a linear and quadratic effect of percent emergent vegetation cover (emergent), and an interaction between emergent and survey week (week). Week and year were included as fixed effects in every model but are not shown unless included in an interaction. Models with a ΔAIC < 2 are shown, along with their AIC, model weights (w_i), and number of parameters (K).

Model	AIC	ΔAIC	w_i	K
Geese/Swans				
YSR + area	1013.91	0.00	0.68	32
Dabbling ducks				
YSR + area + water change + emergent*week	4807.89	0.00	0.26	46
area + water change + emergent*week	4807.91	0.02	0.26	45
Diving ducks				
YSR + area + water change + emergent^2*week	5106.21	0.00	0.42	59
area + water change + emergent^2*week	5107.22	1.01	0.25	58
Secretive Marsh Birds				
YSR + area	1374.39	0.00	0.69	32
Shorebirds				
water change	454.29	0.00	0.20	7
area	455.66	1.37	0.10	7
Total Waterbird Abundance				
YSR + area + water change + emergent^2	6125.65	0.00	0.50	35
area + water change + emergent^2	6127.12	1.47	0.22	34
YSR + area + water change	6127.59	1.94	0.18	33
Species Richness				
area + water change + emergent^2*week	4707.45	0.00	0.42	58
area + emergent^2*week	4708.79	1.34	0.22	57

weeks that portray this contrasting interaction the most were the first week in March in 2017, when emergent vegetation had a negative influence on dabbling duck abundance, and the third and fourth week in March and the first week in April, when there was a positive effect on abundance (Fig. 4B). Years-since-restoration did not influence dabbling duck abundance.

For diving ducks, the highest-ranking models included years-since-restoration, wetland area, water level, and an interaction between survey week and a quadratic trend in percent emergent vegetation (Table 3). Wetland area ($F_{1, 25.4} = 17.05$, $P < 0.01$; Table 4) and water level ($F_{1, 166} = 17.05$, $P = 0.03$) had positive effects on diving duck abundance (Fig. 5A). The interaction between survey week and a quadratic trend in percent emergent vegetation cover had a significant influence on diving duck abundance ($F_{12, 52} = 3.36$, $P < 0.01$). Abundance tended to peak around 40% emergent vegetation cover. This effect was strongest during the second and fourth weeks in March, and it gradually weakened after the second week in April (Fig. 5B). Years-since-restoration did not affect diving duck abundance.

The highest-ranking models for secretive marsh bird abundance included wetland area and years-since-restoration (Table 3). Wetland area ($F_{1, 23.8} = 11.18$, $P < 0.01$; Table 4) and years-since-restoration ($F_{1, 27.3} = 9.31$, $P = 0.01$; Fig. 3B) positively influenced secretive marsh bird abundance.

The highest-ranking models for shorebird abundance included water level and wetland area (Table 3). The greatest shorebird numbers tended to occur at sites with low water levels and exposed mud, and water level had a negative relationship with shorebird abundance. However, this and other covariates did not have a significant influence on shorebird abundance.

For total waterbird abundance, the highest-ranking models included years-since-restoration, wetland area, water level, and a quadratic effect of percent emergent vegeta-

Table 4. Beta coefficients (SE) of covariate effects on spring migrant waterbirds surveyed in the Prairie Pothole Region of Iowa, 2016-2018. Estimates are from the top linear mixed model. An asterisk (*) indicates a significant ($P < 0.05$) effect. Survey week was included as a factor, so we showed beta estimates from three different weeks when we found a significant effect of emergent and week. Survey week is represented by the week and the month in which the survey took place (e.g., 1st for the first week of the month).

Covariate	Geese/Swans	Dabbling ducks	Diving ducks	Secretive marsh birds	Total waterbird abundance	Species richness
years since restored	*0.21 (0.05)	0.49 (0.35)	0.60 (0.36)	*0.10 (0.03)	1.40 (0.78)	
wetland area	*0.18 (0.06)	0.70 (0.34)	*1.31 (0.32)	*0.12 (0.03)	*3.46 (0.73)	*2.64 (0.52)
water level		*-0.23 (0.10)	*0.27 (0.13)		*0.69 (0.22)	0.29 (0.16)
emergent		*0.53 (0.40)	-0.72 (1.52)		*1.42 (0.69)	*0.80 (1.91)
emergent^2			*-0.75 (0.40)		-0.64 (0.32)	-0.47 (1.91)
emergent x week		*	*			*
1st March		-1.99 (3.42)	2.36 (3.80)			-0.39 (2.21)
1st April		1.79 (0.87)	2.75 (1.85)			-0.28 (1.94)
1st May		0.12 (0.35)	1.35 (1.51)			1.28 (1.89)
emergent^2 x week			*			*
1st March			-2.90 (3.78)			0.38 (2.23)
1st April			-2.00 (1.80)			0.06 (1.96)
1st May			0.57 (1.53)			-0.47 (1.92)

tion (Table 3). Wetland area ($F_{1, 24.7} = 22.59$, $P < 0.01$; Table 4) and water level ($F_{1, 138} = 9.77$, $P < 0.01$; Fig. 6A) positively influenced total waterbird abundance (Table 4). Percent emergent vegetation did not influence total waterbird abundance in the top model, but there was a significant influence in the second-best model ($F_{1, 71.7} = 5.97$, $P = 0.02$). Total waterbird abundance was predicted to peak around 60% emergent vegetation cover.

Finally, the highest-ranking models for species richness included wetland area, water level, and an interaction between survey week and a quadratic trend in percent emergent vegetation (Table 3). Wetland area had a positive effect on species richness ($F_{1, 25.4} = 25.76$, $P < 0.01$; Table 4). The interaction between percent emergent vegetation and survey week also influenced species richness ($F_{12, 51.2} = 2.36$, $P = 0.02$). This quadratic effect tended to be negative or nearly zero throughout the season. The strongest negative effect occurred during the second week in March, when abundance peaked around 40% emergent vegetation cover (Fig. 6B). However, during the last two weeks in April, the quadratic effect was positive, with species richness peaking at very low or very high emergent vegetation cover, but this was a weaker effect. Water level did not influence species richness.

DISCUSSION

While much wetland restoration in the PPR has focused on smaller, temporary or seasonal wetlands, the restoration of large, lacustrine wetlands (i.e., shallow lakes) is also beneficial to waterbirds (Hanson and Butler 1994; Anteau and Afton 2009; Fox *et al.* 2018). This is particularly true for migrant waterbirds that require adequate stopover locations to rest, refuel, and acquire energy reserves for breeding (Krapu *et al.* 1995; LaMontagne *et al.* 2001; Alisauskas 2002). In fact, the decline in some waterbirds, such as the Lesser Scaup (*Aythya affinis*), may be attributed to the degradation of these shallow lakes and loss of invertebrate diversity (Anteau and Afton 2004, 2008, 2009). Due

Figure 3. The predicted effect of years-since-restoration ($n = 604$ waterbird surveys) on goose/swan abundance (A) and secretive marsh bird (SMB) abundance (B) at shallow lakes in the Iowa Prairie Pothole Region, 2016-2018. The shaded ribbons represent 95% confidence intervals.

to their large size and the resulting availability of microhabitats, these sites have the potential to accommodate a greater variety of waterbirds, especially during migration (Hansson *et al.* 2010). Additionally, the practice of managing shallow lakes to mimic the

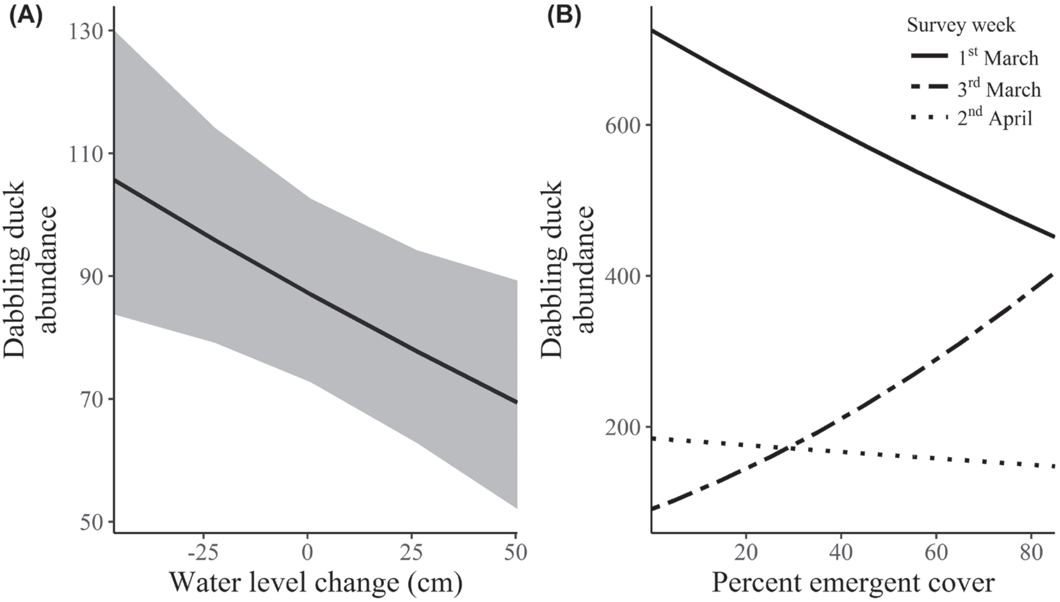

Figure 4. The predicted effects of water level (A) ($n = 604$ waterbird surveys) and an interaction between survey week and emergent vegetation (B) on the abundance of dabbling ducks at shallow lakes in the Iowa Prairie Pothole Region, 2016-2018. The shaded ribbons represent 95% confidence intervals, but these are not shown for B to improve clarity of the relationship. The number of waterbird surveys conducted for each week differed, with 16 surveys for the first week in March 2017, 71 surveys each for the third week in March (all three years), and 81 surveys in the second week in April (all three years).

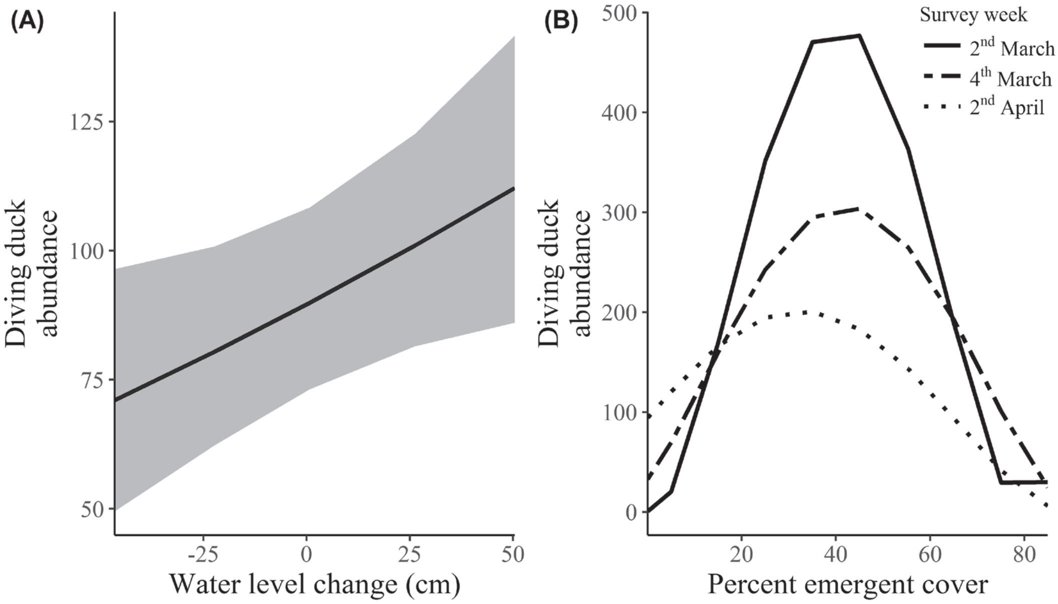

Figure 5. The predicted effects of water level (A) (*n* = 604 waterbird surveys) and an interaction between survey week and a quadratic effect of emergent vegetation (B) (*n* = 90 waterbird surveys for each week) on the abundance of diving ducks at shallow lakes in the Iowa Prairie Pothole Region, 2016-2018. The shaded ribbons represent 95% confidence intervals, but these are not shown for B to improve clarity of the relationship. The number of waterbird surveys conducted for each week differed, with 20 surveys for the second week in March 2017, 77 surveys each for the fourth week in March (all three years), and 81 surveys in the second week in April (all three years).

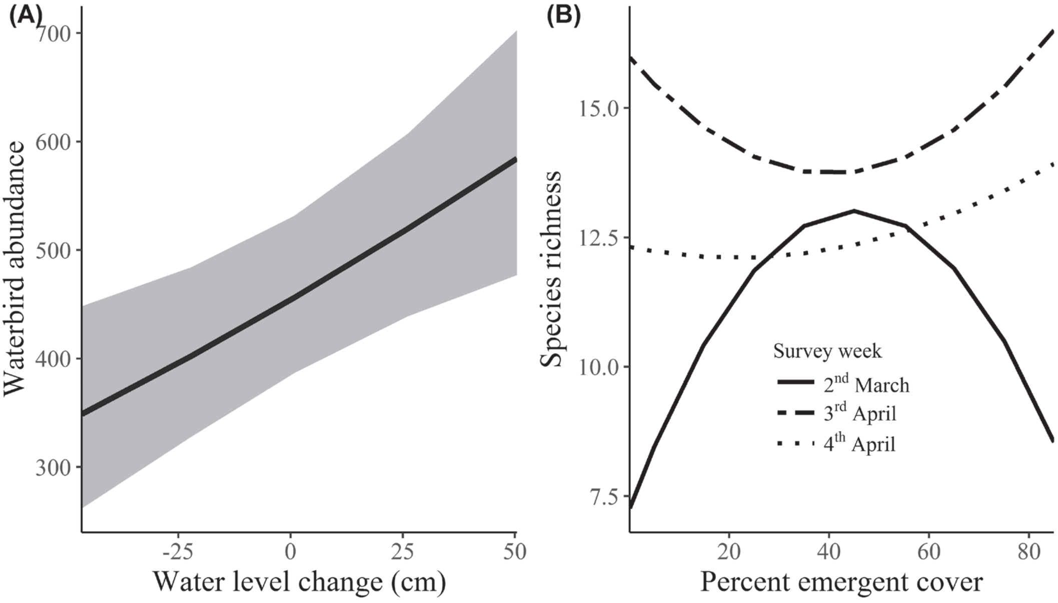

Figure 6. The predicted effects of water level on total waterbird abundance (A) (*n* = 604 waterbird surveys) and an interaction between survey week and a quadratic effect of emergent vegetation (*n* = 90 waterbird surveys for each week) on waterbird species richness (B) at shallow lakes in the Iowa Prairie Pothole Region, 2016-18. The shaded ribbons represent 95% confidence intervals, but these are not shown for B to improve clarity of the relationship. The number of waterbird surveys conducted for each week differed, with 20 surveys for the first week in March 2017 and 83 surveys each for the third and fourth weeks in April (all three years).

natural hydrological, wet-dry cycle provides different habitats through time and supports a greater number of species and individuals than if they were to remain in an open, turbid state (Hargeby *et al.* 1994; Murkin and Caldwell 2000; Hansson *et al.* 2010). Restored sites host a variety of plant life, such as emergent vegetation, which can provide shelter for waterbirds, and submersed aquatic vegetation, which can provide forage and a substrate for invertebrates (Murkin and Caldwell 2000; Paszkowski and Tonn 2000).

Several habitat variables have been associated with abundance, density, or richness of waterbirds (Fairbairn and Dinsmore 2001; Webb *et al.* 2010), and understanding these relationships is important when managing restored wetlands (Ma *et al.* 2010). In our study, shallow lake area was an influential variable for several waterbird groups, total waterbird abundance, and species richness. In all cases, area had a strong positive effect for geese and swans, diving ducks, secretive marsh birds, total waterbird abundance, and species richness. This relationship has been demonstrated previously for several waterfowl species and total waterfowl abundance (LaGrange and Dinsmore 1989; Colwell and Taft 2000; Webb *et al.* 2010) and for secretive marsh birds such as the Least Bittern and Pied-billed Grebe (Tozer *et al.* 2010; Baschuk *et al.* 2012; Harms and Dinsmore 2013; Monfils *et al.* 2014). During spring migration, waterfowl feed on a variety of food items, including waste corn, moist soil seeds, and invertebrates (Anteau and Afton 2008; Pearse *et al.* 2013; Tidwell *et al.* 2013). The propensity for certain forage varies by availability, species (Baldassarre and Bolen 1994; Tidwell *et al.* 2013), and breeding condition (Krapu *et al.* 1995; Pearse *et al.* 2011). Secretive marsh birds also feed on both plant and animal material during spring migration (Conway 19995; Muller and Storer 1999). With a larger area, these shallow lakes have a high degree of water level and vegetation complexity and are able to support various species with different nutritional requirements (Weller and Spatcher 1965; Kantrud and Stewart 1984).

At the same time, the positive association of area with several waterbird groups contrasts with other studies that found that a complex of several smaller wetlands supported a similar, if not greater, number of waterbirds and species than a single large wetland (Brown and Dinsmore 1986; Fairbairn and Dinsmore 2001). Indeed, small, seasonally flooded wetlands or a complex of both large and small wetlands are considered important for several species of waterbirds (Kantrud and Stewart 1977; Fairbairn and Dinsmore 2001; Naugle *et al.* 2001; Tozer *et al.* 2010). However, with an average size of 125 ha, all of our shallow lakes were much larger than the smaller wetlands considered by some of these studies, which examined wetlands as small as 1 ha or less (Brown and Dinsmore 1986). Therefore, we conclude that the shallow lakes in our study area may provide a greater variety of food items that can accommodate more individuals and species than complexes of small wetlands (Kantrud and Stewart 1984; Brown and Smith 1998).

Another important variable for some groups was the percent cover of emergent vegetation. We found emergent cover to be important for dabbling ducks, diving ducks, total waterbird abundance, and species richness. The importance of emergent vegetation has been well documented for waterbirds that use wetlands during migration and breeding (Weller and Spatcher 1965; VanRees-Siewert and Dinsmore 1996; Webb *et al.* 2010; Harms and Dinsmore 2013). Emergent vegetation provides shelter and a substrate for invertebrates (Murkin *et al.* 1992), and there is evidence that invertebrate abundance is greater when open water is interspersed with emergent vegetation (Voigts 1976). Indeed, waterbird abundance tends to be greatest when emergent vegetation and open water are present at a 1:1 ratio (Weller and Spatcher 1965; Kaminski and Prince 1984; Webb *et al.* 2010). We found that total waterbird abundance and the abundance of diving ducks had a quadratic relationship with emergent vegetation, with abundance peaking around 40-60% vegetation throughout the season. An equal interspersion of open water and emergent vegetation likely provides diverse habitat for different diving duck species. For example, Ring-necked Ducks (*Aythya collaris*) tend to prefer to forage in habitat interspersed with vegetation, while Ruddy Ducks (*Oxyura jamaicense*) are more commonly found in open water areas (Bergan and Smith 1989). Additionally, some degree of open water improves visibility of potential predators, while emergent vegetation provides protection against other disturbances, such as weather and human disturbance. (Kaminski and Prince 1981; Austin *et al.* 2017).

Species richness also had a quadratic relationship with emergent vegetation with most weeks showing a negative quadratic effect. Similar to abundance, previous studies have found that species richness of waterbirds is highest in wetlands with 50% emergent vegetation cover (Weller and Spatcher 1965; Webb *et al.* 2010), and we found a similar relationship throughout most of the season. The last two weeks in April showed the opposite relationship with the highest numbers of species occurring at low and high emergent coverage. Although change in waterbird species composition was not reported for this study, this variability was likely due to the changing species composition throughout the migration period. For example, waterfowl species numbers were declining slightly in April and May, but species richness for shorebirds and secretive marsh birds was higher during this time period. Migrant shorebirds tend to prefer sites with little to no vegetation and open water (Velasquez 1992; Taft *et al.* 2002), while secretive marsh birds rely on areas with emergent vegetation (Harms and Dinsmore 2013; Blake-Bradshaw 2018; Fournier *et al.* 2018; Wilson *et al.* 2018). Such preferences could explain the change in the relationship between species richness and emergent vegetation.

On the other hand, dabbling ducks showed a linear relationship with emergent vegetation cover. This pattern was negative early in the season but became more positive in the mid- to late-season. Other studies have found that dabbling ducks tend to a have positive linear relationship with emergent vegetation cover (Stafford *et al.* 2007; Webb *et al.* 2010). Along with geese, the Mallard (*Anas platyhynchos*) and Northern Pintail (*Anas acuta*) are the earliest spring migrants in the PPR, and they often arrive along with the spring thaw (Drilling *et al.* 2002; Haukos *et al.* 2006). Indeed, these two species made up a large proportion of the waterbirds we counted early in the season, and they often appeared on thawed areas of mostly frozen shallow lakes. In such cases the presence of open water seemed more important than emergent vegetation, and this could explain this relationship early in the season.

Water level was also an influential predictor for several groups. Published studies have identified water depth as an important variable predicting waterbird use (Pöysa 1983; Colwell and Taft 2000; Isola *et al.* 2000). It can directly affect the ability of some birds to forage (Pöysa 1983) and influence the food items available (Murkin and Ross 2000). Managers can manipulate water levels, but water level changes in the PPR can still be highly variable and unpredictable within a given year (van der Valk 2005), especially since many of these shallow lakes are isolated and the main source of water input is precipitation (Winter 1989). In our study, dabbling duck abundance was negatively influenced by water level. This relationship has been demonstrated by other studies (Colwell and Taft 2000; Murkin and Caldwell 2000; Taft *et al.* 2002; Baschuk *et al.* 2012). Because dabbling ducks generally feed along the surface of the water or just a few centimeters below the surface, they are constrained by relatively shallow waters (< 25 cm; Colwell and Taft 2000). Contrastingly, diving ducks and total waterbird abundance showed a positive relationship with water level. Compared to dabbling ducks, diving ducks tend to forage for macroinvertebrates and tubers in deeper water (Afton *et al.* 1991; Colwell and Taft 2002). Additionally, nearly half of the observed waterbirds were diving ducks and American Coots, a species that can forage in relatively deep water during migration (Brisbin and Mowbray 2002). This group and species could have been driving the relationship between water level and total waterbird abundance.

We originally anticipated that several groups might be positively influenced by years-since-restoration, but only secretive marsh birds and geese and swans showed this relationship. Some of the earliest migrants in the spring in Iowa are geese and swans, not long after wetlands and ponds begin to thaw. The primary diet of midcontinent, migrant geese consists of agricultural items, such as waste corn and shoots of winter wheat (Krapu *et al.* 1995; Pearse *et al.* 2013). As such, wetlands appear to mostly be used for roosting by geese and less for foraging in the spring in the PPR (Krapu *et al.* 1995; Pearse *et al.* 2013). Thus, older restorations with increased emergent vegetation cover may provide better protection from predators or cover from weather than more open sites. On the other hand, older restorations tended to have more areas with thicker vegetation, and this could explain the positive relationship between secretive marsh birds and years-since-restoration. However, we did not find emergent vegetation to influence either geese and swans or secretive marsh birds, so there may be another habitat variable related to years-since-restoration that we did not measure that influences these groups. We found this to be particularly surprising for secretive marsh birds. This could partly be due to our sampling scheme, which may not have been appropriate for getting accurate counts of many secretive marsh birds. Future studies of migration for secretive marsh birds should use playback recordings, which have been shown to improve detection of species in this group (Gibbs and Melvin 1993; Lor and Malecki 2002).

Management Implications

This study highlights some of the habitat requirements of waterbirds migrating through the PPR in Iowa in spring, and the importance of restoring large shallow lakes by the SLRP to meet these requirements. There are two major components managers should consider when restoring large prairie wetlands and managing them for waterbirds. First, restoring wetlands that have lost major natural hydrological fluctuations will provide habitat for a greater number of birds and species during migration. Shallow lakes that remain in the lake phase of the wetland wet-dry cycle are the least productive when compared to wetlands with more emergent and submersed aquatic vegetation (Murkin and Caldwell 2000). After dewatering a shallow lake, the natural changes in the vegetation throughout the next few years provides habitat for different birds. Initially, the low water levels attract many shorebirds and some dabbling ducks (Taft *et al.* 2002). With gradual reflooding, conditions improve for waterfowl and other wetland-associated migrants. Second, additional periodic drawdowns could be implemented to further mimic the hydrological cycle. Ideally, restored shallow lakes will host emergent vegetation for a few years, then begin to die back due to persistent inundation and muskrat activity, which would prevent the "choking out" of wetlands by aggressive emergent vegetation (i.e., *Typha* sp.; Van der Valk and Davis 1976). At this time, another drawdown might be appropriate.

ACKNOWLEDGMENTS

This project was funded by a grant from the U.S. Fish and Wildlife Service (Prairie Pothole Joint Venture) with additional support from the Iowa Department of Natural Resources. We thank Sarah Moodie, David Jabot, Jacob Newton, and Jason Newton for assistance with field work. We thank Brian J. Wilsey and Timothy W. Stewart for providing edits and advice on field methods and analyses. We also thank Mark Gulick, Todd Bishop, Doug Janke, Bryan Hellyer, Steve Woodruff, TJ Herrick, Clint Maddix, Chris LaRue, Karen Kinkead, Kevin Murphy, and Tyler Harms for help with planning and logistics. We thank Katherine Goode and Philip M. Dixon for assistance with statistical modeling. We thank two anonymous reviewers for constructive comments to improve the manuscript. We followed all applicable ethical guidelines for the use of birds in research, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010). This paper is a product of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. IOW05438 is sponsored by Hatch Act and State of Iowa funds.

LITERATURE CITED

Aagard, K., S. M. Crimmins, W. E. Thogmartin, B. G. Tavernia and J. E. Lyons. 2015. Evaluating predictors of local dabbling duck abundance during migration: managing the spectrum of conditions faced by migrants. Wildfowl 65: 100-120.

Afton, A. D., R. H. Hier and S. L. Paulus. 1991. Lesser Scaup diets during migration and winter in the Mississippi flyway. Canadian Journal of Zoology 69: 328-333.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 276-281 *in* International symposium on information theory (B. N. Petran and F. Csaki, Eds.). Akad éiai Kiad ó Budapest, Hungary.

Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent Lesser Snow Geese. Journal of Wildlife Management 66: 181-193.

Ankney, C. D., A. D. Afton and R. T. Alisauskas. 1991. The role of nutrient reserves in limiting waterfowl reproduction. Condor 93: 1029-1032.

Anteau, M. J. 2012. Do interactions of land use and climate affect productivity of waterbirds and prairie-pothole wetlands? Wetlands 32: 1-9.

Anteau, M. J. and A. D. Afton. 2004. Nutrient reserves of Lesser Scaup (*Aythya affinis*) during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis. Auk 121: 917-929.

Anteau, M. J. and A. D. Afton. 2008. Amphipod densities and indices of wetland quality across the upper-Midwest, USA. Wetlands 28: 184-196.

Anteau, M. J. and A. D. Afton. 2009. Wetland use by Lesser Scaup during spring migration across the Upper Midwest, USA. Wetlands 29: 704-712.

Anteau, M. J., A. D. Afton, A. C. E. Anteau and E. B. Moser. 2011. Fish and land use influence *Gammarus lacustris* and *Hyallela azteca* (Amphipoda) densities in large wetlands across the upper Midwest. Hydrobiologia 664: 69-80.

Arnold, T. W. 2010. Uniformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175-1178.

Austin, J. E., S. T. O'Neil and J. M. Warren. 2017. Habitat selection by postbreeding female diving ducks: influence of habitat attributes and conspecifics. Journal of Avian Biology 48: 295-308.

Baker, L. A. 1992. Introduction to nonpoint source pollution in the United States and prospects for wetland use. Ecological Engineering 1: 1-26.

Baldassarre, G. A. and E. G. Bolen. 1994. Waterfowl ecology and management. John Wiley & Sons, Inc., New York, New York.

Bärlocher F., R. J. Mackay and G. B. Wiggins. 1978. Detritus processing in a temporary vernal pool in southern Ontario Canada. Archiv fuer Hydrobiologie 81: 269-295.

Baschuk, M. S., N. K. Koper, D. A. Wrubleski and G. Goldsborough. 2012. Effects of water depth, cover, and food resources on habitat use of marsh birds and waterfowl in boreal wetlands of Manitoba, Canada. Waterbirds 35: 44-55.

Beerens, J. M., D. E. Gawlik, G. Herrgin and M. I. Cook. 2011. Dynamic habitat selection by two wading bird species with divergent foraging strategies in a seasonally fluctuating wetland. Auk 128: 651-662.

Bergan, J. F. and L. M. Smith. 1989. Differential habitat use by diving ducks wintering in South Carolina. Journal of Wildlife Management 53: 1117-1126.

Bishop, R. A. 1981. Iowa's wetlands. Proceedings of the Iowa Academy of Science 88: 11-16.

Blake-Bradshaw, A. G. 2018. Wetland suitability for waterbirds in Illinois. M.S. Thesis, University of Illinois at Urbana Champagne, Urbana, Illinois.

Brinson, M. M. and S. D. Eckles. 2011. U. S. Department of Agriculture conservation program and practice efforts on wetland ecosystem services: a synthesis. Ecological Applications 21: S116-S127.

Brisbin, I. L., Jr. and T. B. Mowbray. 2002. American Coot (*Fulica americana*). No. 697 *in* The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.697a, accessed 4 April 2018.

Brown, M. and J. J. Dinsmore. 1986. Implications of marsh size and isolation for marsh bird management. Journal of Wildlife Management 50: 392-397.

Brown, S. C. and C. R. Smith. 1998. Breeding season bird use of recently restored versus natural wetlands in New York. Journal of Wildlife Management 62: 1480-1491.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information theoretic approach. Springer, New York, New York.

Colwell, M. A. and O. W. Taft. 2000. Waterbird communities in managed wetlands of varying water depth. Waterbirds 23: 45-55.

Conway, C. J. 1995. Virginia Rail (*Rallus limicola*). No. 173 *in* The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.173, accessed 4 April 2018.

Conway, C. J. 2009. Standardized North American bird monitoring protocols, version 2009-2. Wildlife Research Report #2009-02. U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, Arizona.

Conway, C. J. 2011. Standardized North American marsh bird monitoring protocol. Waterbirds 34: 319-346.

Cowardin, L. M., V. Carter and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of Interior, Fish and Wildlife Service Report FWS/OBS-79/31, Washington, D.C.

Dahl, T. E. 1990. Wetlands losses in the United States 1780's to 1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington D.C.

Dahl, T. E. 2014. Status and trends of prairie wetlands in the United States 1997 to 2009. U.S. Department of the Interior, Fish and Wildlife Service, Washington D.C.

Devries, J. H., L. M. Armstrong, R. J. MacFarlane, L. Moats and P. T. Thoroughgood. 2008. Waterfowl nesting in fall-seeded and spring-seeded cropland in Saskatchewan. Journal of Wildlife Management 72: 1790-1797.

Dimalexis, A. and M. Pyrovetsi. 1997. Effect of water level fluctuations on wading bird foraging habitat use at an irrigation reservoir, Lake Kerkini, Greece. Colonial Waterbirds 20: 244-252.

Drilling, N., R. D. Titman and F. McKinney. 2002. Mallard/Mexican Duck (*Anas platyrhynchos/diazi*). No. 658 *in* The Birds of North American (A. G. Poole and F. B. Gill, Eds.). Cornell Lab of Ornithology, Ithaca, New York. https://doi.org/10.2173/bna.658, accessed 13 November 2018.

Environmental Systems Research Institute (ESRI). 2014. ArcGIS v. 10.3. ESRI, Redlands, California.

Euliss, N. H., Jr. and D. M. Mushet. 1999. Influence of agricultural on aquatic invertebrate communities of temporary wetlands in the Prairie Pothole Region of North Dakota, USA. Wetlands 19: 578-583.

Fair, J., E. Paul and J. Jones (Eds.). 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C.

Fairbairn, S. E. and J. J. Dinsmore. 2001. Local and landscape-level influences on wetland bird communities of the Prairie Pothole Region of Iowa, USA. Wetlands 21: 41-47.

Fournier, A. M. V, Mengel, D. C. and Krementz, D. G. 2018. Sora (*Porzana carolina*) autumn migration habitat use. Royal Society Open Science. 5: 171664.

Fox, A. D., T. J. S. Balsby, H. E. Jørgensen, T. L. Lauridsen, E. Jeppesen, M. Søndergaard, K. Fugl, P. Myssen and P. Clausen. 2018. Effects of lake restoration on breeding abundance of globally declining common pochard (*Aythya ferina* L.). Hydrobiologia 830: 33-44.

Fronemen, A., M. J. Mangnal, R. M. Little and T. M. Crowe. 2001. Waterbird assemblages and associated habitat characteristics of farm ponds in the Western Cape, South Africa. Biodiversity and Conservation 10: 251-270.

Geisthardt, E., J. Gautsch and B. Harland. 2013. Shallow lakes summary report. Iowa Department of Natural Resources, Watershed Monitoring and Assessment Section, Des Moines, Iowa. 65 pages.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27: 2865-2873.

Gibbs, J. P. and S. M. Melvin. 1993. Call-response surveys for monitoring breeding waterbirds. Journal of Wildlife Management 57: 27-34.

Gleason, R. A., N. H. Euliss, Jr., D. E. Hubbard and W. G. Duffy. 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23: 26-34.

Hanson, M. A. and M. G. Butler. 1994. Responses to food web manipulation in a shallow waterfowl lake. Hydrobiologia 279/280: 457-466.

Hanson, M. A. and M. R. Riggs. 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. Wetlands 15: 167-175.

Hanson, M. A., K. D. Zimmer, M. G. Butler, B. A. Tangen, B. R. Herwig and N. H. Euliss, Jr. 2005. Biotic interactions as determinants of ecosystem structure in prairie wetlands: an example using fish. Wetlands 25: 764-775.

Hansson, L.-A., A. Nicolle, C. Brönmark, A. Hargeby, Å. Lindström and G. Andersson. 2010. Waterfowl, macrophytes, and the clear water state of shallow lakes. Hydrobiologia 646: 101-109.

Hargeby, A., G. Andersson, I. Blindow and S. Johansson. 1994. Trophic structure in a shallow eutrophic lake during a dominance shift to submerged macrophytes. Hydrobiologia 279/280:83-90.

Harms, T. M. and S. J. Dinsmore. 2013. Habitat associations of secretive marsh birds in Iowa. Wetlands 33: 561-571.

Harris, S. W. and W. H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44: 331-343.

Haukos, D. A., M. R. Miller, D. L. Orthmeyer, J. Y. Takekawa, J. P. Fleskes, M. L. Casazza, W. M. Perry and J. A. Moon. 2006. Spring migration of northern pintails from Texas and New Mexico, USA. Waterbirds 29: 127-136.

Hopps, E. C. 2012. Avian diversity and habitat use on Wetland Reserve Program lands in the Lower Missouri River Valley. The Prairie Naturalist 44: 79-97.

Igl, L. D. and D. H. Johnson. 1997. Changes in breeding bird populations in North Dakota: 1967 to 1992-93. Auk 114: 74-92.

Iowa Association of Naturalists (IAN). 2001. Iowa Wetlands. http://www.extension.iastate.edu/Publications/IAN204.pdf, accessed 2 October 2017.

Isola, C. R., M. A. Colwell, O. W. Taft and R. J. Safran. 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Jaoquin Valley. Waterbirds 23: 196-203.

Jenni, L. and S. Jenni-Eiermann. 1998. Fuel supply and metabolic constraints in migrating birds. Journal of Avian Biology 29: 521-528.

Johnson, D. H., S. D. Haseltine and L. M. Cowardin. 1994. Wildlife habitat management on the northern prairie landscape. Landscape and Urban Planning 28: 5-21.

Kent, T. H. and J. J. Dinsmore. 1996. Birds in Iowa. Thomson-Shore, Inc., Dexter, Michigan.

Kaminski, R. M. and H. H. Prince. 1981. Dabbling duck activity and foraging responses to aquatic macroinvertebrates. Auk 98: 115-126.

Kaminski, R. M. and H. H. Prince. 1984. Dabbling duck-habitat associations during spring in Delta Marsh, Manitoba. Journal of Wildlife Management 48: 37-50.

Kantrud, H. A. and R. E. Stewart. 1977. Use of natural basin wetlands by breeding waterfowl in North Dakota. Journal of Wildlife Management 41: 243-253.

Kantrud, H. A. and R. E. Stewart. 1984. Ecological distribution and crude density of breeding birds on prairie wetlands. Journal of Wildlife Management 48: 426-437.

Kantrud, H. A., G. L. Krapu and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.28).

Krapu, G. L., K. J. Reinecke, D. G. Jorde and S. G. Simpson. 1995. Spring-staging ecology of midcontinent

Greater White-fronted Geese. Journal of Wildlife Management 59: 736-746.

Krapu, G. L. 1981. The role of nutrient reserves in mallard reproduction. Auk 98: 29-38.

LaGrange, T. G. and J. J. Dinsmore. 1989. Plant and animal community responses to restored Iowa wetlands. Prairie Naturalist 21: 39-48.

LaMontagne, J. M., R. M. R. Barclay and L. J. Jackson. 2001. Trumpeter Swan behavior at spring-migration stopover areas in southern Alberta. Canadian Journal of Zoology 79: 2036-2042.

Loges, B. W., B. G. Tavernia, *et al.* 2015. National protocol framework for the inventory and monitoring of nonbreeding waterbirds and their habitats, an Integrated Waterbird Management and Monitoring Initiative (IWMM) approach. Natural Resources Program Center, Fort Collins, Colorado.

Lor, S. and R. A. Malecki. 2002. Call-response surveys to monitor marsh bird population trends. Wildlife Society Bulletin 30: 1195-1201.

Lor, S. and R. A. Malecki. 2006. Breeding ecology and nesting habitat associations of five marsh bird species in western New York. Waterbirds 29: 427-436.

Luke, S. G. 2017. Evaluating significance in linear mixed effects models in R. Behavioral Research 49: 1494-1502.

Ma, Z., Y. Cai, B. Li and J. Chen. 2010. Managing wetland habitats for waterbirds: an international perspective. Wetlands 30: 15-27.

Main, A. R., J. V. Headley, K. M. Peru, N. L. Michel, A. J. Cessna and C. A. Morrissey. 2014. Widespread use and frequent detection of neonicotinoid insecticides in wetlands of Canada's Prairie Pothole Region. PLoS ONE 9, e92821.

Martin, D. B. and W. A. Hartman. 1987. The effect of cultivation on sediment composition and deposition in prairie pothole wetlands. Water, Air, and Soil Pollution 34: 45-53.

Miller, B. A., W. G. Crumpton and A. G. van der Valk. 2009. Spatial distribution of historical wetland classes on the Des Moines Lobe, Iowa. Wetlands 29: 1146-1152.

Monfils, M. J., P. W. Brown, D. B. Hayes, G. J. Soulliere and E. N. Kafcas. 2014. Breeding bird use and wetland characteristics of diked and undiked coastal marshes in Michigan. Journal of Wildlife Management 78: 79-92.

Muller, M. J. and R. W. Storer. 1999. Pied-billed Grebe (*Podilymbus podiceps*). No. 410 *in* The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.410, accessed 4 April 2018.

Murkin, H. R. and P. J. Caldwell. 2000. Avian use of prairie wetlands. Pages 249-286 *in* Prairie wetland ecology: the contribution of the marsh ecology research program (H. R. Murkin, A. G. van der Valk and W. R. Clark, Eds.). Iowa State University Press, Ames, Iowa.

Murkin, H. R. and L. C. Ross. 2000. Invertebrates in prairie wetlands. Pages 201-247 *in* Prairie wetland ecology: the contribution of the marsh ecology research program (H. R. Murkin, A. G. van der Valk and W. R. Clark, Eds.). Iowa State University Press, Ames, Iowa.

Murkin, E. J., H. R. Murkin and R. D. Titman. 1992. Nektonic invertebrate abundance and distribution at the emergent vegetation-open water interface in the Delta Marsh, Manitoba, Canada. Wetlands 12: 45-52.

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

Murphy, K. T. and S. J. Dinsmore. 2014. Stopover dynamics of fall migrant Pectoral Sandpipers in Iowa. Wader Study Group Bulletin 121: 186-192.

Myers, J. P., R. I. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. Sallaberry, S. E. Senner and A. Tarak. 1987. Conservation Strategy for Migratory Species. American Scientist 75: 18-26.

Naugle, D. E., R. R. Johnson, M. E. Etsy and K. F. Higgins. 2001. A landscape approach to conserving wetland bird habitat in the Prairie Pothole Region of eastern South Dakota. Wetlands 21: 1-17.

Naugle, D. E., K. F. Higgins, S. M. Nusser and W. C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology 14: 267-276.

Neely, R. K. and J. K. Baker. 1989. Nitrogen and phosphorous dynamics and the fate of agricultural runoff. Pages 92-131 *in* Northern Prairie Wetlands (A. G. van der Valk, Ed.). Iowa State University press, Ames, Iowa.

Ntiamoa-Baidu, Y., T. Piersma, P. Wiersma, M. Poot, P. Battley and C. Gordon. 1998. Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. Ibis 140: 89-103.

O'Neal, B. J., E. J. Heske and J. D. Stafford. 2008. Waterbird response to wetlands restored through the Conservation Enhancement Program. Journal of Wildlife Management 72: 654-664.

Paszkowski, C. A. and W. M. Tonn. 2000. Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors. Freshwater Biology 43: 421-437.

Pearse, A. T., G. K. Krapu and R. R. Cox., Jr. 2013. Comparative spring-staging ecology of sympatric arctic-nesting geese in south-central Nebraska. American Midland Naturalist 169: 371-381.

Pearse, A. T., G. L. Krapu, R. R. Cox, Jr. and B. E. Davis. 2011. Spring-migration ecology of Northern Pintails in south-central Nebraska. Waterbirds 24: 10-18.

Pearse, A. T., R. M. Kaminski, K. J. Reinecke and S. J. Dinsmore. 2012. Local and landscape associations between wintering dabbling ducks and wetlands complexes in Mississippi. Wetlands 32: 859-869.

Pinheiro, J. and D. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York, New York.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team. 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme.

Pöysa, H. 1983. Morphology-mediated niche organization in a guild of dabbling ducks. Ornis Scandinavica 14: 317-326.

R Core Team. 2018. R: a language and environment for statistical computing v. 3.4.4. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/, accessed 15 March 2018.

SAS Institute, Inc. 2008. SAS Statistical Software v. 9.4. SAS Institute, Inc., Cary, North Carolina.

Schabenberger, O. and F. Pierce. 2002. Contemporary statistical models for the plant and soil sciences. CRC Press, Boca Raton, Florida.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Tree 8: 275-279.

Skagen, S. K., D. A. Granfors and C. P. Melcher. 2008. On determining the significance of ephemeral continental wetlands to North American migratory shorebirds. Auk 125: 20-29.

Skagen, S. K. and F. L. Knopf. 1993. Toward conservation of midcontinental shorebird migrations. Conservation Biology 7: 533-541.

Sprague, A. J., D. J. Hamilton and A. W. Diamond. 2008. Site safety and food affect movements of semipalmated sandpipers (*Calidris pusilla*) migrating through the upper Bay of Fundy. Avian Conservation and Ecology 3(2):4. http://www.ace-eco.org/vol3/iss2/art4/.

Stafford, J. D., A. K. Janke, M. J. Anteau, A. T. Pearse, A. D. Fox, J. Elmberg, J. N. Straub, M. W. Eichholz and C. Arzel. 2014. Spring migration of waterfowl in the northern hemisphere: a conservation perspective. Wildfowl 4: 70-85.

Stafford, J. D., M. M. Horath, A. P. Yetter, C. S. Hine and S. P. Havera. 2007. Wetland use by mallards during spring and fall in the Illinois and Central Mississippi River Valleys. Waterbirds 30: 394-402.

Stewart, R. E. and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. In F. a. W. S. U.S. Department of the Interior (Ed.). Bureau of Sport Fisheries and Wildlife, Washington, D.C.

Taft, O. W., M. A. Colwell, C. R. Isola and R. J. Safran. 2002. Waterbird responses to experimental drawdown: implications for the multispecies management of wetland mosaics. Journal of Applied Ecology 39: 987-1001.

Tidwell, P. R., E. B. Webb, M. P. Vrtiska and A. A. Bishop. 2013. Diets and food selection of female Mallards and Blue-Winged Teal during spring migration. Journal of Fish and Wildlife Management 4: 63-74.

Tiner, R. W., Jr. 1984. Wetlands of the United States: current status and recent trends. U.S. Department of the Interior, Fish and Wildlife Service. 59 p.

Tozer, D. C., E. Nol and K. F. Abraham. 2010. Effects of local and landscape-scale habitat variables on abundance and reproductive success of wetland birds. Wetlands Ecology Management 18: 679-693.

U. S. Fish and Wildlife Service. 2009. National Wetlands Inventory website. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. http://www.fws.gov/wetlands/, accessed 15 September 2015.

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

Van der Valk, A. G. 2005. The prairie potholes of North America. Pages 393-423 *in* The world's largest wetlands: ecology and conservation (L. H. Fraser and P. A. Keddy, Eds.). Cambridge University Press, New York, NY, USA.

Van der Valk, A. G. and C. B. Davis. 1976. The seed banks of prairie glacial marshes. Canadian Journal of Botany 54: 1832-1838.

Van der Valk, A. G. and C. B. Davis. 1978. The role of seed banks in vegetation dynamics of prairie glacial marshes. Ecology 59: 322-335.

Van Meter, K. J. and N. B. Basu. 2015. Signatures of human impact: size distributions and spatial organization of wetlands in the Prairie Pothole landscape. Ecological Applications 25: 451-465.

Velasquez, C. R. 1992. Managing artificial saltpans as a waterbird habitat: species' responses to water level manipulation. Colonial Waterbirds 15: 43-55.

Voigts, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. American Midland Naturalist 95: 313-322.

Watson, D. M. 2003. The 'standardize search': an improved way to conduct bird surveys. Austral Ecology 28: 515-525.

Webb, E. B., L. M. Smith, M. P. Vrtiska and T. G. Lagrange. 2010. Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. Journal of Wildlife Management 74: 109-119.

Weber, L. M. and S. M. Haig. 1996. Shorebird use of South Carolina managed and natural coastal wetlands. Journal of Wildlife Management 60: 73-82.

Weller, M. W. and C. S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa Agriculture and Home Economics Experiment Station Report 43, Ames, Iowa.

Wilson, R. R., D. J. Twedt and A. B. Elliott. 2000. Comparison of line transects and point counts for monitoring spring migration in forested wetlands. Journal of Field Ornithology 71: 345-355.

Winter, T. C. 1989. Hydrologic studies of wetlands in the northern prairie. Pages 16-54 *in* Northern Prairie Wetlands (A. G. van der Valk, Ed.). Iowa State University Press, Ames, Iowa.

Zar, J. H. 2010. Biostatistical analysis, 5th ed. Pearson Prentice Hall, Upper Saddle River, New Jersey.

Zimmer, K. D., M. A. Hanson and M. G. Butler. 2002. Effects of fathead minnows and restoration on prairie wetland ecosystems. Freshwater Biology 47: 2071-2086.

Zuur, A. F., E. N. Ieno and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York.

Appendix 1. Names and counties of shallow lakes in the Iowa PPR surveyed for spring migrant waterbirds, 2016-2018 (restored lakes indicated by an asterisk). All properties are managed by the Iowa Department of Natural Resources ("WMA" represents wildlife management area). Locations and shapefiles of these properties can be found at https://geodata.iowa.gov/dataset/national-wetlands-inventory-iowa.

Name	County
Big Wall Lake WMA*	Wright
Burr Oak Lake WMA*	Emmet
D.U. Marsh*	Clay
Dan Green Slough WMA*	Clay
Diamond Lake WMA*	Dickinson
Elk Lake	Clay
Elm Lake WMA	Wright
Four Mile Lake*	Emmet
Garlock Slough WMA	Dickinson
Jemmerson Slough*	Dickinson
Jensen Slough	Emmet
Little Storm Lake*	Buena Vista
Little Swan Lake	Dickinson
Lizard Lake*	Pocahontas
Marble Lake*	Dickinson
McQuown's Slough*	Emmet
Meredith Marsh WMA*	Hancock
Morse Lake WMA	Wright
Pickerel Lake WMA*	Buena Vista
Pleasant Lake WMA	Dickinson
Prairie Lake WMA	Dickinson
Rice Lake WMA*	Winnebago and Worth
South Twin Lake WMA	Calhoun
Trumbull Lake*	Clay
Twelve Mile Lake WMA	Emmet
Ventura Marsh WMA*	Cerro Gordo and Hancock
Virgin Lake WMA*	Palo Alto
West Hottes Lake*	Dickinson
West Slough*	Emmet
West Swan Lake WMA	Emmet