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Predictions of future ephemeral springtime waterbird stopover habitat availability under global change

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Abstract. In the present period of rapid, worldwide change in climate and landuse (i.e., global change), successful biodiversity conservation warrants proactive management responses, especially for long-distance migratory species. However, the development and implementation of management strategies can be impeded by high levels of uncertainty and low levels of control over potentially impactful future events and their effects. Scenario planning and modeling are useful tools for expanding perspectives and informing decisions under these conditions. We coupled scenario planning and statistical modeling to explain and predict playa wetland inundation (i.e., presence/absence of water) and ponded area (i.e., extent of water) in the Rainwater Basin, an anthropogenically altered landscape that provides critical stopover habitat for migratory waterbirds. Inundation and ponded area models for total wetlands, those embedded in rowcrop fields, and those not embedded in rowcrop fields were trained and tested with wetland ponding data from 2004 and 2006–2009, and then used to make additional predictions under two alternative climate change scenarios for the year 2050, yielding a total of six predictive models and 18 prediction sets. Model performance ranged from moderate to good, with inundation models outperforming ponded area models, and models for non-rowcrop-embedded wetlands outperforming models for total wetlands and rowcrop-embedded wetlands. Model predictions indicate that if the temperature and precipitation changes assumed under our climate change scenarios occur, wetland stopover habitat availability in the Rainwater Basin could decrease in the future. The results of this and similar studies could be aggregated to increase knowledge about the potential spatial and temporal distributions of future stopover habitat along migration corridors, and to develop and prioritize multi-scale management actions aimed at mitigating the detrimental effects of global change on migratory waterbird populations.

Key words: Central Flyway; climate change; landuse change; mixed models; playa wetlands; ponding; Rainwater Basin; scenarios; shorebirds; stopover habitat; waterfowl.

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INTRODUCTION

Global-scale changes in climate and landuse (i.e., global change) stress ecosystems through processes such as habitat destruction, degradation and fragmentation; biological invasions; and long-term changes in average temperature and precipitation (Millennium Ecosystem Assessment [MEA] 2005, Melillo et al. 2014). The consequences of change for wildlife may be greatest in landscapes that have already experienced substantial human modification (e.g., agricultural landscapes). Successfully conserving biodiversity, in spite of these large-scale challenges, warrants proactive management responses at multiple scales; however, the development and implementation of management strategies can be impeded by high levels of uncertainty and low levels of control over potentially impactful future events. Scenario planning is a useful tool for expanding perspectives and informing decisions under these conditions, as it allows for the consideration of multiple, alternative, plausible futures, instead of just one expected future, that in reality, will probably not occur (Peterson et al. 2003, Chermack 2004, Carpenter et al. 2005). The practice of adaptive management is also commonly used to address management uncertainties (Allen et al. 2011); however, it is less effective when managers have limited control over the phenomena at hand (e.g., global change; Cumming and Peterson 2005).

An excellent example of wildlife management under uncertainty, intensive landscape modification, and unfolding climatic change is provided in North American waterbird populations, many of which undertake semi-annual, cross-continental migrations between northern breeding grounds and southern wintering grounds (Bellrose 1980, Newton 2008). Despite potential advantages (e.g., better resources and/or environmental conditions), long-distance migration is energetically expensive and dangerous, and tradeoffs between its benefits and costs influence survival and reproductive success (Lind and Cresswell 2006, Newton 2006). Rapidly changing climatic conditions and landscape alterations introduce additional stressors that complicate the phenology of long-distance migration (Moller et al. 2008, Fontaine et al. 2009). Although quality breeding and wintering habitats are

critical (Robbins et al. 1989), waterbirds also rely on wetland stopover habitat along migratory routes, especially during spring migration, to replenish energy reserves and improve body condition prior to arriving at breeding sites (LaGrange and Dinsmore 1988, Moore et al. 2005, Webb et al. 2010). Several studies have documented positive relationships between nutrient reserves acquired in stopover areas and annual recruitment (Alisauskas 2002, Klaassen et al. 2006, Devries et al. 2008); therefore, active conservation of remnant and restored stopover habitats is critical for maintaining viability in North American migratory waterbird populations, now and in the future.

The ephemeral nature of wetlands (i.e., tendency to alternate between wet and dry) makes stopover habitat availability variable among years and locations (Euliss et al. 2004, Johnson et al. 2004). Historically, the effects of fluctuating habitat area on waterbird populations were at least partially smoothed by high densities of wetlands with continually shifting habitat types (e.g., transitions between relatively deep water, shallow water, and exposed mudflat; Gibbs 2000, Euliss et al. 2004). In many landscapes, this relatively consistent provisioning of heterogeneous habitat decreased markedly as wetlands were drained and degraded for urban development, and agricultural conversion and intensification (Zedler and Kercher 2005, Smith et al. 2011, Anteau 2012). Climate change could further exacerbate landuse change-imposed habitat deficiencies (Johnson et al. 2005, Mitsch and Hernandez 2013). Although the direction, location and timing of climatic changes are largely uncertain (Hawkins and Sutton 2011, Deser et al. 2012, Trenberth et al. 2014), uncertainty should not preclude proactive management.

Addressing management-impeding uncertainties related to future wetland stopover habitat availability in altered landscapes calls for the consideration of wetland ponding processes under alternative levels of climate and landuse change. In other words, landscape-specific knowledge of the factors that were influential in driving wetland ponding prior to human modification and climate change, after human modification but before substantial climate change, and under the present circumstances of coupled landuse and climate change, could lead to a fuller

understanding of wetland ponding and waterbird habitat availability under future global change. Although data limitations preclude modeling wetland ponding before large-scale anthropogenic landuse changes in many locations, there is a wealth of more recent information that could be used to better understand contemporary and future ponding under different degrees of landscape alteration. Beneath the umbrella of scenario planning, statistical models of wetland ponding could be used to understand and predict the consequences of putative changes in annual weather events and trends (e.g., mean maximum winter temperature increases) for future waterbird habitat availability. Furthermore, comparing wetland ponding predictions from alternative, plausible scenarios of future change, at different positions along major waterbird migratory paths, could yield a range of future habitat availability possibilities for use in the development of multi-scale management objectives and strategies.

An illustration of how uncertainties over future waterbird stopover habitat availability could be addressed is presented in the North American Central Flyway migration corridor. Identifying and quantifying the factors influencing local- and landscape-scale wetland ponding has been a subject of active research throughout the flyway (e.g., Larson 1995, Sorenson et al. 1998, Johnson et al. 2004, 2005, 2011, Voldseth et al. 2009, Bartzen et al. 2010, Wilson 2010, Cariveau et al. 2011, Liu and Schwartz 2011, 2012, Bartuszevige et al. 2012, Collins et al. 2014). In addition to informing current wetland and waterbird management, aggregating the findings of these and related studies could provide insights into how waterbird habitat availability and its drivers vary spatially and temporally within the flyway, and when coupled with projections of climate and landuse change, could be used to make predictions about future, continental-scale stopover habitat availability. This information is highly relevant to waterbird management in North America, given the potentially dire consequences of global change for waterbird populations and the limited monetary resources available for accomplishing conservation objectives, such as those outlined in the North American Waterfowl Management Plan (U.S. Fish and Wildlife Service 2014). Although

ponding studies have been completed for several important stopover locations along the Central Flyway, information from other critical sites is missing.

In this study, we address knowledge gaps related to the drivers of playa wetland ponding in the Rainwater Basin, an intensively cultivated landscape within the Central Flyway that provides critical waterbird stopover habitat, but for which predictive ponding models have not yet been developed. Our objectives were threefold: (1) develop and validate predictive models of Rainwater Basin wetland inundation (i.e., presence/absence of water) and ponded area (i.e., extent of water) at peak spring waterbird migration; (2) construct scenarios of future climate change in the Rainwater Basin for the year 2050; and (3) predict wetland stopover habitat availability in the Rainwater Basin in the year 2050 under scenarios of future climate change. Results from this and similar studies could be collectively used to inform continental-scale wetland and waterbird management aimed at mitigating the detrimental effects of global change on North American migratory waterbird populations.

METHODS

Study area

This study was conducted within the Rainwater Basin, a region that covers 15,800 km² in all, or portions of, 21 counties in south-central Nebraska, USA (Fig. 1; LaGrange 2005). This intensively farmed landscape is dominated by corn (*Zea mays*) and soybean (*Glycine max*) production, and water for irrigation is obtained from surface and groundwater sources (Dunnigan et al. 2011). Soil surveys from the early 20th century document the existence of as many as 1,000 major and 10,000 minor shallow, precipitation-fed playa wetlands at the time of European resettlement, less than 10% of which remain today (Gersib 1991, Bishop and Vrtiska 2008). Playa wetlands are depressional recharge wetlands that only receive water from precipitation and runoff (Smith 2003, LaGrange et al. 2011, Smith et al. 2011). Technological advances and agricultural intensification during the 20th century resulted in wetland loss and degradation via draining, development, culturally accelerated

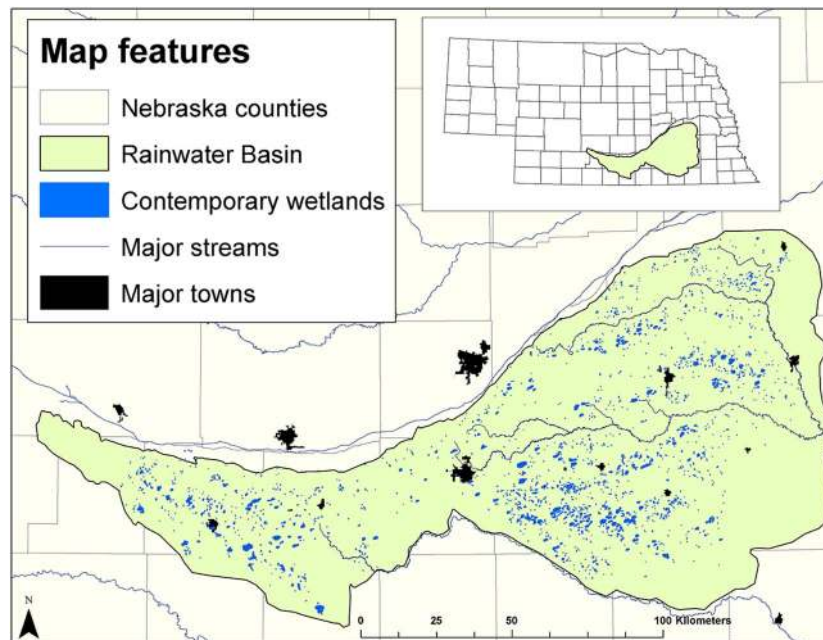


Fig. 1. Location and features of the Rainwater Basin in south-central Nebraska, USA.

sediment accumulation, and conversion to agriculture (Gersib et al. 1989, LaGrange et al. 2011). Remaining wetland habitats are highly dynamic, and the degree of ponding varies within and among years.

Wetlands are commonly classified as semi-permanent, seasonal or temporary, according to hydric soil series, water retention, and plant community composition (Gersib et al. 1989, Gilbert 1989). Semi-permanent wetlands are the largest, are inundated for the longest time periods, and provide waterfowl roosting and loafing areas, whereas the smaller seasonal and temporary wetlands are generally inundated for shorter durations and offer ideal foraging conditions for dabbling ducks (Gersib et al. 1989, Bishop and Vrtiska 2008). During wetter periods, seasonal and temporary wetlands provide reliable habitat and foraging resources for migrants, whereas only semi-permanent wetlands are dependable during drier times.

Rainwater Basin wetlands serve as an important stopover location for migratory waterbirds traveling along a narrow stretch of the Central Flyway. It is estimated that 7–14 million waterfowl, including 90% of continental white-fronted geese (*Anser albifrons*), 50% of mid-continental

mallards (*Anas platyrhynchos*), 30% of continental northern pintails (*Anas acuta*), and various shorebird species (Gersib et al. 1989, Farmer and Parent 1999, LaGrange 2005, Rainwater Basin Joint Venture [RWB JV] 2013) utilize these wetlands as staging sites during spring and fall migrations. Flooded wetlands provide birds an opportunity to rest, court, and increase lipid reserves by feeding on invertebrates, wetland vegetation, moist-soil vegetation seeds, and corn, which can be found in farmed-through wetlands and adjacent rowcrop fields (Tidwell et al. 2013).

Numerous hydrologic, geomorphic, and weather-related factors influence the magnitude, frequency and duration of playa wetland ponding, including precipitation, runoff, evapotranspiration, infiltration, soil type, and surrounding landuse (Cariveau et al. 2011, Johnson et al. 2011, Smith et al. 2011, Bartuszevige et al. 2012, Collins et al. 2014). However, the ways in which these drivers interact with one another and other factors, in addition to how they may change in the future, are not fully understood. Playa wetlands are typically inundated by runoff or snowmelt following major precipitation events (Cariveau et al. 2011, Smith et al. 2011), and retention of accumulated water is facilitated by

clay-based hydric soils which, when wet, form a seal that slows infiltration of water into soils (Starks 1984, Gersib et al. 1989, Wilson 2010). Rainwater Basin playa wetlands differ from wetlands within other regions of the Central Flyway (e.g., the Prairie Potholes, as studied by Larson 1995, Sorenson et al. 1998, Johnson et al. 2004, 2005, Voldseth et al. 2007, 2009, Liu and Schwartz 2011, 2012, Werner et al. 2013), in that they are closed basins that do not receive inflows from springs or groundwater (Smith 2003). During extended dry periods, desiccation cracks may form in the playa wetland clay pan (Bagarello et al. 1999, Smith 2003, Gurdak and Roe 2009, Wilson 2010), inducing rapid infiltration and limiting inundation, even when major precipitation events occur (Gurdak and Roe 2009, Wilson 2010). Air temperature, humidity and plant growth also indirectly influence ponding through their regulation of evapotranspiration rates (Wilson 2010).

Data sources

Annual Habitat Survey (AHS) wetland ponding data from 2004 and 2006–2009 was provided by the Rainwater Basin Joint Venture (RWBJV). The AHS data quantifies the extent of wetland ponding during peak spring bird migration in late February or early March using an image-object classification method of high-resolution (0.61 m) color-infrared aerial photography (Bishop 2010). The RWBJV also provided hydric soil footprints and rowcrop irrigation type data. Weather data from 2003–2009 were downloaded from the Yellowstone Ecological Research Center's Customized Online Aggregation and Summarization Tool for Environmental Rasters (COASTER) website (Weiss et al. 2012). Data pertaining to the artificial flooding of wetlands with groundwater wells was provided by a number of regional wetland managers. Downscaled climate change projection data for the Great Plains in the mid-21st century was obtained from Groisman et al. (2012), High Plains Regional Climate Center (HPRCC; 2013), Bathke et al. (2014), and Shafer et al. (2014).

Surrounding landcover

Landscape context is an important driver of wetland ponding. Most Rainwater Basin wetlands are located within rowcrop fields, but

others are not. Rowcrop production can decrease wetland area and water retention capability by increasing culturally accelerated sedimentation rates over those that would exist in grasslands and other natural habitats (Skagen et al. 2008, Johnson et al. 2011, LaGrange et al. 2011, Smith et al. 2011, Collins et al. 2014); however, extremely dense, ungrazed grass stands can inhibit runoff into wetlands (Cariveau et al. 2011, Bartuszevige et al. 2012). Wetlands embedded in rowcrop fields tend to have more variable water levels than those in natural environments (Voldseth et al. 2007, 2009), although these influences may differ among wetland and grassland types (Bartzen et al. 2010, Anteau 2012, Collins et al. 2014).

Non-rowcrop wetlands are primarily embedded in restored grasslands that mimic the original tallgrass and mixedgrass prairies of the region. On older, state owned Wildlife Management Areas, federally owned Waterfowl Production Areas, and NRCS Wetland Reserve Program (WRP, now WRE) tracts, the uplands, which were predominantly under rowcrop agriculture prior to acquisition, have been re-seeded to low diversity mixes of native, warm-season grass and forb species (e.g., big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), upright prairie coneflower (*Ratibida columnifera*), and Maximilian sunflower (*Helianthus maximiliani*)). More recent wetland acquisitions have had the uplands surrounding them reseeded to high diversity, local ecotype, prairie mixtures consisting of upwards of 100 species of native grasses and forbs. Non-rowcrop wetlands on private property other than WRP tracts primarily exist in remnant grasslands and pastures, which are often overgrazed by cattle (*Bos taurus*). Cool season grasses and forbs (e.g., smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), snow-on-the-mountain (*Euphorbia marginata*) and ironweed (*Vernonia fasciculata*)) dominate the upland vegetative community on these sites. Therefore, although by no means isolated from anthropogenic influences, ponding in wetlands not embedded in rowcrop fields is hypothesized to better approximate historical ponding than ponding in rowcrop-embedded wetlands.

All non-rowcrop properties containing wetlands were grouped and designated as such, and

rowcrop fields containing wetlands were grouped and classified according to the following rowcrop irrigation system types: center-pivots, gravity, or none (i.e., dryland). Approximately 35% of wetlands were embedded in non-rowcrop surroundings, ~36% in pivot-irrigated fields, ~15% in gravity-irrigated fields, and ~14% in dryland fields. Gravity irrigation systems are generally associated with landscape alterations like wetland draining, land leveling, and irrigation reuse pit excavation. It is likely that these alterations negatively affect hydroperiods within watersheds by diverting or catching precipitation runoff that might otherwise fill wetlands.

Weather data (2003–2009)

Seasonal groupings.—Weather data from 2003–2009 was divided into four annual time periods (i.e., seasons) representing proximate shifts in weather patterns: April 1–June 30 (i.e., spring), July 1–September 30 (i.e., summer), October 1–November 30 (i.e., autumn) and December 1–March 31 (i.e., winter). In the Rainwater Basin, winter snowmelt—which is hypothesized to be a major contributor to springtime wetland ponding—occurs throughout late winter and early spring. Because the AHS aims to capture information on wetland ponding at peak spring bird migration, the date of the survey varies among years. To help ensure that the effect of snowmelt on wetland ponding at peak migration was captured in the data, the winter season was extended through March 31st, which is similar to the May–April definition of the year used by Larson (1995) when studying the drivers of wetland ponding in the Prairie Potholes Region, north of the Rainwater Basin.

Precipitation.—Both total precipitation and the number of days with major precipitation events were used to assess the influence of seasonal precipitation on wetland inundation the following spring. Major precipitation event days were represented by the number of 24-hour periods in which precipitation met or exceeded season-specific threshold values recognized as generally necessary for generating rain or snow-melt runoff. Threshold values were ~51 mm for spring and summer, and ~25 mm for autumn and winter. These thresholds were based on extensive experience of the authors observing wetland ponding in the Rainwater Basin follow-

ing precipitation events, and the 51 mm threshold is similar to the precipitation quantities that Wilson (2010) observed inundating a Rainwater Basin wetland. In addition, Groisman et al. (2012) defined heavy precipitation events as days with ~26–76 mm of precipitation. Finally, our thresholds are comparable to those for rowcrop agriculture from the precipitation runoff model developed by the U. S. Department of Agriculture, Soil Conservation Service (USDA NRCS) (1972), which calculates runoff according to rainfall amount, soil type, and land use. The mean water retention potentials for soils with moderate, slow, and very slow infiltration rates (i.e., hydrologic soil groups B, C and D) in straight-row rowcrop fields is ~49 mm, and the mean retention potential for the same three soil classes in straight-row rowcrop fields with crop residue cover is ~62 mm (USDA NRCS 1999). Although the mean value for the same three soil classes in fair-condition grassland (~77 mm) is greater than our thresholds, ~65% of the Rainwater Basin wetlands considered in the study are embedded in rowcrop fields, and those that are not likely still receive runoff from rowcrop fields. Therefore, we posit that our ~51 mm and ~25 mm thresholds are reasonable indicators of major precipitation events. The format of the downloaded precipitation data did not allow for differentiation between snowfall and rain, so it is unclear which of these precipitation forms is represented in the winter and spring data.

Temperature.—Temperature can affect evapotranspiration during the growing season and evaporation and formation of frost layers in winter. Mean minimum and maximum temperature data for all seasons and the number of winter days when the maximum temperature was <0 degrees Celsius (°C) were used to represent temperature effects on ponding.

Wetland shape complexity

Wetland shape-complexity may influence the amount of water lost to evaporation because wetlands with a more complex shape generally have a greater proportion of the water's surface area exposed to air (Wilson 2010). We calculated the perimeter-to-area ratio of wetland hydric soil footprints and used it as a measure of shape complexity.

Wetland pumping

To increase stopover habitat availability in drier years, wetland managers often artificially inundate wetlands with autumn and/or spring groundwater pumping (Bishop 2010). To prevent pumping from introducing bias into the analyses, inundation and ponded area records for wetlands where pumping had been conducted during the preceding autumn or corresponding spring were excluded.

Data manipulation

Data aggregation and manipulation was conducted in the programs Microsoft Excel (Microsoft, Redmond, Washington, USA), ArcGIS (ESRI, Redlands, California, USA) and R (R Core Team 2015). Predictor variable values were extracted to the centroids of individual wetland hydric soil footprints. Nominal predictor variables treated as factors consisted of individual wetland identifier (ID), year, wetland type (i.e., semi-permanent, seasonal and temporary), and surrounding landuse (i.e., non-rowcrop, center-pivot irrigated, gravity-irrigated and dryland) (Appendix: Table A1). To reduce bias from extreme observations, non-factor predictor variables with outlying values were log-transformed. The response variable ponded wetland area (i.e., m² of water) was also log-transformed, so that it better approximated a normal distribution. Following transformations, all non-categorical predictor variables were standardized (i.e., centered and scaled) to facilitate model convergence and the direct comparison of model parameter coefficient estimates (Zuur et al. 2009). Thus, some predictors were log-transformed and standardized, while others were only standardized. Standardization was accomplished with the function

$$\frac{x_i - \bar{x}}{\sigma}$$

where x_i is the i th value of variable x , \bar{x} is the mean of x , and σ is the standard deviation of x .

After standardizations, correlations among predictor variables were examined visually with pairplots (Zuur et al. 2007, 2009) and numerically with Pearson's correlation coefficient (Pearson 1895). When two predictors had a correlation with absolute value >0.5, only one of them—usually the one most strongly correlated with the

response—was retained. In these ways, response and predictor variables were selected and prepared for analysis. A list of all response and predictor variables considered is provided in Appendix: Table A1.

Model development

Our objectives of explaining and predicting wetland inundation (i.e., presence/absence of water) and ponded area (i.e., extent of water) under varying intensities of climate and landuse change led to the development of six datasets and models for the years 2004 and 2006–2009: (1) inundation of all (i.e., total) wetlands; (2) ponded area in all inundated wetlands; (3) inundation of all wetlands embedded in rowcrop fields; (4) ponded area in all inundated wetlands embedded in rowcrop fields; (5) inundation of all wetlands not embedded in rowcrop fields; and (6) ponded area in all inundated wetlands not embedded in rowcrop fields. The two datasets and models for rowcrop-embedded wetlands were used to assess inundation and ponded area in wetlands where the effects of landuse change were expected to be greatest, whereas the two datasets and models for non-rowcrop-embedded wetlands were used to assess inundation and ponded area in wetlands where the effects of landuse change were expected to be least. Although non-rowcrop-embedded wetlands are certainly not exempt from the influences of rowcrop production and other landuse change effects, we used them as proxies for region-specific wetland ponding under reduced anthropogenic influence. In addition to the explanation and prediction of wetland inundation and ponded area in 2004 and 2006–2009, the six models were used to make predictions about wetland inundation and ponded area in the year 2050 under two plausible scenarios of regional climate change—yielding 18 total sets of predictions (i.e., nine inundation and nine ponded area). Of the nine sets of predictions for each of the two responses, three pertained to observed weather events in 2004 and 2006–2009, three pertained to modest projections of climate change for the year 2050, and three pertained to extreme projections of climate change for the year 2050 (Fig. 2).

To ensure that non-inundation (i.e., water absence) records in datasets did not bias ponded

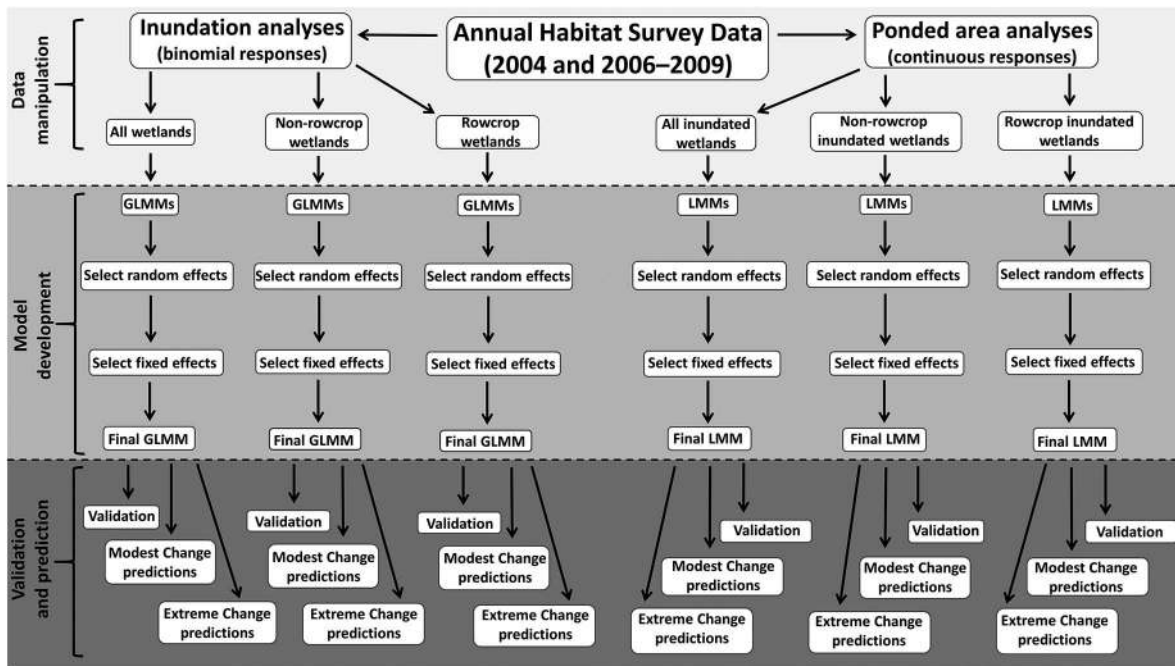


Fig. 2. Three-stage framework used to model wetland inundation and ponded area in the Rainwater Basin in 2004 and 2006–2009, as well as in 2050 under Modest and Extreme Change Scenarios. In the data manipulation stage, Annual Habitat Survey data was split into binomial inundation and continuous ponded area responses and datasets, each of which were subdivided into datasets for total, rowcrop-embedded and non-rowcrop-embedded wetlands. In the model development stage, generalized linear mixed models and linear mixed models were used to model the binomial and continuous responses, respectively. The best-supported random and fixed effects structure was combined into a final model for each response. Finally, in the validation and prediction stage, each of the final six models was cross-validated and used to make predictions under Modest and Extreme Change Scenarios in the year 2050.

area model estimates, we employed a customized version of the two-step process described by Welsh et al. (1996), Barry and Welsh (2002), and Zuur et al. (2009) when developing each model pair (i.e., inundation and ponded area). In the first step of this process, a single generalized linear mixed model (GLMM) was developed to identify and quantify drivers of the binomial inundation response at hand. In the second step, absence records (i.e., ponded area = 0 m²) were removed from the dataset and a single linear mixed model (LMM) was developed to identify and quantify drivers of the continuous ponded area response in remaining inundated wetlands (i.e., those with ponded area > 0 m²). In effect, we used the two-step process to consider the factors driving wetland inundation, and given that wetlands were inundated, the factors driving the extent of ponding within them (Fig. 2).

GLMMs and LMMs are subsets of mixed effects models, which contain both fixed effects and random effects structures, and as such, are well-suited for analyzing hierarchical (i.e., nested) data (Zuur et al. 2007, 2009, Bolker et al. 2008). Fixed effects structures are comprised of specific predictor variables about which inferences are to be made, whereas random effects structures consist of predictor variables about which inferences are not to be made, but by which the model intercept and/or fixed effect variable parameter estimates may vary (i.e., receive individual estimates). Random effects can help explain additional variation in hierarchically organized datasets, conserve degrees of freedom that would otherwise be used to generate coefficient estimates for individual levels of random effects, and account for spatial autocorrelation between observations. In the case

of our dataset, repeated inundation and ponded area observations for individual wetlands are nested within study years. Yet, it is not the effects of specific years or wetlands on wetland inundation and ponded area that are of interest, but rather the effects of seasonal weather events, landuse practices, and general wetland characteristics. Therefore, we considered wetland identifier (ID) and year as random effects, and all other predictors as fixed effects. All mixed models were formulated in the lme4 Package for R (Bates et al. 2014).

Within the two-step process described above—in order to specify appropriate fixed and random effects structures in each of the final six models—we employed a customized version of the top-down process described by Fitzmaurice et al. (2004) and Zuur et al. (2009). This method entails: (1) identification of the best-supported random effects structure via the comparison of alternative models with the same global fixed effects structure, but different random effects structures; (2) identification of the best-supported fixed effects structure via comparison of alternative models with the same, previously identified, best-supported random effects structure, but different fixed effects structures; and (3) combination of the best-supported random and fixed effects structures into a final explanatory/predictive model.

In step 1 of the top-down process, for each of the six datasets, we compared three alternative models with the same global fixed effects structure, but different random effects structures, for explaining variation in the response. The three random effects structures, by which the parameter estimate for each model intercept was permitted to vary, were: (1) wetland ID; (2) year; and (3) wetland ID and year. Competing models were ranked with Akaike's information criterion, corrected for small sample size (AIC_c) scores and weights (Burnham and Anderson 2004), and only the model with the best-supported random effects structure was retained. In step 2, backwards selection was used to iteratively remove individual predictor variables from the fixed effects structure of the retained model. At each iteration, the variable whose removal yielded the greatest improvement (i.e., decrease) in AIC_c was eliminated, until eliminations no longer resulted in a better AIC_c score. Therefore, the resulting

final model for each of the three inundation and ponded area responses contained the random and fixed effects structures best-supported by their respective datasets (Fig. 2). Backwards selection was carried out with the drop1 function in the stats package for R (R Core Team 2015).

For training wetland inundation models, there were 7,358 observations in the total wetlands dataset, 4,818 observations in the rowcrop-embedded wetlands dataset, and 2,540 observations in the non-rowcrop-embedded wetlands dataset. The logit link function was used to model each binomially distributed inundation response as a continuous probability between 0 and 1 (Zuur et al. 2007). For training the corresponding ponded area models, there were 4,420 observations in the total wetlands dataset, 2,713 observations in the rowcrop-embedded wetlands dataset, and 1,707 observations in the non-rowcrop-embedded wetlands dataset. For each of the six models, plots of model residual and predictor variable values were used to visually detect major violations of linear model assumptions, none of which were evident after variable transformations, standardizations, and random effect incorporations.

Marginal and conditional pseudo R^2 values were used to estimate the proportion of variation that each of the six best-supported models explained in their respective response variables and datasets. Marginal pseudo R^2 values approximated the proportion of variation explained by fixed effects alone, whereas conditional pseudo R^2 values approximated the proportion of variation explained by fixed and random effects together. This distinction between the proportion of variation explained by fixed effects alone versus combined fixed and random effects highlights a key difference in using models for prediction versus explanation. Because the extrapolation of model predictions in space and/or time can preclude the estimation of individual random effect predictor variable coefficient estimates (e.g., the effect of the future year 2050)—although not estimates for the effects of entire random effects populations (e.g., years in general)—fixed effects alone are often used for prediction extrapolation. All R^2 values were calculated with the r.squaredGLMM function in the MuMIn package for the program R (Barton 2015), which draws calculations from Nakagawa

and Schielzeth (2013) and Johnson (2014).

Model validation

In addition to pseudo R^2 values, we used 10-fold cross-validation to independently assess the predictive performance of each of the six best-supported models. This method evaluates predictive error in models by randomly subsetting data into training (90%) and testing (10%) sets, refitting the best-supported model at hand with the training data, making predictions with the testing data, comparing predictions for the testing data with its known values, replacing observations, and repeating the process nine more times (Kohavi 1995, Fushiki 2011). For each of the three best-supported inundation models, a receiver operating characteristic (ROC) plot and the area under the curve (AUC) statistic, which are threshold independent, were used to determine the ability of the model to assign higher inundation probabilities to wetlands from the testing sets that were actually inundated (Fielding and Bell 1997, McPherson and Jetz 2007). In addition, the maximum Kappa statistic (Cohen 1960, Manel et al. 2001) was used to identify the optimal threshold value for classifying wetlands as inundated or non-inundated, according to model-generated continuous inundation probabilities. For each of the three best-supported ponded area models, the Pearson correlation coefficient (PCC; Pearson 1895) was used to determine the degree of similarity between ponded area predictions and their corresponding observed values.

Scenarios of future change

For scenarios of climate change in the year 2050, we assumed changes in weather-related predictor variables consistent with HPRCC (2013), Kunkel et al. (2013), Bathke et al. (2014), and Shafer et al. (2014), which report downscaled general circulation model projections for the Great Plains in the mid-21st century, according to the Special Report on Emissions Scenarios (SRES) developed by the Intergovernmental Panel on Climate Change (IPCC 2007). In general, changes in total mean annual precipitation are uncertain; however, a greater proportion of precipitation is expected to arrive in major precipitation events, especially during winter and spring. Meanwhile, seasonal mean temper-

atures are projected to increase substantially. Considering a range of plausible climatic changes—instead of mid-range projections alone—can help account for inherent uncertainty in climate change studies (Wuebbles and Hayhoe 2004). Indeed, in previous wetland ponding studies for Great Plains landscapes, Poiani and Johnson (1991), Larson (1995), Sorenson et al. (1998), Johnson et al. (2005), Voldseth et al. (2009), Smith et al. (2011), and Werner et al. (2013) considered climate change scenarios within the range of +2–6°C temperature change and $\pm 20\%$ precipitation.

We used downscaled projections of temperature and precipitation change in the Great Plains to develop two alternative, plausible, climate change-based scenarios for the Rainwater Basin in the year 2050 (Table 1). In a Modest Change Scenario, we assumed an increase of 20% in the number of spring days with major precipitation events, no change in total summer precipitation, an increase of 2°C in mean maximum daily temperature in autumn, an increase of 10% in total winter precipitation, an increase of 3°C in mean maximum daily temperature in winter, and a decrease of 10% in the number of winter days with maximum temperatures $<0^\circ\text{C}$. In an Extreme Change Scenario, we assumed an increase of 40% in the number of spring days with major precipitation events, a decrease of 20% in mean total summer precipitation, an increase of 4°C in mean maximum daily temperature in autumn, an increase of 30% in total winter precipitation, an increase of 5°C in mean maximum daily temperature in winter, and a decrease of 20% in the number of winter days with maximum temperatures $<0^\circ\text{C}$. These changes were applied to predictions of wetland inundation and ponded area in total, rowcrop-embedded and non-rowcrop-embedded wetlands via the six final predictive models, yielding 12 sets of predictions under assumed future climatic changes.

RESULTS

Inundation models

Within the final inundation models for total, rowcrop-embedded and non-rowcrop-embedded wetlands, the best-supported random effects structures allowed the coefficient estimate for model intercepts to vary among wetlands (Appendix: Tables A2–A4). With the exception of

Table 1. Assumed changes in pertinent weather variables under the Modest Change and Extreme Change Scenarios for the Rainwater Basin region of Nebraska for the year 2050.

Predictor variable	Modest	Extreme
Number of spring days precipitation > 50 mm	+20%	+40%
Total summer precipitation	+0%	-20%
Mean autumn maximum temperature	+2°C	+4°C
Total winter precipitation	+10%	+30%
Mean winter maximum temperature	+3°C	+5°C
Number of winter days maximum temperature < 0°C	-10%	-20%

Note: Scenario development was informed by High Plains Regional Climate Center (HPRCC; 2013), Kunkel et al. (2013), Bathke et al. (2014) and Shafer et al. (2014).

surrounding landcover—which was limited to cropland in the rowcrop-embedded model and was not considered in the non-rowcrop-embedded wetlands inundation model—the predictor variables present in the finalized fixed effects structures of all three inundation models were identical, as were the direction of their effects (Tables 2–4). All three models indicated that semi-permanent wetlands were the wetland type most-likely to be inundated, although this effect was not significantly greater than seasonal wetlands in the rowcrop-embedded or non-rowcrop-embedded models. Seasonal wetlands were more likely to be inundated than temporary wetlands in all three models. Also, each of the three models showed the likelihood of wetland inundation to: decrease with more complex hydric footprint shapes; increase with more total precipitation in the previous summer; decrease with warmer mean maximum daily temperatures

in the previous autumn; increase with more total precipitation in the previous winter; and decrease with warmer mean maximum daily temperatures in the previous winter.

The effects of surrounding landcover on inundation likelihood were only incorporated into the total wetlands and rowcrop-embedded wetlands inundation models. The total wetlands model showed inundation to be most likely in gravity-irrigated rowcrop fields, although this effect was not significantly greater than the likelihood of inundation in non-rowcrop surroundings, the landcover class with the next greatest inundation likelihood (Table 2). Following non-rowcrop surroundings, the total wetlands model showed wetlands embedded in pivot-irrigated fields as more likely to be inundated than those in dryland fields. In the rowcrop-embedded wetlands inundation model, wetlands in gravity-irrigated fields were more

Table 2. Predictor variable coefficient, standard error, and 95% confidence interval estimates for the best-supported generalized linear mixed model for predicting inundation (i.e., presence/absence of water) in total Rainwater Basin wetlands at peak spring bird migration.

Parameter	Estimate ± SE	95% CI	
		Lower	Upper
Intercept	2.06566* ± 0.16592	1.74045	2.39088
Semi-permanent	0.76577* ± 0.34450	0.09056	1.44098
Temporary	-1.42203* ± 0.16991	-1.75507	-1.08900
Pivots	-0.38474* ± 0.16824	-0.71450	-0.05498
Dryland	-0.69119* ± 0.21791	-1.11829	-0.26409
Gravity	0.04405 ± 0.21944	-0.38605	0.47415
Perimeter-to-area ratio†‡	-1.32091* ± 0.08848	-1.49433	-1.14750
Total summer precipitation†‡	0.45222* ± 0.04828	0.35759	0.54685
Mean autumn maximum temperature†	-0.70633* ± 0.04554	-0.79558	-0.61707
Total winter precipitation†‡	0.43724* ± 0.04000	0.35885	0.51564
Mean winter maximum temperature†	-0.95336* ± 0.04673	-1.04495	-0.86178

Notes: Non-categorical variables were log-transformed and/or standardized (i.e., centered and scaled). Log transformations were conducted before standardizations.

* $P < 0.05$, based on the 95% confidence interval not containing 0.

† Log-transformed.

‡ Standardized.

Table 3. Predictor variable coefficient, standard error, and 95% confidence interval estimates for the best-supported generalized linear mixed model for predicting inundation (i.e., presence/absence of water) in rowcrop-embedded Rainwater Basin wetlands at peak spring bird migration.

Parameter	Estimate \pm SE	95% CI	
		Lower	Upper
Intercept	1.82601* \pm 0.20741	1.41949	2.23254
Semi-permanent	0.78335 \pm 0.57172	-0.33723	1.90392
Temporary	-1.73349* \pm 0.21601	-2.15688	-1.31011
Dryland	-0.33092 \pm 0.20889	-0.74035	0.07850
Gravity	0.45676* \pm 0.21218	0.04088	0.87263
Perimeter-to-area ratio $\dagger\dagger$	-1.07370* \pm 0.09555	-1.26098	-0.88641
Total summer precipitation $\dagger\dagger$	0.45429* \pm 0.05994	0.33680	0.57178
Mean autumn maximum temperature \dagger	-0.75777* \pm 0.05665	-0.86881	-0.64673
Total winter precipitation $\dagger\dagger$	0.56492* \pm 0.04962	0.46766	0.66218
Mean winter maximum temperature \dagger	-0.98802* \pm 0.05818	-1.10205	-0.87398

Notes: Non-categorical variables were log-transformed and/or standardized (i.e., centered and scaled). Log transformations were conducted before standardizations. Symbols are as in Table 2.

likely to be inundated than those in pivot-irrigated fields, and wetlands in dryland fields were less likely to be inundated than those in pivot-irrigated fields, although this difference was not significant (Table 3).

The total wetlands inundation model yielded a pseudo R^2 value of 0.42 when only fixed effects were used to explain variation in inundation (i.e., marginal R^2) and a pseudo R^2 value of 0.75 when both fixed and random effects were used to explain variation in inundation (i.e., conditional R^2). The rowcrop-embedded wetlands inundation model yielded marginal and conditional pseudo R^2 values of 0.38 and 0.74, respectively, and the non-rowcrop-embedded wetlands inundation model yielded values of 0.46 and 0.78, respectively (Table 5). This means when fixed effects alone are considered, the models explained 42%, 38% and 46% of the total variation

in inundation in their respective datasets, and that the addition of random effects explained 33%, 36% and 32% more of the variation.

Inundation model validations.—During 10-fold cross-validation, the inundation model for total wetlands yielded an AUC score of 0.79, the inundation model for rowcrop-embedded wetlands yielded an AUC score of 0.78, and the inundation model for non-rowcrop-embedded wetlands yielded an AUC score of 0.82 (Fig. 3). This means that given a randomly selected pair of wetlands, one of which was inundated and the other that was not, the fixed effects structures of the models would assign higher inundation probabilities to the wetland that was actually inundated 79%, 78% and 82% of the time, respectively. Thus, although the model for non-rowcrop-embedded wetlands was the most successful, all three models exhibited good

Table 4. Predictor variable coefficient, standard error, and 95% confidence interval estimates for the best-supported generalized linear mixed model for predicting inundation (i.e., presence/absence of water) in non-rowcrop-embedded Rainwater Basin wetlands at peak spring bird migration.

Parameter	Estimate \pm SE	95% CI	
		Lower	Upper
Intercept	1.96446* \pm 0.21653	1.54007	2.38886
Semi-permanent	0.71939 \pm 0.45357	-0.16961	1.60839
Temporary	-0.87143* \pm 0.28312	-1.42634	-0.31652
Perimeter-to-area ratio $\dagger\dagger$	-1.76324* \pm 0.18120	-2.11840	-1.40809
Total summer precipitation $\dagger\dagger$	0.42099* \pm 0.08154	0.26117	0.58081
Mean autumn maximum temperature \dagger	-0.60281* \pm 0.07750	-0.75471	-0.45091
Total winter precipitation $\dagger\dagger$	0.16996* \pm 0.06949	0.03377	0.30616
Mean winter maximum temperature \dagger	-0.92181* \pm 0.07996	-1.07853	-0.76509

Notes: Non-categorical variables were log-transformed and/or standardized (i.e., centered and scaled). Log transformations were conducted before standardizations. Symbols are as in Table 2.

Table 5. Marginal and conditional pseudo R^2 values for the best-supported total wetlands and non-rowcrop-embedded wetlands inundation and ponded area models.

Model	Marginal R^2	Conditional R^2
Total wetlands inundation	0.42	0.75
Rowcrop-embedded wetlands inundation	0.38	0.74
Non-rowcrop-embedded wetlands inundation	0.46	0.78
Total wetlands ponded area	0.27	0.62
Rowcrop-embedded wetlands ponded area	0.22	0.56
Non-rowcrop-embedded wetlands ponded area	0.34	0.66

Notes: Marginal pseudo R^2 values indicate the proportion of variance in the response explained when only fixed effects are considered, whereas conditional pseudo R^2 values indicate the proportion of variance in the response explained when both fixed and random effects are considered. Values were calculated with the `r.squaredGLMM` function in the `MuMIn` package for R (Barton 2015), which draws calculations from Nakagawa and Schielzeth (2013) and Johnson (2014).

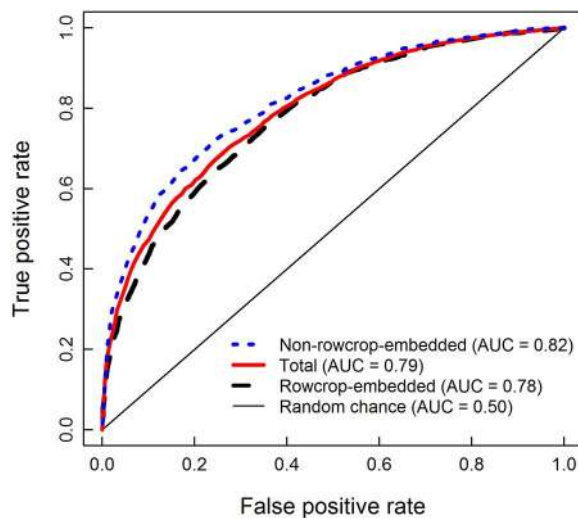


Fig. 3. Receiver operating characteristic (ROC) plot and associated area under the curve (AUC) statistics obtained by comparing the agreement between the predictions of the fixed effects portions of the non-rowcrop-embedded, total, and rowcrop-embedded wetland inundation models and observed inundation events in their associated testing sets in 2004 and 2006–2009. The curved lines represent the success of the three inundation models in assigning higher probabilities of inundation to wetlands that were actually inundated than those that are not, and the straight line represents the same success expected with a random guess. The AUC scores of 0.82, 0.79 and 0.78 mean that for any randomly selected pair of inundated and non-inundated wetlands, the non-rowcrop-embedded, total, and rowcrop-embedded inundation models will assign a higher probability of inundation to the wetland that was actually inundated 82%, 79% and 78% of the time, respectively.

predictive performance, especially considering that only fixed effects structures were used during validation. The optimum threshold values for assigning continuous inundation probabilities to inundation or non-inundation classes in the total wetlands, rowcrop-embedded and non-rowcrop-embedded datasets—according to the maximum kappa statistic—were 0.58, 0.55 and 0.73, respectively. These threshold values were used to assign wetlands an “inundated” or “non-inundated” status under scenarios of future change.

Ponded area models

In both the total and rowcrop-embedded wetlands ponded area models, the best-supported random effects structures allowed the coefficient estimates for the model intercepts to vary among wetlands and years, whereas the best-supported random effects structure in the non-rowcrop-embedded ponded area wetlands model allowed the coefficient estimate for the model intercept to vary among wetlands (Appendix: Tables A5–A7). The set of predictor variables comprising the finalized fixed effects structures for the three final models, as well as the directions of their effects, were similar, although not identical (Tables 6–8). In all three models, increasing wetland shape complexity was associated with less ponded area, whereas increasing total summer precipitation, increasing total winter precipitation, and an increasing number of winter days with maximum temperatures below freezing were all associated with more ponded area. The ponded area model for rowcrop-embedded wetlands did not incorporate the effect of major spring precipitation events; however, an increasing number of major spring

Table 6. Predictor variable coefficient, standard error, and 95% confidence interval estimates for the best-supported linear mixed model for predicting ponded area in all inundated Rainwater Basin wetlands at peak spring bird migration.

Parameter	Estimate \pm SE	95% CI	
		Lower	Upper
Intercept	8.25906* \pm 0.30260	7.66596	8.85215
Semi-permanent	1.32752* \pm 0.16898	0.99632	1.65872
Temporary	-0.76114* \pm 0.10509	-0.96711	-0.55517
Pivots	-0.28251* \pm 0.10907	-0.49629	-0.06873
Dryland	0.36406* \pm 0.14282	0.08414	0.64399
Gravity	-0.56592* \pm 0.14109	-0.84246	-0.28939
Perimeter-to-area ratio $\dagger\dagger$	-0.40144* \pm 0.05194	-0.50325	-0.29964
Spring days with major precipitation event \dagger	0.07812* \pm 0.02793	0.02338	0.13286
Total summer precipitation $\dagger\dagger$	0.30366* \pm 0.04609	0.21333	0.39398
Total winter precipitation $\dagger\dagger$	0.26013* \pm 0.07935	0.10460	0.41565
Winter days with maximum temperature $< 0^\circ\text{C}$ \dagger	0.77571* \pm 0.07047	0.63758	0.91383

Notes: Non-categorical variables were log-transformed and/or standardized (i.e., centered and scaled). Log transformations were conducted before standardizations. Symbols are as in Table 2.

Table 7. Predictor variable coefficient, standard error, and 95% confidence interval estimates for the best-supported linear mixed model for predicting ponded area in rowcrop-embedded and inundated Rainwater Basin wetlands at peak spring bird migration.

Parameter	Estimate \pm SE	95% CI	
		Lower	Upper
Intercept	8.04202* \pm 0.29123	7.47121	8.61284
Semi-permanent	0.97839* \pm 0.29100	0.40803	1.54875
Temporary	-0.90915* \pm 0.12822	-1.16047	-0.65783
Dryland	0.66729* \pm 0.13672	0.39933	0.93526
Gravity	-0.20840 \pm 0.13641	-0.47577	0.05897
Perimeter-to-area ratio $\dagger\dagger$	-0.18190* \pm 0.05730	-0.29421	-0.06959
Total summer precipitation $\dagger\dagger$	0.30557* \pm 0.05764	0.19260	0.41854
Total winter precipitation $\dagger\dagger$	0.41977* \pm 0.10063	0.22254	0.61701
Winter days with maximum temperature $< 0^\circ\text{C}$ \dagger	0.70207* \pm 0.08732	0.53093	0.87321

Notes: Non-categorical variables were log-transformed and/or standardized (i.e., centered and scaled). Log transformations were conducted before standardizations. Symbols are as in Table 2.

Table 8. Predictor variable coefficient, standard error, and 95% confidence interval estimates for the best-supported linear mixed model for predicting ponded area in non-rowcrop-embedded and inundated Rainwater Basin wetlands at peak spring bird migration.

Parameter	Estimate \pm SE	95% CI	
		Lower	Upper
Intercept	8.25802* \pm 0.11877	8.02522	8.49081
Semi-permanent	1.22951* \pm 0.22428	0.78992	1.66909
Temporary	-0.57479* \pm 0.18125	-0.93003	-0.21955
Perimeter-to-area ratio $\dagger\dagger$	-0.72171* \pm 0.09553	-0.90895	-0.53448
Spring days with major precipitation event \dagger	0.10567* \pm 0.04061	0.02609	0.18527
Total summer precipitation $\dagger\dagger$	0.26324* \pm 0.04458	0.17587	0.35061
Mean autumn maximum temperature \dagger	-0.53600* \pm 0.04582	-0.62581	-0.44618
Total winter precipitation $\dagger\dagger$	0.17197* \pm 0.03870	0.09611	0.24782
Winter days with maximum temperature $< 0^\circ\text{C}$ \dagger	0.63935* \pm 0.04289	0.55528	0.72342

Notes: Non-categorical variables were log-transformed and/or standardized (i.e., centered and scaled). Log transformations were conducted before standardizations. Symbols are as in Table 2.

precipitation events increased ponded area in both the total and non-rowcrop-embedded models. Mean maximum daily autumn temperature had a negative effect on ponded area, but was only included in the model for non-rowcrop-embedded wetlands. Semi-permanent wetlands were associated with the greatest ponded area in all three models, and seasonal wetlands were associated with more ponded area than temporary wetlands. Surrounding landuse was not included in the model for non-rowcrop-embedded wetlands, and only cropland-related landuses were included in the model for rowcrop-embedded wetlands. In the total wetlands model, wetlands situated in dryland fields tended to pond more water than wetlands embedded in non-rowcrop surroundings, and wetlands in both pivot-irrigated and gravity-irrigated fields were associated with less ponded area than wetlands in non-rowcrop surroundings, with those in gravity-irrigated fields being associated with the least ponded area. Similarly, in the model for rowcrop-embedded wetlands, the greatest amount of ponding tended to occur in wetlands embedded in dryland fields, whereas lesser amounts of ponding tended to occur in wetlands within pivot-irrigated and gravity-irrigated fields, respectively, although there was no significant difference in ponded area between wetlands in pivot-irrigated and gravity-irrigated fields.

The total wetlands ponded area model yielded marginal and conditional pseudo R^2 values of 0.27 and 0.62, respectively, whereas the model for rowcrop-embedded wetlands had pseudo R^2 values of 0.22 and 0.56, and the non-rowcrop-embedded wetlands model had values of 0.34 and 0.66 (Table 5). Thus, the fixed effect structures of the models explained 27%, 22% and 34% of the variation in ponded area in their respective datasets, and the addition of random effects explained 35%, 34% and 32% more variation, respectively.

Ponded area model validations.—During 10-fold cross-validation, the total wetlands ponded area model yielded a PCC of 0.49 between predicted ponded area values and their associated observed values, when only fixed effects were used as predictors (Fig. 4). Meanwhile, the ponded area models for rowcrop-embedded and non-rowcrop-embedded wetlands yielded PCC val-

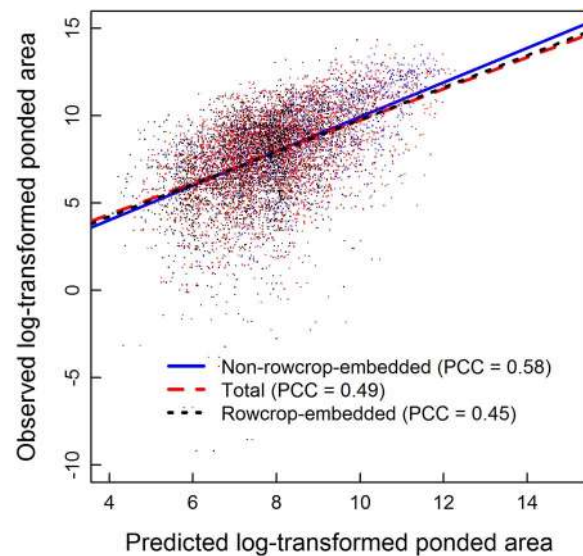


Fig. 4. Model-predicted versus observed log-transformed ponded wetland area in the testing sets for the non-rowcrop-embedded, total, and rowcrop-embedded wetland ponded area models in 2004 and 2006–2009, with best straight-line fits. The Pearson's correlation coefficient (PCC) values between predicted and observed values for the non-rowcrop-embedded, total, and rowcrop-embedded wetland ponded area models were 0.58, 0.49 and 0.45, respectively. Original data were in square meters.

ues of 0.45 and 0.58, respectively. Even when only fixed effects were used as predictors, all three ponded area models displayed moderate levels of predictive ability, with the performance of non-rowcrop-embedded wetlands model being best.

Predictions under climate change scenarios

Inundation predictions.—All three inundation models predicted decreases in the number of inundated wetlands in 2050 under scenarios of climate change (Fig. 5). In the Modest Change Scenario, the greatest number of inundation events was predicted by the total wetlands model, which was followed by the non-rowcrop-embedded and rowcrop-embedded models, respectively. This ranked order is identical to the number of predicted inundation events produced by the three inundation models under the Extreme Change Scenario, as well as the sample sizes of the three datasets.

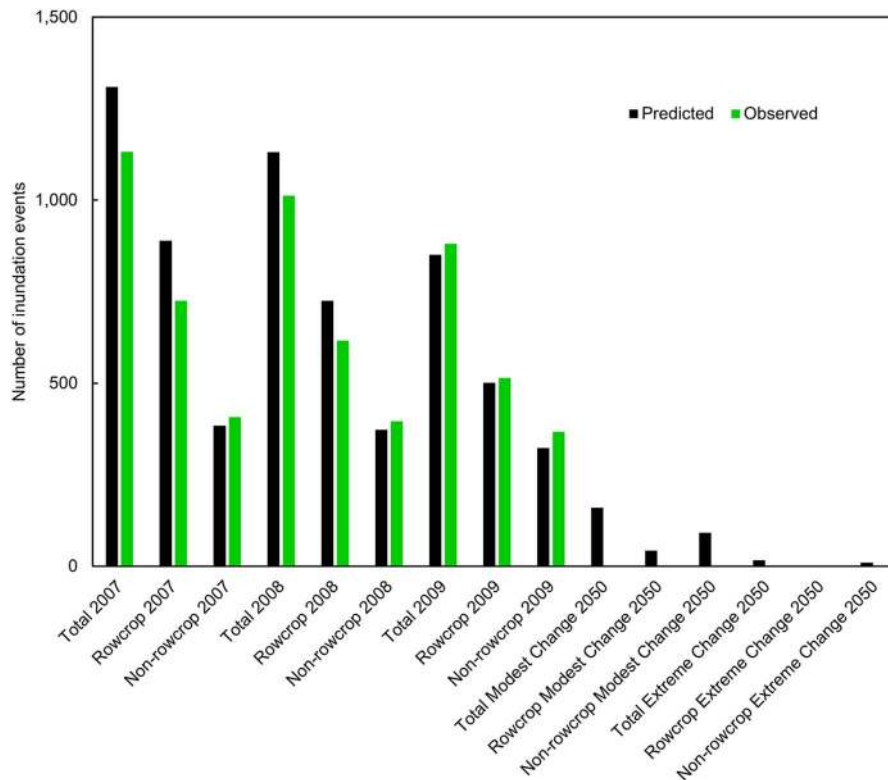


Fig. 5. Predicted and observed number of inundation events for total, rowcrop-embedded and non-rowcrop-embedded wetlands in 2007–2009, as well as in 2050 under the Modest Change and Extreme Change Scenarios. The number of inundation events for 2004 and 2006 are not displayed because the extent of the Annual Habitat Survey increased from 2004–2007. Inundation probability thresholds for classification as inundated or non-inundated were 0.58, 0.55 and 0.73 for the total, rowcrop-embedded and non-rowcrop-embedded wetlands datasets, respectively. Values were calculated for entire datasets, not just validation sets. In general, the number of inundation events decreased under more extreme climatic changes.

Although the greatest number of inundation events was predicted by the total wetlands model under both scenarios, the non-rowcrop-embedded wetlands model predicted the highest proportion of wetlands inundated under both scenarios, whereas the rowcrop-embedded wetlands model predicted the lowest proportion of wetlands inundated under both scenarios (Fig. 6). Similarly, the greatest mean wetland inundation probability was predicted by the non-rowcrop-embedded model under both scenarios (Fig. 7). In summary, all three inundation models predicted fewer inundation events, a lower proportion of wetlands inundated, and lower mean inundation probabilities under both climate change scenarios than under any 2004–2009 study year, with inundation likelihoods being

generally lower under the Extreme Change Scenario than the Modest Change Scenario, and inundation likelihoods being generally greater in non-rowcrop-embedded wetlands than rowcrop-embedded wetlands.

Ponded area predictions.— All three ponded area models predicted substantial decreases in overall ponded wetland area under scenarios of future climate change (Fig. 8); however, mean ponded area predictions did not show as great of decreases (Fig. 9). Under the Modest Change Scenario, the greatest total and mean ponded areas were predicted by the model for non-rowcrop-embedded wetlands, whereas the least total and mean ponded areas were predicted by the model for rowcrop-embedded wetlands (Figs. 7 and 8). The same order of the models in

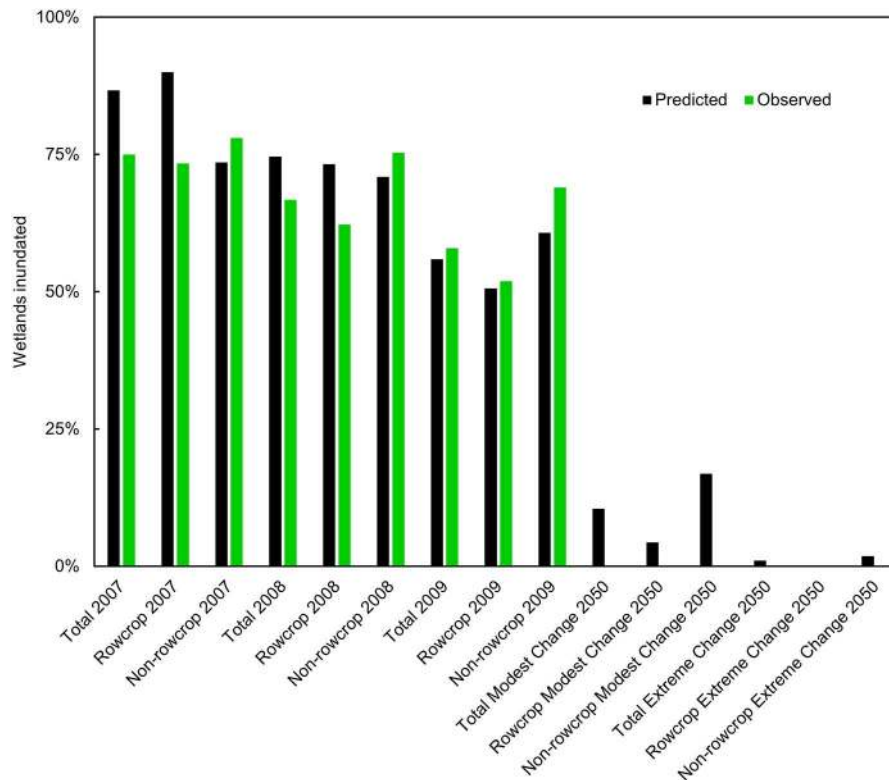


Fig. 6. Predicted and observed percentage of total, rowcrop-embedded and non-rowcrop-embedded wetlands inundated in 2007–2009, as well as in 2050 under the Modest Change and Extreme Change Scenarios. In general, the proportion of wetlands inundated events decreased under more extreme climatic changes.

predicting mean and total ponded area was observed under the Extreme Change Scenario.

DISCUSSION

Playa wetland inundation and ponded area in the Rainwater Basin vary among sites and years, and are influenced by wetland characteristics (i.e., wetland type and hydric footprint shape complexity), anthropogenic landscape alterations (i.e., surrounding landuse), and seasonal weather events and trends (i.e., number of days with major precipitation events, total precipitation, mean maximum temperature, and number of days with maximum temperature below freezing; Tables 2–4, 6–8). Model predictions indicate that if the temperature and precipitation changes assumed under our climate change scenarios occur, future spring migratory waterbird stop-over habitat in the landscape may decrease. In general, greater hydric footprint shape complex-

ity, and warmer and drier weather patterns appear to negatively influence wetland inundation and ponded area in the Rainwater Basin. However, because substantial uncertainty exists over the exact nature, direction, timing and effects of regional-scale climate change, associated changes in habitat availability are also largely unclear. These potentially detrimental, yet highly uncertain, large-scale future changes necessitate proactive management strategies for mitigating the effects of global change on migratory waterbirds. The consideration of a range of regional climate change possibilities (Wuebbles and Hayhoe 2004) and the comparison of model predictions to those from other landscapes within the migration corridor (Werner et al. 2013) could provide additional insights into drivers of wetland ponding. Furthermore, information-sharing among landscapes could provide early indicators of climate change effects on wetland inundation and waterbird habitat avail-

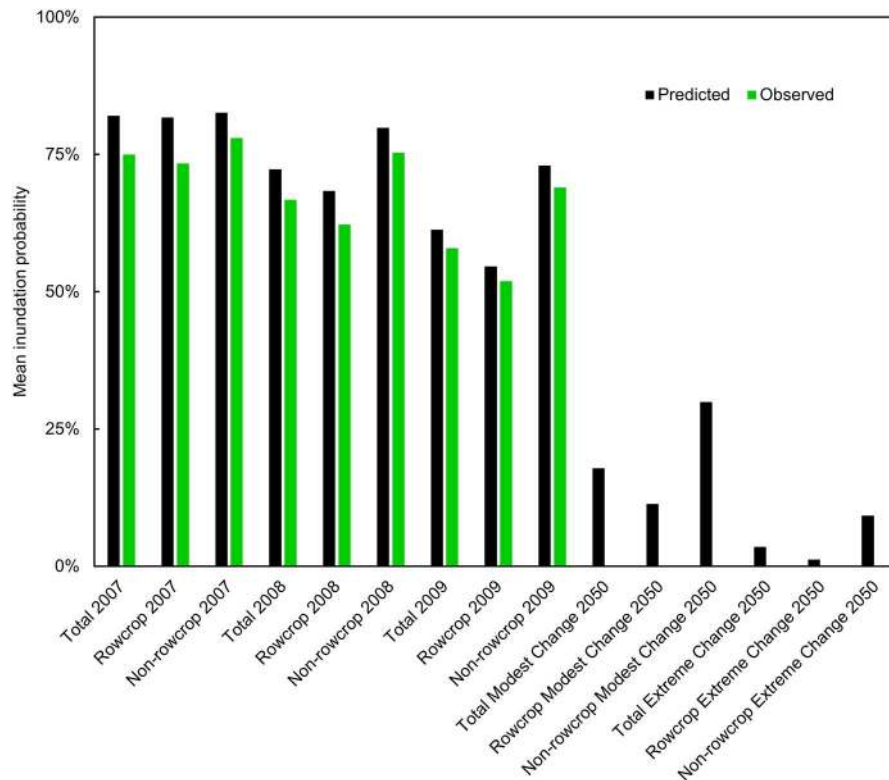


Fig. 7. Predicted and observed mean probabilities of inundation for total, rowcrop-embedded and non-rowcrop-embedded wetlands in 2007–2009, as well as in 2050 under the Modest Change and Extreme Change Scenarios. In general, the mean predicted probability of inundation decreased under more extreme climatic changes.

ability (Werner et al. 2013).

In regard to weather-related drivers of wetland ponding, Poiani and Johnson (1991), Larson (1995), Sorenson et al. (1998), Johnson et al. (2005), and Voldseth et al. (2009) predicted decreases in wetland ponding and waterbird habitat in the Prairie Pothole Region under increased temperature and decreased precipitation—results that are consistent with ours for the Rainwater Basin. However, they also found that the negative effects of temperature increases could be partially or entirely offset by simultaneous precipitation increases. Our model predictions indicate that even with seasonal precipitation increases (Table 1), accompanying temperature increases could decrease the number of inundation events (Fig. 5), inundation likelihood (Fig. 6), and total ponded area (Fig. 7). There could be a number of reasons for this difference between these studies and ours,

including the fact that unlike Rainwater Basin playa wetlands, many Prairie Pothole wetlands are fed by groundwater (Smith 2003). In addition, different seasonal temperature and precipitation changes would affect their predictions (Johnson et al. 2005). In playa wetlands of the southern plains, Johnson et al. (2011) determined mean annual rainfall and total rainfall in the year prior to be the most important weather-related drivers of playa wetland inundation, and Bartuszevige et al. (2012) found the amount of rainfall in the previous two weeks and variation in the amount of rainfall to be most important. However, neither of these studies extrapolated their results to scenarios of future climate change.

In regard to surrounding landuse, Voldseth et al. (2007) and (2009) reported that in the Prairie Potholes, rowcrop agriculture affects wetland hydrology by increasing water inflows and sedimentation rates, thereby making water levels

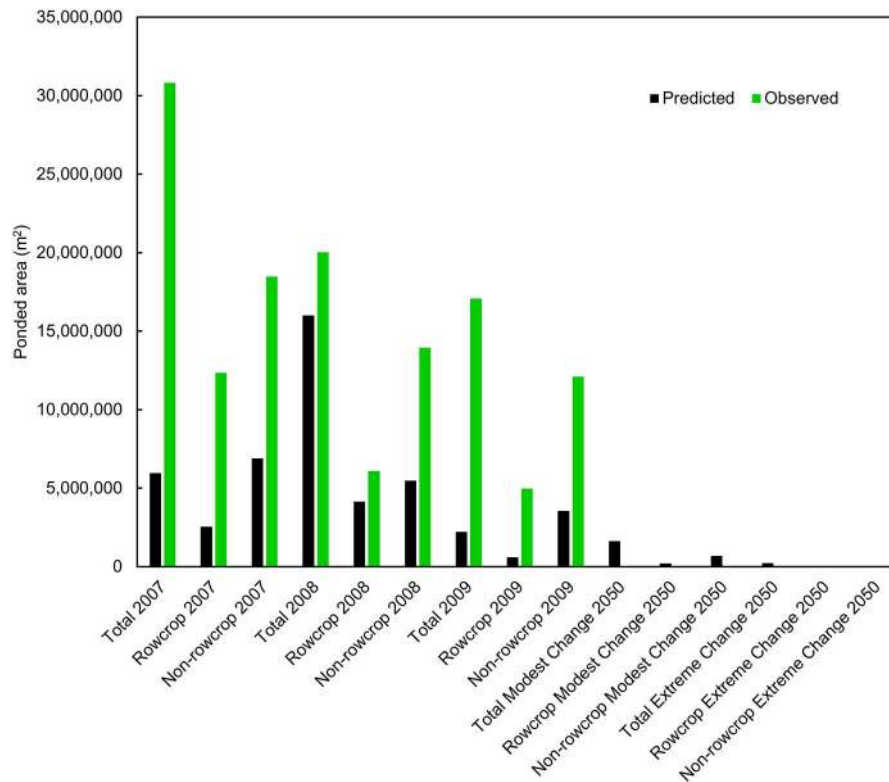


Fig. 8. Predicted and observed ponded area sums for total, rowcrop-embedded and non-rowcrop-embedded wetlands in 2007–2009, as well as in 2050 under the Modest Change and Extreme Change Scenarios. In general, the predicted sum of ponded area decreased under more extreme climatic changes.

more variable. They also found that dense stands of non-grazed grass impeded overland flows of precipitation runoff into wetlands, which resulted in wetlands in unmanaged grasslands being less likely to pond water than those in rowcrop fields—a conclusion supported by Cariveau et al. (2011) and Bartuszevige et al. (2012) in playas surrounded by dense stands of conservation plantings in the southern plains. Alternatively, Collins et al. (2014) determined that playa wetlands embedded in shortgrass prairie pastures of the southern plains are more likely to be inundated than playas embedded in rowcrop fields, and that wetlands in rowcrop fields have shorter hydroperiods. Highlighting the importance of landscape context for playa wetland inundation in the Southern High Plains, Smith et al. (2011) found that the negative effects of sedimentation on playa wetland inundation—a result of rowcrop production in and around the wetland—outweighed those of projected future

temperature increases.

Our results indicate that both wetland type and surrounding landuse are important drivers of wetland inundation and ponded area in the Rainwater Basin. Although the direction of the effects of surrounding landuse were not consistent among models, the effects of wetland type were (Tables 2–4, 6–8). Semi-permanent wetlands were more likely to be inundated and likely to pond more water than seasonal wetlands, and seasonal wetlands were more likely to be inundated and likely to pond more water temporary wetlands. Temporary wetlands tend to be located in agricultural fields, where they are farmed through in drier years, whereas semi-permanent wetlands tend to be embedded in non-rowcrop properties that are not farmed (LaGrange et al. 2011). Indeed, ~75% of the temporary wetlands in our total wetlands inundation dataset were located in rowcrop fields and ~75% of the semi-permanent wetlands in the

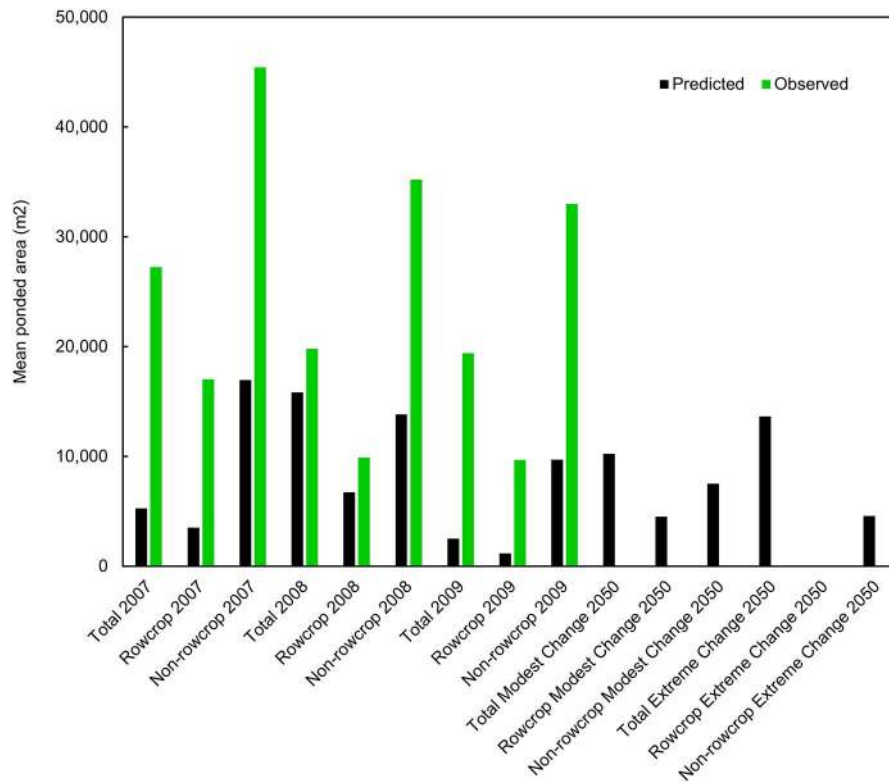


Fig. 9. Predicted and observed mean ponded area for total, rowcrop-embedded and non-rowcrop-embedded wetlands in 2007–2009, as well as in 2050 under the Modest Change and Extreme Change Scenarios. In general, mean ponded area decreased under more extreme climatic changes.

same dataset were located in non-rowcrop surroundings. Temporary wetlands were predicted as the least likely of the wetland types to be inundated in all three inundation models (Tables 2–4), as well as the wetland type with the lowest ponded areas in the three ponded area models (Tables 6–8), whereas semi-permanent wetlands were the most likely to be inundated and were likely to contain the most water in the same three models. Although decreased inundation frequency and ponded area is a defining characteristic of temporary wetlands, frequent soil disturbances in rowcrop fields may further decrease inundation frequency and ponded area within them—an interpretation of our results that is consistent with previous studies conducted throughout the Central Flyway that have reported negative effects of agriculture on ephemeral wetlands (e.g., Voldseth et al. 2007, 2009, Bartzen et al. 2010, Smith et al. 2011, Collins et al. 2014). Thus, the effects of climate change on wetland ponding

may be intensified or reduced by surrounding landcover and landuse.

Approximately 80% of total landcover in the Rainwater Basin is currently enrolled in rowcrop production, and of those rowcrops, ~59% are pivot-irrigated, ~15% are gravity-irrigated, and ~26% are not irrigated (i.e., dryland). Recent landuse change trends in the region have involved converting grassland to pivot-irrigated rowcrop production, as well as converting gravity-irrigated and dryland rowcrop fields to pivot-irrigation. The already intensive cultivation of this landscape makes additional large-scale conversion of grassland to rowcrops unlikely; however, both rowcrop fields and remnant grasslands may be subject to further changes (e.g., bioenergy feedstock production; Uden et al. 2015), especially if more limitations are placed on groundwater irrigation in response to future climatic changes (Uden et al. 2013). Wetlands embedded in these properties would certainly be

affected, yet the nature of the effects is likely to depend largely on the kind and intensity of landuse change.

Although the majority of natural wetlands are likely to benefit migratory birds, certain characteristics may promote specific sites as conservation and/or restoration targets at the local scale. Focusing conservation and restoration efforts on wetlands with high likelihoods of continued ponding will help ensure the future availability of these habitats, whereas focusing efforts on wetlands that currently provide habitat, but that may not under future conditions, may or may not be effective for preventing future habitat losses (Bartzen et al. 2010). Furthermore, wetland and waterbird managers in landscapes with closed-basin wetlands and access to groundwater pumping, such as the Rainwater Basin, may focus on increasing funds for artificially flooding wetlands, as well as continuing watershed restoration projects. In watershed restorations, special emphasis may also be placed on sediment removal and the restoration of native grass waterways, so that sediment loading from intense precipitation events is reduced (Skagen et al. 2008, Smith et al. 2011). Finally, filling irrigation reuse pits, re-contouring waterways, and replacing culverts could be used to maximize overland flows to wetlands.

Landscape-scale conservation objectives (e.g., securing sufficient stopover habitat for migratory waterbirds) may be accomplished by seizing opportunities afforded by fluctuations in agricultural commodity and land prices (Powell 2012, 2015). Avenues for securing additional habitat under future environmental and economic changes may include: developing collaborative partnerships among private landowners, corporations, and government entities; establishing private reserves for nature-based recreational activities; and continuing to promote water and soil conservation programs (Smith et al. 2011, Powell 2012, 2015). Conservation and restoration activities are likely to increase the long-term provisioning of ecosystem services by wetlands, especially in intensive agricultural landscapes, which are common throughout the Central Flyway (Smith et al. 2011). A modeling framework for quantifying changes in wetland ecosystem services as a result of conservation program enrollment has been proposed by Euliss et al.

(2011).

Means for improving understanding and predictions of stopover habitat availability at the continental scale could involve the aggregation and comparison of stopover habitat availability-related predictions from this and similar studies spanning the Central Flyway (e.g., Larson 1995, Sorenson et al. 1998, Johnson et al. 2004, 2005, 2011, Voldseth et al. 2009, Bartzen et al. 2010, Cariveau et al. 2011, Smith et al. 2011, Liu and Schwartz 2011, 2012, Bartuszevige et al. 2012, Werner et al. 2013, Collins et al. 2014). In general, wetland ponding studies in the Central Flyway have shown the probability of inundation to be negatively impacted by surrounding rowcrop agriculture, dense grass stands of conservation plantings, and warmer and drier weather conditions. Meanwhile, increased rainfall and surrounding native grassland increased inundation likelihood. These and forthcoming insights and predictions concerning habitat availability under alternative levels of landuse and climate change could help determine how migratory waterbirds might be differentially affected by future changes at different spatial and temporal scales. This information, in turn, could be used to spatially prioritize management efforts for the greatest benefit to migratory waterbird populations (Heglund and Skagen 2005). For example, focusing habitat protection, restoration and enhancement efforts on strategically located wetlands that may serve as stepping stones between other stopover habitats (Urban and Keitt 2001). It will also be important to ensure that sufficient conservation actions are completed within core stopover habitats to provide sufficient habitat and food resources.

In regard to the performance of our predictive models for the Rainwater Basin, the three wetland inundation models performed better than the three wetland ponded area models, with the model for inundation in non-rowcrop-embedded wetlands being best and the model for ponded area in rowcrop-embedded wetlands being worst, as indicated by AUC scores (Fig. 3), PCC values (Fig. 4), and pseudo R^2 values (Table 5). For both the inundation and ponded area responses, the models for non-rowcrop-embedded wetlands performed best and the models for rowcrop-embedded wetlands performed worst. Although differences in perfor-

mance were not great, the poorer performance of the models for rowcrop-embedded wetlands could be due in part to increased anthropogenic influence within them, an assertion supported by the tendency of water levels in rowcrop-embedded wetlands to be more variable than those of wetlands in natural surroundings (Voldseth et al. 2007, 2009, Collins et al. 2014).

In addition to serving as an indicator of model performance, differences between the marginal and conditional pseudo R^2 values for the six final models (Table 5) illustrate the important role of random effects in explaining variation in both responses. When only fixed effects were used for explanation and prediction, all three wetland inundation models still performed well; however, the fixed effects structures of the ponded area models tended to under-predict ponded area from 2004–2009, which means that it is also likely that predictions for the Modest and Extreme Change scenarios are also consistently low. The decreased predictive ability of the ponded area models could be partially the result of a number of landuse change-related variables (e.g., roadways and associated infrastructure, surface drains, irrigation reuse pits, depth of culturally accelerated sediment, and agricultural tillage practices) that were not included as predictor variables. Despite these limitations, predictions from the ponded area models are still useful for informing global change mitigation efforts in the Rainwater Basin wetlands landscape, especially when used in tandem with the more accurate wetland inundation models.

This study adds to the existing literature that has been published in regard to playa wetland functioning in the Great Plains, establishes a baseline for additional wetland ponding studies, and provides a foundation for developing a robust set of conservation tools for prioritizing wetland conservation actions at multiple scales, in order to ensure reliable habitat for wetland dependent migratory birds. We did not consider inundation or ponded area in wetlands that were artificially flooded with groundwater in the year preceding migration. However, given the predicted decreases in habitat availability in non-pumped wetlands, pumped wetlands are likely to become even more important for securing habitat in the future—assuming that groundwater can continue to be allotted for these purposes.

Therefore, future studies should examine the effects of artificial autumn and spring wetland flooding on wetland inundation and ponded area throughout the year. The role of interactions among explanatory variables, especially temperature, precipitation, and hydric footprint shape complexity, should also be explored further. Stopover habitat availability predictions may be extended to the calculation of waterbird food availability during stopover, due to differences in vegetative communities and invertebrate densities among wetland types (Bishop and Vrtiska 2008), and wetland inundation and ponded area predictions may be coupled with region-specific functional connectivity assessments for wetland-dependent species (e.g., Uden et al. 2014).

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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