# Avian Response to Weather in the Central U.S. Grasslands

By

Jessica Gorzo

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This dissertation is approved by the following committee:

Anna Pidgeon, Professor, Forest & Wildlife Ecology

Volker Radeloff, Professor, Forest & Wildlife Ecology

Benjamin Zuckerberg, Professor, Forest & Wildlife Ecology

Steven Ackerman, Professor, Atmospheric & Oceanic Sciences

Stephen Vavrus, Senior Scientist, Atmospheric & Oceanic Sciences

## Abstract

My dissertation focuses on breeding birds in the open-canopy habitats of the north central United States. Grassland birds across the grassland ecoregions of the U.S. share some common life history strategies shaped by natural selection within open habitats. Grassland species also exhibit important differences according to the particulars of their habitat associations. For instance, extreme weather is observed across fire-mediated landscapes in the central U.S., from the Prairie Hardwood Transition to the Badlands and Prairies, and avian communities must be able to cope with the level of weather variability inherent to their region. Avian communities of the Prairie Hardwood Transition region are adapted to a landscape with a sparse tree canopy, whereas the communities of the Eastern Tallgrass Prairie, Prairie Potholes and Badlands and Prairies regions are true grassland avian communities, with minimal varying interspersion of woody cover but varying grass height and density, with both declining from eastern to western regions. Further, prevalence and type of wetland habitat varies within these grassland regions, with a large number of wetlands in the Prairie Potholes supporting most (50 to 80%) of the continent's breeding waterfowl populations. My goal was to characterize the responses of avian communities to weather variability, in light of known life history responses and characteristics of the habitat of regions in the central U.S. grasslands.

In my first analysis, I focused on the Badlands and Prairies, the driest region considered. Natural cover in this region consists primarily of shortgrass prairie, shrub land and bare ground, but spatiotemporal variability at the local scale is high. Weather determines local conditions, such that vegetative structure can change dramatically between years. I quantified the response of annual abundance of 14 grassland birds to weather during the summer breeding season, both within the same year and in the preceding year. Baird's and grasshopper sparrows responded positively to precipitation and negatively to temperature. Eastern kingbird and vesper sparrow responded negatively to precipitation, whereas upland sandpiper responded positively to temperature. With projected warmer, drier weather during summer in the Badlands and Prairies, Baird’s and Grasshopper sparrows may be especially threatened by future climate change.

In my second analysis, I examined the differences in life history strategies of species found in forest, oak savanna and grassland with respect to weather within three regions: the Prairie Hardwood Transition, Eastern Tallgrass Prairie and Prairie Potholes. These regions encompass a gradient of forest to grassland. I compared communities along the gradient of tree cover. Abundance of grassland species was more variable year-to-year where they occurred, and generally responded more strongly to weather than forest species did. This analysis sheds light, at a broad scale, on the possible consequences of differential site fidelity strategies for responses to weather variation at the level of avian communities. As a group, the higher variability of grassland species may be reflective of low site fidelity, which allows them to select different breeding locales year-to-year. The relatively low variability of forest species potentially reflects known higher rates of site fidelity for this group, which means that these species may not as readily move in response to weather, but instead cope in other ways at the same breeding site as the previous year.

In my third analysis, I focused on the Prairie Potholes region. I analyzed the response of waterfowl to land cover and weather, and examined patterns of species movement in response to drought. While waterfowl responded to both presence, configuration and temporal availability of water, there was no evidence of movement patterns in response to drought from my analysis. Since movement in response to drought has been documented previously, it is possible that data sets with finer-scale information and greater spatial coverage are needed to elucidate large-scale movements in times of extreme weather.

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## Introduction

Climates are defined by distributions of precipitation and temperature, whereas weather is an observation from a climate distribution, defined within an arbitrary time window (Strahler 2007). As such, climates can be described by averages and typical variation of weather in a given year (Monkhouse 2007). Within the U.S., climate generally grades from wetter to drier moving from the coast toward the interior of the country (Guttman and Quayle 1996). The “Df” type (humid continental) climates dominate the northeastern U.S., whereas “B” (arid) type climates occur in the interior west (Kottek et al. 2006). With the westward shift in precipitation and temperature from the east coast to the interior U.S. comes a shift in dominant vegetative cover, from forest to grasslands (Myneni et al. 2002). There are many ways to define ecoregions such as these depending on the goal of the classification, and various scales at which to make distinctions (CEC 1997). Focusing on bird communities, Bird Conservation Regions (BCRs) have been defined to encompass regions that harbor distinct avian communities of North America (Committee 2000). In terms of BCRs, the ecotone between U.S. eastern forest and central grassland is the Prairie Hardwood Transition (BCR 23), which is characterized by oak savanna (Thogmartin et al. 2014). Thus, this BCR harbors a bird community that exploits landscapes with some tree cover and tall herbaceous ground cover (Murray et al. 2008). From east to west, the Eastern Tallgrass Prairie (BCR 22) is the easternmost grassland BCR, though it is mostly dominated by forest and oak savanna in the eastern portion of the region (Sauer et al. 2003). The Eastern Tallgrass Prairie is dominated by a “Dfa” climate, which differs from the “b” type climate to the north based on temperature regime. The Eastern Tallgrass Prairie hosts warmer average temperatures than the Prairie Potholes (BCR 11) to the north, and is generally both more topographically homogeneous and productive. This region provides key habitat for eastern grassland birds, as well as some oak savanna and forest species in the east (Link and Sauer 2002). The Prairie Potholes (BCR 11), which is the north-easternmost grassland ecoregion in the U.S., is dominated by “Dfb” type climate and extends north into southern Canada (Skagen and Thompson 2007). Prehistoric temperature also defines the ecoregion, in that former glaciation created the Prairie Potholes, which are depressions that seasonally fill with water (Sloan 1972). Thus, the Prairie Potholes (BCR 11) is the core breeding region for most of the continent’s waterfowl (Forcey et al. 2007). To the west, the “BSk” climate dominates and produces the Badlands and Prairies (BCR 17) (Bunkers et al. 1996). This region represents a mixed-grass prairie, with taller grass in the east and shortgrass prairie in the west (Millsap et al. 2013). Further, within BCR 17, there is much variation in vegetation height and community at the local scale across the region (Coupland 1961). The Badlands and Prairies (BCR 17) supports a diverse assemblage of western grassland birds, because of the diversity of available niches (Nielson et al. 2012).

Weather differentially affects the habitat types encompassed by the U.S. central grassland BCRs (Xiao and Moody 2004). Variability across a biome generally translates to greater spatiotemporal variability in sites within the biome (Frank and Inouye 1994). Overall, the forests in the east are less variable than grasslands in above-ground net primary productivity, which varies with weather (Knapp and Smith 2001). Woody vegetation persists on the landscape in times of drought, whereas grassland structure is highly sensitive to weather (Webb et al. 1978). In keeping with climatic relationships, vegetative height and density in grasslands is dependent on inter-annual weather, with sufficient precipitation required to promote growth (Baldocchi et al. 2004). Thus, grasslands are inter-annually dynamic, with conditions varying spatiotemporally in accordance with weather (Yang et al. 1998). Similarly, the Prairie Potholes region depends on adequate seasonal and inter-annual precipitation to refill the potholes with water in the spring (Ballard et al. 2014). In regions such as these that are highly variable with respect to weather, weather may be a proxy to measure habitat condition (Burke et al. 1997). The response of the ecosystems in the BCRs to weather variation in turn mediates the response of the indwelling bird communities.

Avian response to weather may be due to either direct effects such as physiological stress, or may be mediated by changes in habitat characteristics. Avian response to weather often varies in magnitude with the severity of the event. Several aspects of breeding life history vary within normative bounds of weather. For example, Florida scrub-jays showed a positive linear relationship between rainfall and clutch size (Woolfenden 1984). Grassland birds are known to have low site fidelity, likely to allow flexibility in choosing a site based on annual conditions (Ahlering et al. 2006). A particularly severe event, however, may warrant an extreme response. For example, northern pintail have moved to the Arctic when surface water is too scarce within their normal breeding range (Henny 1973). Some species may forgo breeding in times of extreme weather (Bolger et al. 2005). Thus, though likely through a variety of mechanisms, weather can affect avian breeding strategies and ultimately productivity. Both studies of bird response to singular extreme events and studies of an observed relationship between weather variables and avian parameters are useful for determining the nature of the relationship between climate variables and avian response. Studies that capture deviations over time provide a richer source of information than those that simply compare outcomes in an extreme year to those in a normal year, but the latter type due shed light on conditions that definitively influence avian life history strategies.

This dissertation is divided into three chapters, investigating questions of breeding bird response to weather in the central U.S. grasslands. For my **1st chapter**, I investigated the response of the 14 most commonly-encountered grassland birds in the Badlands and Prairies to weather variability, hypothesizing that species' response to weather would depend on niche requirements. The weather variability inherent in the prevailing climate, as well as the variation in habitats at local scales across this region made it an ideal setting to investigate the response of birds with varying requirements to changes in inter-annual conditions. For my **2nd chapter**, I compared the response of grassland birds and forest birds to weather variability, in relation to differential life history strategies. Forest birds and grassland birds have evolved different life history traits based on both the climate and resulting land cover that form their native ecosystems, so I hypothesized that their responses to weather would vary accordingly. For my **3rd chapter**, I quantified the response of waterfowl in the Prairie Potholes to weather and land cover, and investigated long-term movements of waterfowl populations in times of drought in their core breeding range. It is well-known that waterfowl species depend on water and wetland habitats, though weather responses are less well-quantified. Some North American waterfowl species are known to make long-distance movements in times of extreme drought, and many have ranges that extend to northern Canada and Alaska. As such, I hypothesized that species would be more abundant at range edges with increasing drought severity. My dissertation was overall motivated by the implications of climate change in the central grasslands, and how changing weather regimes would affect birds. By understanding grassland birds' past response to weather over a long temporal record of variation, I can better understand how species will respond under predicted climate regimes.

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# Chapter 1: Using the North American Breeding Bird Survey to assess broad-scale response of the continent's most imperiled avian community, grassland birds, to weather variability

## Abstract

Avian populations can respond dramatically to extreme weather such as droughts and heat waves. However, patterns of response to weather at broad scales remain largely unknown. Our goal was to evaluate annual variation in abundance of 14 grassland bird species breeding in the northern mixed-grass prairie, in relation to annual variation in precipitation and temperature. I modeled avian abundance during the breeding season using North American Breeding Bird Survey (BBS) data for the U.S. Badlands and Prairies Bird Conservation Region (BCR 17) from 1980 to 2012. I used hierarchical Bayesian methods to fit models and estimate the candidate weather parameters standardized precipitation index (SPI) and standardized temperature index (STI) for the same year and the previous year. Upland Sandpiper (*Bartramia longicauda*) responded positively to within-year STI ($\beta$=0.101). Baird's Sparrow (*Ammodramus bairdii*) responded negatively to within-year STI ($\beta$=-0.161) and positively to within-year SPI ($\beta$=0.195). The parameter estimates were superficially similar (STI $\beta$=-0.075, SPI $\beta$=0.11) for Grasshopper Sparrow (*Ammodramus savannarum*), but the best-selected model included an interaction between SPI and STI. The best model for both Eastern Kingbird (*Tyrannus tyrannus*) and Vesper Sparrow (*Pooecetes gramineus*) included the additive effects of within-year SPI ($\beta$=-0.032 and $\beta$=-0.054, respectively) and the previous-year's SPI ($\beta$=-0.057 and $\beta$=-0.02, respectively), though for Vesper Sparrow the lag effect was insignificant. With projected warmer, drier weather during summer in the Badlands and Prairies, Baird's and Grasshopper sparrows may be especially threatened by future climate change.

## Introduction

Birds experience and respond to a variety of weather conditions during the breeding season, governed in part by the climate of a region. Climate is defined by both averages and variability of precipitation and temperature over a 30-year or longer time period, while weather occurs over minutes to months (Arguez et al. 2012). Drought is defined here as a long-term deficit in precipitation (Palmer 1965, Dai et al. 2004). The magnitude of avian population response to weather is often proportional to the extremity of the weather experienced, though the type of response varies by species, biome, and type of weather event. For example, an extreme heat wave in an arid region may kill adult birds (McKechnie and Wolf 2009) due to physiological thresholds. In drought conditions, birds may abandon nests or forgo breeding altogether, as was the case for Bridled Titmice (*Baeolophus wollweberi*) in the southwestern U.S. (Christman 2002). Thus, avian settlement and productivity may depend strongly on inter-annual variation in weather.

Droughts are common in temperate semi-arid regions and have long played a role in creating grasslands (Peel et al. 2007). Because spring precipitation in the mixed-grass prairie strongly influences primary productivity (Sala et al. 1988, Yang et al. 2008), deviation from normal conditions influences vegetative density and height (Lane et al. 1998). Given that birds rely on vegetative condition for habitat and food production, and grassland vegetation varies in response to precipitation, grassland birds must cope with both spatial and temporal habitat variability (Andrews et al. 2015). Above-average temperature can exacerbate the effects of droughts such that major, prolonged deviations from normal temperature may impose physiological stress on birds. Therefore, avian breeding success in semi-arid grasslands greatly depends on the weather (Lloyd 1999).

Extreme weather, such as drought and heat waves, is projected to increase in frequency and intensity in many regions as climate changes (Meehl and Tebaldi 2004). Understanding how changes in extreme weather may affect the grassland bird communities in the future can be greatly aided by the analysis of bird responses to past extreme events. The most extreme drought in the temperate grasslands of the U.S. after the Dust Bowl was in 1988, and coincided with the era of rigorous bird data collection (Giorgi et al. 1996). The 1988 drought caused stress in many sectors, including human food production, and breeding birds were also affected (Krapu et al. 2006). For example, during the drought, there was 61% lower breeding bird density in June of 1988 compared to June of 1987 in North Dakota (George et al. 1992). Furthermore, Horned Larks (*Eremophila alpestris*), Western Meadowlarks (*Sturnella neglecta*) and Vesper Sparrows (*Pooecetes gramineus*) stopped nesting in mid-June of 1988 (George et al. 1992). However, prior empirical evidence on the effects of extreme weather on grassland bird communities was largely limited to case studies (Ludlow et al. 2015).

Our goal was to quantify the broad-scale pattern of grassland bird response to weather in the breeding range. I aimed to determine if weather is an important driver of species-specific annual abundance. I predicted that grassland birds may respond to precipitation conditions preceding the breeding season and temperatures in the early breeding season because these conditions ultimately determine the environmental conditions experienced by birds during the breeding season. Also, I predicted that weather in the previous breeding season may influence bird abundance the following year because of its potential effect on the previous season’s reproductive success.

## Methods

### *Study Area*

Our study area was Bird Conservation Region (BCR) 17, the Badlands and Prairies, which stretches from central South Dakota to western Montana, and includes parts of North Dakota and Wyoming, encompassing over 36.7 million ha (Figure 1). The Badlands and Prairies are characterized by large, contiguous tracts of mixed-grass prairie, composed of a mosaic of tall grass, mixed grass, and short grass vegetation.

### *Bird Data*

The North American Breeding Bird Survey (BBS) is based on annual counts of birds along 39.4 km routes conducted by skilled volunteers (Keller and Scallan 1999). All birds seen and heard during each 3-minute stop (spaced every 0.8 km along the route) are counted. The BBS counts are considered an index of abundance, rather than a true tally of abundance, because the area sampled by a route is difficult to assess (Boulinier et al. 1998). I used BBS data from 1966 through 2010, in accordance with the time record of an available weather dataset (Maurer et al. 2002). I analyzed the subset of birds that George et al. (1992) most commonly encountered during their local scale line-transect sampling of the same general geographic area, and for which there was adequate representation in the BBS dataset. Thus, I excluded Sharp-tailed Grouse, (*Tympanuchus phasianellus*) leaving 14 grassland bird species (Table 2). For each species, I only considered routes on which the species occurred at least once. The Badlands and Prairies BCR includes 117 routes, but the number of routes on which each species was detected differed. I excluded route runs that did not meet quality standards, as indicated in the dataset. I also only used standard BBS route runs, and did not include resampling efforts or non-standard protocols.

*Weather Data*

We analyzed weather data from the gridded meteorological dataset produced by Maurer et al. (2002) algorithm, which covers the contiguous U.S. at 1/8th degree spatial resolution (~140 $km^2$ per grid cell) from 1949-2010 (Maurer et al. 2002). I used data from 1965 through 2010 to match the temporal record of BBS data, and extracted values for the route centroid of each BBS route per year. I considered weather both leading up to a given year's breeding season, and weather from the previous year as potentially influential for avian abundance.

**Precipitation.** I used the Standardized Precipitation Index (SPI) to characterize inter-annual variation in precipitation totals preceding the breeding season. The SPI is standardized so that values can be compared among areas with different precipitation patterns, and the study period during the year can be customized to the study system (McKee et al. 1993). Our metric was the precipitation totals during the 90-day period ending June 1 (i.e. spring, March-May) in the same year as the BBS count. To capture conditions in the prior year's breeding season, I used summer (i.e. June-August) SPI. I fit annual totals to the Pearson-III distribution, and transformed each annual total to a standard deviation from a standard normal distribution. Full details of these calculations are available in Allstadt et al. (*unpublished*) though the data are available online (http://silvis.forest.wisc.edu/climate-averages-and-extremes). In some cases, precipitation values were so anomalous that they did not fit the distribution, and those were recoded as 7 or -7 depending on whether or not the anomaly was positive or negative, respectively.

**Temperature.** I calculated the Standardized Temperature Index (STI) for the month of June, which is the first summer month in which extreme temperatures (i.e. record heat anomalies) are possible (e.g., a record high of 43.9°C in Bismarck, North Dakota, in the northerly portion of our range). Extreme temperatures could either have direct effects on survival or exacerbate an extant precipitation deficit. I standardized average daily maximum temperature into the Standardized Temperature Index (STI) to account for differences in temperature mean and inter-annual variability among locations (Allstadt et al. *unpublished*). The STI is analogous to the SPI, with positive deviations indicating the magnitude of these temperatures above normal conditions.

### *Vegetation Data*

To investigate the relationship between rainfall and vegetation anomaly in BCR 17, I calculated a measure of standardized seasonal greenness (SSG) from the Moderate Resolution Imaging Spectro-radiometer (MODIS) Enhanced Vegetation Index (EVI) monthly product (MYD13A3 https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/myd13a3). Vegetation indices are designed to measure vegetative vigor (Ji and Peters 2003). I averaged and calculated standard deviations per pixel of June EVI from 2003 through 2012. Then, I subtracted the mean and divided by the standard deviation for each pixel, giving a standard score per pixel for each June from 2003 through 2012. I averaged the pixels of the SSG image within 400 m of each BBS route in order to characterize vegetative anomaly for each route per year in 2003 through 2012. I hypothesized that spring (March-May) SPI would be positively associated with June SSG.

### *Statistical Analysis*

We employed Bayesian hierarchical models because they provide a good framework for analyzing BBS data by allowing for multiple levels of variance in nuisance variables that are likely to affect the counts (Link and Sauer 2002). While the goal of the BBS is to detect all breeding birds along a route, routes are run by different observers, which influences the detection and ultimately the tally of species’ abundances recorded. Bayesian methods allow for unknown and unknowable influences to be considered as random variables (LaDeau et al. 2007).

We completed all analyses in R 3.1.3 using integrated nested Laplace approximations (INLA) via the R-INLA package (Blangiardo et al. 2013). I modeled species' counts as an over-dispersed Poisson distribution, with a log-link function to relate the mean predicted count to linear predictors (Wilson et al. 2011). I modeled nuisance effects such as year, route and observer as independent random variables, and assigned standard non-informative priors via the half-Cauchy distribution to the hyper-parameters (Gelman 2006). I also incorporated a linear trend and a binary variable to indicate an observer's first year of counting birds on a given BBS route. The basic model was as follows:

$$\log(\mu) = \beta_0 + \beta_1 year + \beta_2 firstyear + route + observer + year$$

The candidate models included single weather variables, as well as their additive and interactive combinations (Table 1). I performed model selection for each species, with the goal of selecting the best model explaining each species' variation in abundance index. I ranked the models based on the Watanabe-Akaike information criterion (WAIC) which is a  Bayesian information criterion (Watanabe 2010). If the model best explaining a species' abundance patterns included a weather variable, I assessed its significance by examining the 95% credible interval (CI) of the posterior distribution. If the CI did not include zero, I considered the weather variable to have a statistically significant effect on species' abundance.

## Results

Our analysis included a total of 109 BBS routes surveyed from 1966 to 2010 across the Badlands and Prairies. These routes were surveyed between May 15 and August 4 over the study period, though 99% of routes were surveyed in June or later. The number of routes considered per species ranged from 30 to 103 (Table 2). The 14 species under consideration had total counts ranging from 614 for Sprague's Pipit (*Anthus spragueii*) to 368,814 (Western Meadowlark) across all routes from 1966–2010 (Table 2). Western Meadowlark had also by far the highest average count per route (173.15 ±145.22). Horned Lark had the second highest average count per route (48.28 ±64.19), but the standard deviation was larger than the average, indicating high variability in occurrence and detection on BBS routes in the Badlands and Prairies. The species occurring on the fewest number of routes were also those with the lowest average annual counts: Baird's Sparrow (*Ammodramus bairdii*) at an estimated (1.31 ±3.68) individuals per year, and Sprague's Pipit, at an estimated (0.79 ±2.84) individuals per year. Because differences in species detectability are not taken into account, the number of individuals are not directly comparable, but are provided to give a sense of relative abundances.

### *Extreme Weather Events*

The precipitation baselines from which spring and summer SPI were derived differed inherently because of the temporal windows considered, and dry spring observations did not correlate perfectly with dry summer years. The 50 lowest route-level spring SPI values (i.e. the strongest spring droughts) occurred in: 1967-9, 1974, 1979, 1980, 1985, 1988, 1992, 1994, 1998, 2001, 2002 and 2004. The 50 lowest route-level summer SPI values (i.e., the strongest summer droughts) occurred in 1970-1, 1973-4, 1976, 1979, 1985, 1987-8, 1990-1, 1994, 1996, 2002, and 2006-7. Thus, of the spring SPI drought years, 43% were also summer SPI drought years. The year 1980 produced 22% of the most severe spring SPI values, including the overall most extreme drought value on a route which could not be placed within the distribution. Summer SPI included four values that were too extremely negative to be modelled in the distribution, and occurred in 1970, 1994 and 2006-7. The 50 highest spring SPI values observed on a route (i.e. the wettest conditions) occurred in: 1970-1, 1975, 1977-8, 1981-2, 1986, 1991, 1995, 1998, 2005-7, 2008 and 2010. The 50 highest summer SPI values occurred in: 1968-9, 1972, 1976-82, 1984, 1992-3, 1995, 1997-9, 2001, 2004, 2008, and 2009-10. Of the 50 highest STI values observed on a route, the top 47 occurred in 1988, which in part exacerbated the severity of the drought. Of the lowest STI values, 32 of the coldest 50 values observed on routes occurred in 1998.

### *Relationship of Precipitation to Vegetation Greenness*

There was a significant positive linear relationship between SPI and SSG (RSE = 0.49, $P < 0.001$), which appeared to differ by mean EVI per route (Figure 2). Routes with higher average vegetative vigor over the time window considered (2003-2012) had less variable EVI values than routes with comparatively lower average vegetative vigor. The "greenest" points (i.e. those with greatest vegetation vigor) were clustered in a zone of little to no EVI anomaly whereas darker points, representing areas of lower vegetation vigor, were distributed at the extremes of observed values of SPI and EVI. Thus, it appears that the routes of highest mean seasonal greenness were the most consistent in vegetative condition year-to-year, across a gradient of weather conditions, while routes of lower mean seasonal greenness varied inter-annually with weather.

### *Relationship of Raw Species' Counts to Weather*

We plotted species' raw BBS counts in response to SPI (Figure 3) and STI (Figure 4) for visualization purposes. As expected due to the nature of extremes, more bird surveys occurred in average or near-average weather years than in years when extreme weather events occurred.

### *Species' Modelled Response to Precipitation and Temperature*

Of the 14 species considered, the abundances of Upland Sandpiper (*Bartramia longicauda*), Vesper Sparrow, Baird's Sparrow, Grasshopper Sparrow (*Ammodramus savannarum*) and

Eastern Kingbird (*Tyrannus tyrannus*) were significantly associated with weather (Table 4). It appears that weather metrics capturing deviation from normal (SPI and STI) were informative predictors for these 5 species. Grasshopper Sparrow responded to the interaction between within-year SPI and STI and time-lagged STI (model 8), whereas Vesper Sparrow and Eastern Kingbird responded to both within-year SPI and the prior year's SPI (model 12). Upland Sandpiper responded to within-year STI. Baird's Sparrow responded linearly to within-year SPI and STI.

Hierarchy in an interaction can be strong (i.e. both terms are independently significant) or weak (i.e. only one term is significant). Strong hierarchy in the terms of interaction suggests especially high credibility for the effect of the interaction on bird abundance. The weather interaction included in the best-fit model for Grasshopper Sparrow achieved strong hierarchy. The remaining 9 species did not respond significantly to weather. Yet, though the parameter estimates were insignificant, all but one of the best-fit models for these species included a measure of SPI (Table 4). Thus, even though none of the aforementioned species responded to weather in a way that could be substantively interpreted, the best-fit models as determined by WAIC mostly included a measure of SPI, suggesting that weather may be important for these species but I was not able to capture its effects with our datasets and framework.

## Discussion

Our goal was to determine the broad-scale effects of weather on the abundances of 14 bird species within the Badlands and Prairies (i.e. BCR 17). The metrics SPI and STI reflect weather patterns in BCR 17, from 1965 through 2010. Several years were represented in the top 50 driest and wettest route observations, whereas there were relatively few years representing the hottest and coldest observations. This pattern reflects the annual spatial variability in precipitation in this region, as compared to the relative spatial homogeneity of temperature. Variability of SPI observations at the route level is consistent with our knowledge of weather characteristics and patterns, in that precipitation can vary across relatively small spatial and temporal scales (Legates and Willmott 1990). Meanwhile, temperature regimes often prevail over large areas with less spatial and temporal variation (Malcher and Schönwiese 1987). Known drought years were generally well represented by our weather metrics, though temporal windows that best captured these events varied. The drought of 1980 was well captured in spring SPI observations, but was not included in the 50 driest summer route observations. By contrast, the drought of 2002 was captured in both spring and summer SPI extreme negative values. The 1988 drought resulted in both the lowest spring and summer SPI observations. Summer SPI captures more years of this drought period (i.e. 1987-88, 1990). Yet, drought severity can also be defined in part by temperature anomalies, because higher temperatures increase evapotranspiration (Guttman 1998). Concurrent with 1988 SPI values in our data, that year also dominated the extreme temperature observations (47 of the 50 highest STI values on routes). Thus, the severity of the 1988 drought is reflected by both precipitation and temperature extremes in our data. By contrast, 1998 hosted most (32 of 50) of the coolest route observations, and though the northeastern portion of BCR 17 experienced moderate drought during part of the spring, most of the region had normal-to-above average moisture conditions throughout the spring (Alley 1984). Therefore, the conjunctive effects of precipitation and temperature ultimately affect the environment experienced by the avian community in BCR 17, both in terms of physiological and habitat conditions (Gill 2006).

We found that five species responded significantly to weather (Upland Sandpiper, Vesper Sparrow, Baird’s Sparrow, Grasshopper Sparrow, and Eastern Kingbird). Two species are congeneric (Baird’s and Grasshopper sparrows), and responded qualitatively similarly to weather, however the interpretation of Grasshopper Sparrow’s response is not as straightforward, considering the presence of a significant interaction term. Upland Sandpiper was the only species of these five that did not respond significantly to precipitation, but instead responded positively to temperature. Eastern Kingbird and Vesper Sparrow shared the same best model (12), and responded negatively and in similar magnitude to both within-year precipitation and time-lagged precipitation.

The difference among species’ response to weather also included a temporal component. The weather conditions that best explained Eastern Kingbird, Grasshopper Sparrow, and Vesper Sparrow abundance indices occurred in both the same and the previous year. Baird’s Sparrow and Upland Sandpiper responded most strongly to weather conditions, but only in the same year. Different time windows governing weather response may represent different mechanisms driving inter-annual changes in abundance. For instance, weather effects from the prior year explaining abundance may reflect altered productivity. In other words, a time-lagged effect of weather may, on one hand, be due to a significant decrease or increase in the population due to weather during the prior year’s breeding season. On the other hand, a species’ response to weather leading up to and during the early breeding season may instead be due to movement in response to uneven distribution of conditions determined by weather. Nomadism is common in grassland bird species, and is likely a response to the relative unpredictability of habitat suitability at a given location among years (Ahlering et al. 2009).

Species that did not respond significantly to weather were Mourning Dove, Horned Lark, Western Meadowlark, Brewer’s Blackbird, Brown-Headed Cowbird, Lark Sparrow, Clay-Colored Sparrow, Field Sparrow and Sprague’s Pipit. Though severe weather can affect productivity of many species, field studies have suggested that single-year extreme events do not always result in relative abundance declines in the following year. For example, Horned Larks and Western Meadowlarks abandoned nests in mid-June 1988, but this abandonment did not translate to lower counts in the subsequent year (George et al. 1992). Further, given that 12 of the 14 species considered are migratory, conditions during other times in their annual cycle may have affected subsequent-year populations.

Characterizing how birds respond to precipitation and temperature is important in light of predicted changes in frequency and intensity of future extreme weather events (Meehl et al. 2000). Climate change in Badlands National Park, which is in the center of our study area, is projected to result in warmer (3-5°C) weather by the end of the century, and this temperature increase is likely to increase evapotranspiration (Amberg et al. 2012). Thus, although precipitation is actually projected to increase slightly in the region, the temperature increase will likely offset the precipitation increase and result in drier weather in summer months (Cowell and Urban 2010). Declines in response to extreme droughts are thus of particular concern because the grassland bird community has experienced the steepest population declines of any regional avian community within the U.S., primarily due to the loss of grassland habitat as agricultural land use has expanded (Vickery and Herkert 2001). Several bird species of semi-arid grasslands are of conservation concern, including Sharp-tailed Grouse, Upland Sandpiper (Bowen and Kruse 1993), Baird’s Sparrow (Davis and Sealy 1998), Grasshopper Sparrow and Sprague’s Pipit. Of those species, Baird’s and Grasshopper sparrows responded positively to SPI, meaning they were more abundant under wetter conditions. Thus, increased frequency of summer drought, as projected by climate models for these regions (Touma et al. 2015), could negatively impact these species. More in-depth climate vulnerability assessments for the species responding significantly to weather should be conducted to assess further risks posed by climate change, and guide adaptive management strategies.

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Table 1-1. Combinations of precipitation and temperature variables considered to model abundance of 14 grassland bird species in BCR 17. The subscript "lag" indicates the previous year's weather value.

| Model No. | Weather Variables Included |
|---|---|
| 1 | Null |
| 2 | SPI |
| 3 | STI |
| 4 | SPI*STI |
| 5 | SPI + STI |
| 6 | $SPI_{lag}$ + $STI_{lag}$ + SPI*STI |
| 7 | $SPI_{lag}$ + SPI*STI |
| 8 | $STI_{lag}$ + SPI*STI |
| 9 | SPI + STI + $SPI_{lag}$ |
| 10 | SPI + STI + $STI_{lag}$ |
| 11 | SPI + STI + $SPI_{lag}$ + $STI_{lag}$ |
| 12 | SPI + $SPI_{lag}$ |
| 13 | STI + $SPI_{lag}$ |
| 14 | STI + $STI_{lag}$ |
| 15 | SPI + $STI_{lag}$ |
| 16 | SPI + $SPI_{lag}$*$STI_{lag}$ |
| 17 | STI + $SPI_{lag}$*$STI_{lag}$ |
| 18 | STI + SPI + $SPI_{lag}$*$STI_{lag}$ |
| 19 | SPI + $SPI_{lag}$ + $STI_{lag}$ |
| 20 | STI + $SPI_{lag}$ + $STI_{lag}$ |
| 21 | $SPI_{lag}$ |
| 22 | $STI_{lag}$ |
| 23 | $SPI_{lag}$*$STI_{lag}$ |
| 24 | $SPI_{lag}$ + $STI_{lag}$ |
| 25 | $SPI_{lag}$*SPI |
| 26 | $STI_{lag}$*STI |
| 27 | $SPI_{lag}$*STI |
| 28 | $STI_{lag}$*SPI |
| 29 | $SPI_{lag}$*SPI + STI |
| 30 | $STI_{lag}$*STI + SPI |
| 31 | $SPI_{lag}$*STI + SPI |
| 32 | $STI_{lag}$*SPI + STI |
| 33 | $SPI_{lag}$*SPI + $STI_{lag}$ |
| 34 | $STI_{lag}$*STI + $SPI_{lag}$ |
| 35 | $SPI_{lag}$*STI + $STI_{lag}$ |
| 36 | $STI_{lag}$*SPI + $SPI_{lag}$ |
| 37 | $SPI_{lag}$*SPI + $STI_{lag}$ |
| 38 | $STI_{lag}$*STI + $SPI_{lag}$ + SPI |
| 39 | $SPI_{lag}$*SPI + $STI_{lag}$ + STI |

Table 1-2. Combinations of precipitation and temperature variables considered to model abundance of 14 grassland bird species in BCR 17. The subscript “lag” indicates the previous year’s weather value.

| Common Name | Scientific Name | Shrub cover preference | Herbaceous height preference |
|---|---|---|---|
| **Upland Sandpiper** | ***Bartramia longicauda*** | **Minimal/none (<1% cover)** | **Moderate-high (>15 cm)** |
| Mourning Dove | *Zenaida macroura* | Generalist | |
| Eastern Kingbird | *Tyrannus* | Riparian | |
| **Horned Lark** | ***Eremophila alpestris*** | **Minimal/none (<1% cover)** | **Low-moderate (<15 cm)** |
| Sprague’s Pipit | *Anthus spragueii* | Low (<1% cover) | Low (<10 cm) |
| Brown-headed Cowbird | *Molothrus ater* | Generalist | |
| Western Meadowlark | *Sturnella neglecta* | Minimal/none (<1% cover) | Moderate (10-15 cm) |
| Brewer’s Blackbird | *Euphagus cyanocephalus* | Generalist | |
| Vesper Sparrow | *Pooecetes gramineus* | Low shrub (1-5% cover) | Low (<10 cm) |
| **Baird’s Sparrow** | ***Ammodramus bairdii*** | **Minimal/none (<1% cover)** | **Moderate-high (> 15 cm)** |
| Grasshopper Sparrow | *Ammodramus savannarum* | Minimal/none (<1% cover) | High (>15 cm) |
| **Lark Sparrow** | ***Chondestes grammacus*** | **Low (1-5% cover)** | **Low-moderate (< 15 cm)** |
| Clay-Colored Sparrow | *Spizella pallida* | Moderate (>5% cover) | High (>15 cm) |
| Field Sparrow | *Spizella pusilla* | Moderate (>5% cover) | High (>15 cm) |

Table 1-3. Summary statistics for bird species included in this analysis on BBS routes in BCR 17 from 1980 to 2012. For each species I present the total number of birds detected over all routes during the 32 year period, and average annual count (Average). Minimum (min.) and maximum (max.) frequency are the lowest and highest number of routes a species occurred on in a given year. Average frequency is the average number of routes a species is found on per year, and the associated standard deviation.

| Common Name | Scientific Name | Shrub cover preference | Herbaceous height preference |
|---|---|---|---|
| **Upland Sandpiper** | ***Bartramia longicauda*** | **Minimal/none (<1% cover)** | **Moderate-high (>15 cm)** |
| Mourning Dove | *Zenaida macroura* | Generalist | |
| Eastern Kingbird | *Tyrannus tyrannus* | Riparian | |
| **Horned Lark** | ***Eremophila alpestris*** | **Minimal/none (<1% cover)** | **Low-moderate (<15 cm)** |
| Sprague's Pipit | *Anthus spragueii* | Low (<1% cover) | Low (<10 cm) |
| Brown-headed Cowbird | *Molothrus ater* | Generalist | |
| Western Meadowlark | *Sturnella neglecta* | Minimal/none (<1% cover) | Moderate (10-15 cm) |
| Brewer's Blackbird | *Euphagus cyanocephalus* | Generalist | |
| Vesper Sparrow | *Pooecetes gramineus* | Low shrub (1-5% cover) | Low (<10 cm) |
| **Baird's Sparrow** | ***Ammodramus bairdii*** | **Minimal/none (<1% cover)** | **Moderate-high (> 15 cm)** |
| Grasshopper Sparrow | *Ammodramus savannarum* | Minimal/none (<1% cover) | High (>15 cm) |
| **Lark Sparrow** | ***Chondestes grammacus*** | **Low (1-5% cover)** | **Low-moderate (< 15 cm)** |
| Clay-Colored Sparrow | *Spizella pallida* | Moderate (>5% cover) | High (>15 cm) |
| Field Sparrow | *Spizella pusilla* | Moderate (>5% cover) | High (>15 cm) |

Table 1-4. Modeled response of species’ abundance index to weather. The model number corresponds to the list of candidate models provided in Table 1. The value for each parameter is the beta estimate, and the credible interval follows in parentheses. If a given parameter was not included in the model, the cell is empty. The best model was chosen by lowest Watanabe-Akaike information criterion (WAIC). Species in which the best model of abundance index included a significant weather effect (CI of the β estimate did not include 0) are in bold. For the case of Brown-Headed Cowbird, the significant parameter estimate was included in an interaction term, and the interaction only exhibited weak hierarchy (italics).

| Species | Model | SPI | $\text{SPI}_{lag}$ | STI | $\text{STI}_{lag}$ |
|---|---|---|---|---|---|
| **Upland Sandpiper** | **3** | | | **0.101 (0.046, 0.156)** | |
| **Eastern Kingbird** | **12** | **-0.032 (-0.064, 0)** | **-0.057 (-0.086, -0.028)** | | |
| Horned Lark | 25 | -0.005 (-0.038, 0.029) | -0.009 (-0.042, 0.023) | | |
| Sprague's Pipit | 2 | 0.126 (-0.03, 0.279) | | | |
| *Brown-Headed Cowbird* | *30* | *-0.006 (-0.037, 0.025)* | | *0.057 (0.013, 0.101)* | *0.025 (-0.016, 0.066)* |
| Western Meadowlark | 24 | | -0.001 (-0.015, 0.013) | | 0.018 (-0.006, 0.043) |
| Brewer's Blackbird | 10 | -0.034 (-0.082, 0.014) | | 0.027 (-0.029, 0.083) | 0.016 (-0.04, 0.071) |
| **Vesper Sparrow** | **12** | **-0.054 (-0.093, -0.015)** | **-0.02 (-0.057, 0.017)** | | |
| **Baird's Sparrow** | **5** | **0.195 (0.079, 0.311)** | | **-0.161 (-0.297, -0.029)** | |
| **Grasshopper Sparrow** | **8** | **0.11 (0.067, 0.154)** | | **-0.075 (-0.128, -0.023)** | **-0.076 (-0.124, -0.029)** |
| Lark Sparrow | 28 | 0.007 (-0.043, 0.056) | | | 0.022 (-0.04, 0.083) |
| Clay-Colored Sparrow | 1 | | | | |
| Field Sparrow | 25 | -0.031 (-0.11, 0.049) | 0.018 (-0.047, 0.082) | | |

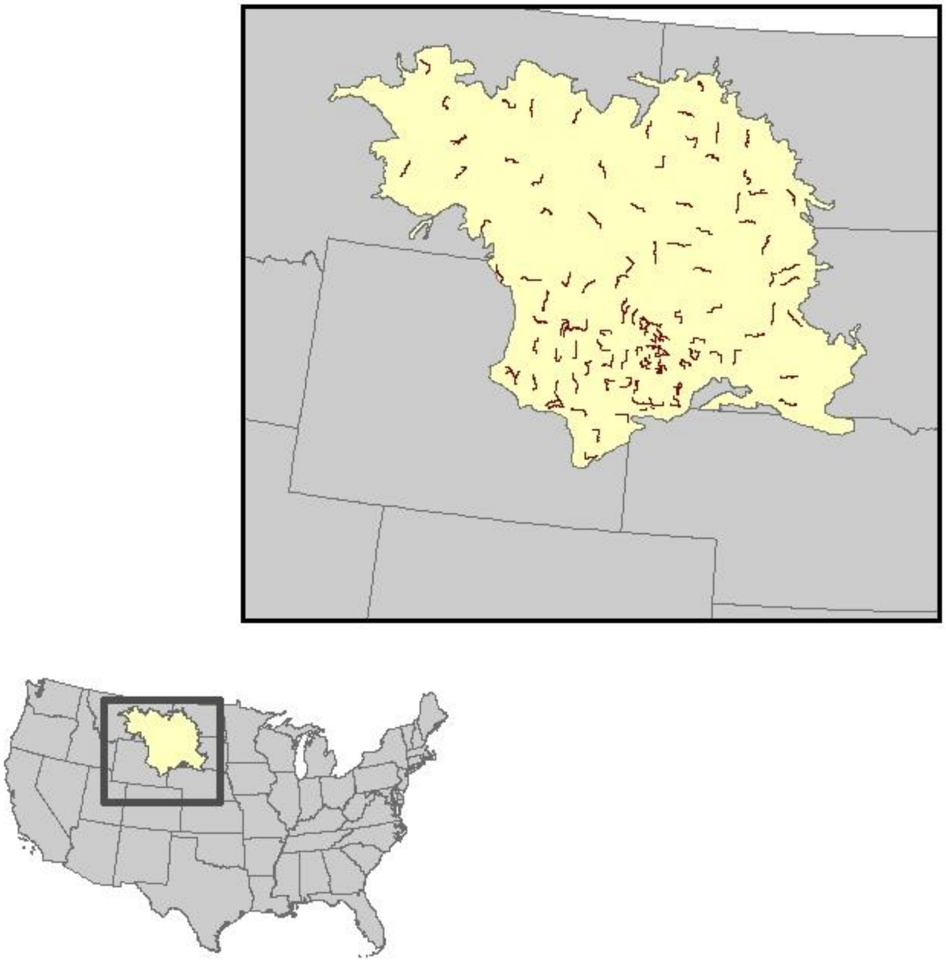

Figure 1-1. Location of Bird Conservation Region 17 within North America. Lines represent BBS routes.

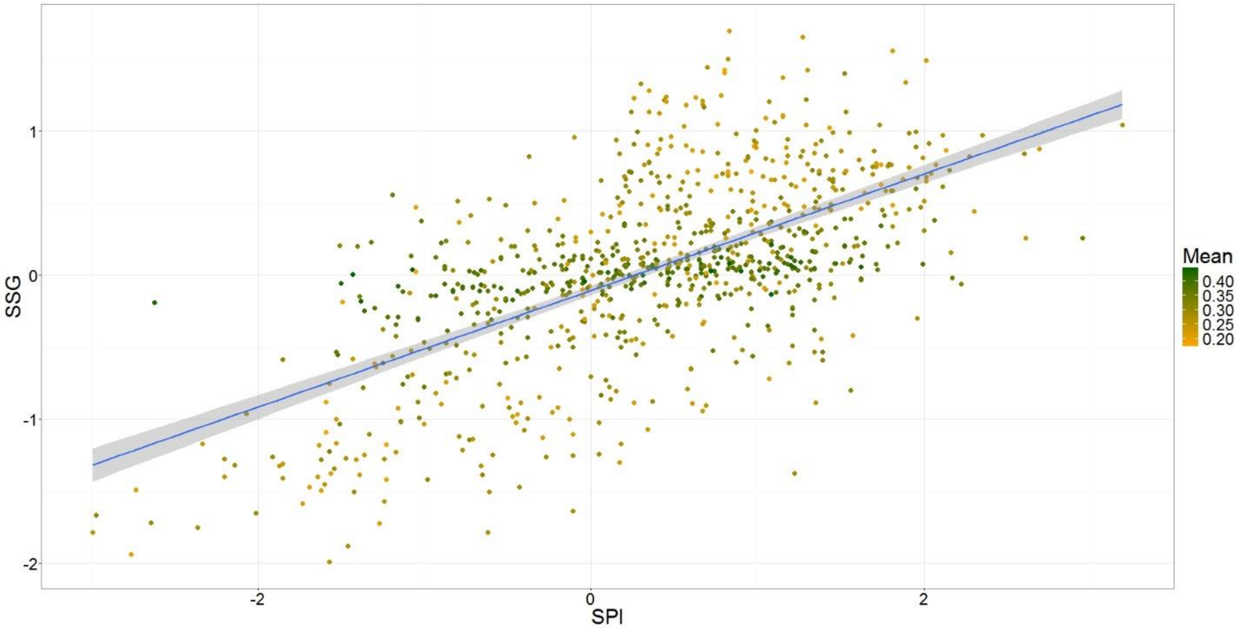

Figure 1-2. The relationship between Standardized Precipitation Index (SPI) and standardized seasonal greenness (SSG) in BCR 17. Dots are a route's observation of both variables (SPI and SSG) in a given year. Color codes are the average EVI for the route from 2003-2012. The residual standard error of the simple linear regression between spring SPI and June SSG was 0.49, and the slope of the line was 0.4047, bracketed by the 95% confidence interval shown in gray.

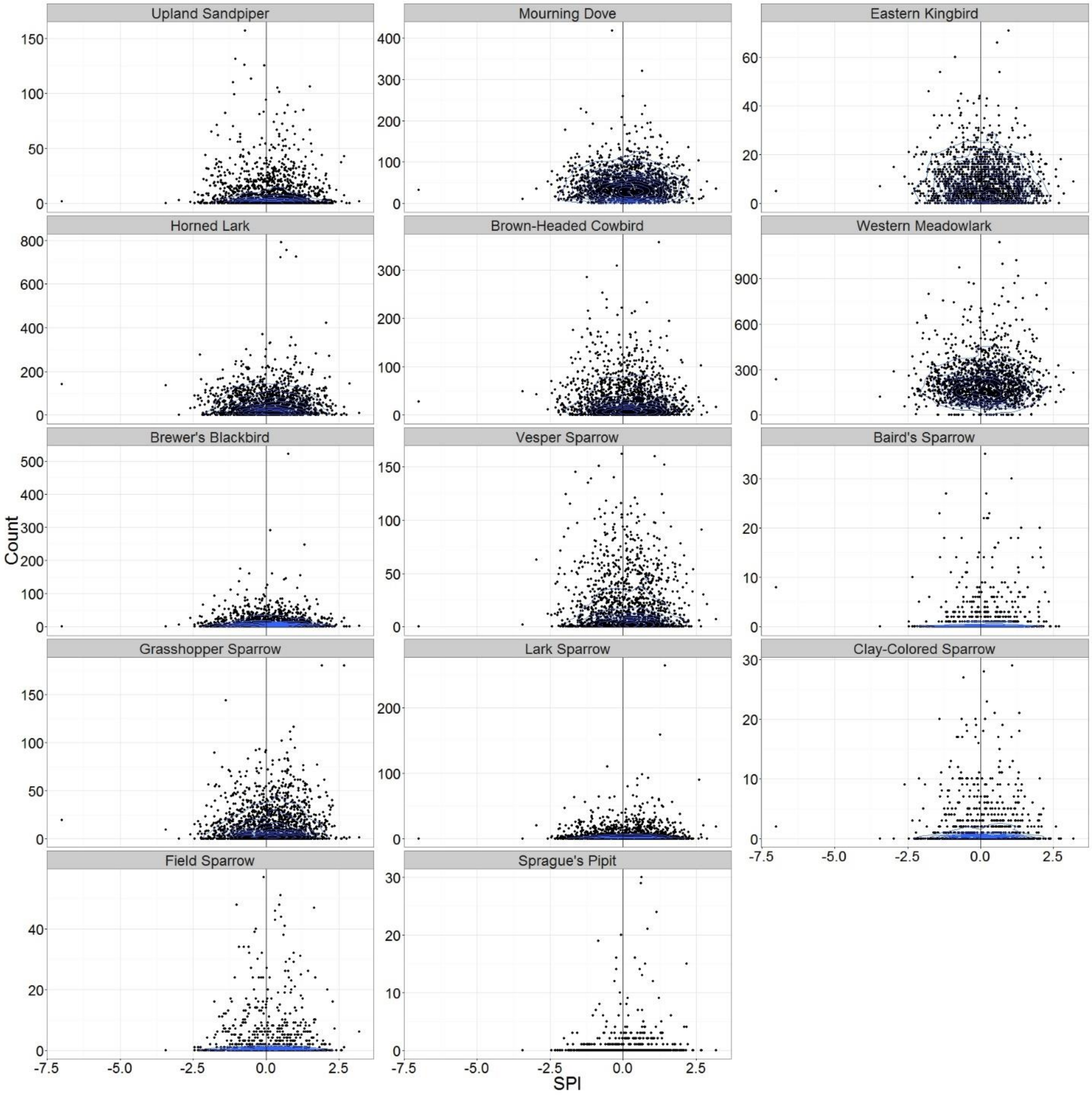

Figure 1-3. Species' raw counts in relation to SPI, with density contours overlain on the point cloud.

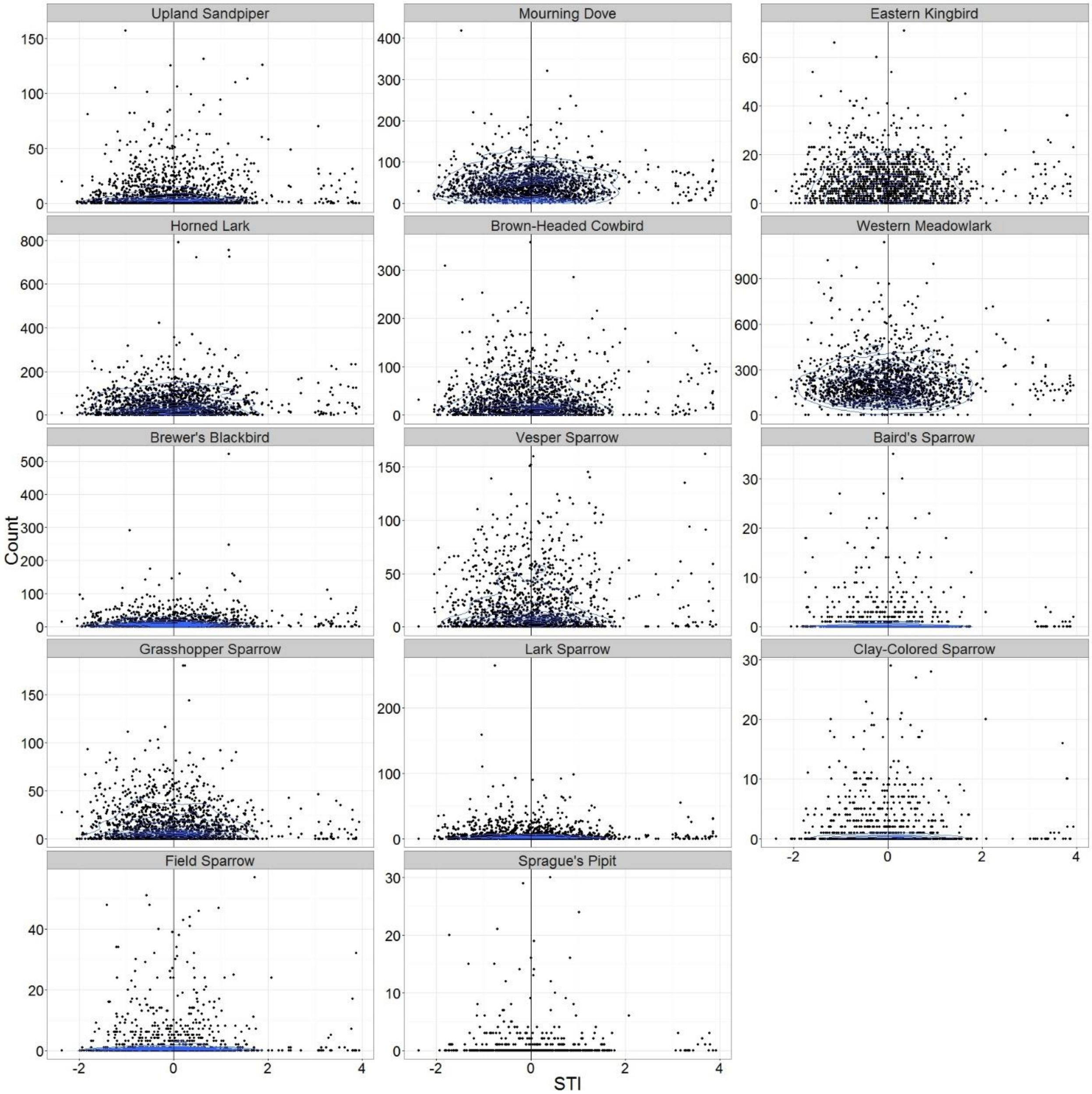

Figure 1-4. Species' raw counts in relation to SPI, with density contours overlain on the point cloud.

# Chapter 2: Response to weather mediated by site fidelity in birds.

## Abstract

Weather can affect avian survival, reproductive output or spatial distribution through its influence on inter-annual movement by birds or on site fidelity. Degree of site fidelity likely varies across a gradient of woody cover, though evidence is available largely from mark-recapture studies at a local scale. I aimed to characterize 1) inter-annual variability in abundance by avian habitat community as a proxy of site fidelity, and 2) how avian communities respond to weather at broad scales. I hypothesized that the abundance of grassland bird species would be more variable on routes where they occur, and would respond to within-year weather, while abundance of forest species would be less variable and exhibit little or no response to weather. I quantified percent tree cover in the landscape, used standardized precipitation index (SPI) and standardized temperature index (STI) to characterize weather. I developed Bayesian hierarchical models to represent relationships between avian abundance indices and these predictor variables, and performed model selection for each species. Bird abundance variability (as measured by coefficient of variation, CV) was negatively related to percent tree cover ($R^2 = 0.455$, $p < 0.0001$). Community response to weather was strongest for grassland birds (12 out of 15 species considered), though weather also affected some open woodland/scrub species (3 of 27) and forest species (5 of 16). Broadly, I saw a pattern of increasing site fidelity with increasing tree cover. Avian communities with low site fidelity generally responded more strongly to inter-annual variation in conditions.

## Introduction

Climate and land cover are spatial phenomena that shape the evolution of animal communities inhabiting a region (Olson 2001). Both averages and variability of precipitation and temperature contribute to regional climate (Peel et al. 2007). Weather events occur with a probability derived from the mean and variation of the climate distribution. In other words, weather is a short-term phenomenon, while climate is essentially average or typical weather (Liston and Elder 2006). Climates with high variance produce wide-ranging weather events, whereas climates with low variance produce comparatively moderate weather. Biomes are largely shaped and defined by the prevailing climate (Sims et al. 1978). Thus, species inhabiting a particular biome must cope with the normative level of weather variability. In terms of inter-annual variation in aboveground net primary productivity, grasslands and forests are at opposite ends of the spectrum, with high variability in grasslands and low variability in forests (Knapp and Smith 2001). Species inhabiting regions in which the land cover spans this continuum thus must adapt to the regime of variability in climate and its effect on land cover.

Species' evolved responses to the characteristics of ecosystem is expressed, in part, through the behavioral plasticity of their response to inter-annual variation in weather. As highly mobile organisms, birds are able to move in response to different inter-annual conditions. If individuals are unable to respond to variation, they may misappropriate energy expenditure, and ultimately die (McKechnie and Wolf 2009) or may fail to reproduce. Thus, it is advantageous for individuals to adjust their strategies according to prevailing conditions. The magnitude and direction of deviation from normative climate conditions in a given year may govern a species' response. For example, in the face of extreme weather, individuals of some species are known to move outside of their normal range (Bateman et al. 2015). A large-scale movement may correspond with forgoing a breeding season (Henny 1973). Alternatively, individuals may remain at the same location but fail to breed if conditions are unsuitable, such as was the case for bridled titmice in an extreme drought year (Christman 2002).

Site fidelity is correlated with spatiotemporal predictability of environmental conditions, such that species inhabiting unpredictable environments typically exhibit low site fidelity (Alerstam and Enckell 1979), whereas species inhabiting predictable environments may have comparatively higher site fidelity (Hoover 2003). It is advantageous for individuals to return to areas that consistently exhibit high site quality (as indicated by high reproductive success) over many years (Schmidt 2004). Therefore, site fidelity may be a mechanism driving a species' response to the weather experienced just before and during the breeding season. Grassland bird site fidelity is known to be low (Askins 1993) while forest bird site fidelity is generally high (Dowsett 1985). Low site fidelity should appear as changing spatial distributions of abundance inter-annually (Mueller and Fagan 2008). In other words, birds that exhibit low site fidelity are likely to relocate annually to where conditions are suitable, leading to concentrations of individuals where habitat conditions are desirable (Reside et al. 2010). The corollary is that species with low site fidelity should also abandon sites that are no longer suitable in a subsequent year. By contrast, species that exhibit high site fidelity should maintain similar densities in a given place from year to year, assuming that habitat quality is consistent and is at or near carrying capacity. Territory occupancy should remain stable, either because individuals return or because other individuals take over a high-quality territory in the absence of a former occupant. Thus, site fidelity tendencies of species should produce patterns of abundance at the population level, such that species that exhibit low site fidelity are variable in abundance across locations among years, whereas species that exhibit high site fidelity exhibit relatively stable abundance across locations among years.

Measures of site fidelity are typically derived from field studies of return rates, which are based on recapturing marked birds in a subsequent year. Mark-recapture is the finest scale and most reliable source of site fidelity data available, because the technique involves directly observing a known individual returning (or not) to a location. Thus, most often, data gathered on site fidelity are limited to a single local population. Sample sizes are often small, and lack of recapture can be due to many factors unrelated to site fidelity (Thogmartin and Knutson 2007). Examining patterns of abundance may allow quantification of avian site fidelity trends over broader scales (Villard et al. 1995). Further, measures available at broad scales allow for simultaneously considering factors that may drive movements of species, thus making it possible to examine how site fidelity may influence species’ response to inter-annual variability in conditions (Winter et al. 2005).

**Our goal was to quantify patterns of abundance variation in response to weather, and to determine the degree to which tree cover affects avian response to weather.** Our objectives were to quantify inter-annual variability per species, and to determine the effects of tree cover and within-year weather on species’ abundance index. In modelling species’ response to percent tree cover, I aimed to quantify species’ tree cover affiliations, in order to describe a continuous as opposed to categorical habitat classification. In order to elucidate degree of site fidelity across a tree cover gradient, I considered inter-annual variability in species’ abundance to be a proxy of site fidelity. I hypothesized that site fidelity would be low for grassland species and high for forest species. I also hypothesized that site fidelity tendencies would be related to within-year weather response, such that species exhibiting low site fidelity would respond significantly to within-year weather. Thus, I expected that grassland bird species would respond negatively to tree cover and have a significant response to weather. By contrast, I expected that forest species would respond strongly positively to tree cover, but would not have a significant response to weather. I hypothesized peak abundance of shrub-affiliated species would occur at intermediate levels of tree cover, thus generating a non-linear response to tree cover.

## Methods

### *Study Area*

Bird Conservation Regions (BCRs) have been delineated by North American Bird Conservation Initiative (NABCI) in keeping with Commission for Environmental Cooperation (CEC) ecological units, and are designed to capture avian communities spatially (Sauer et al. 2003). I analyzed data within Bird Conservation Regions (BCRs) 11, 22, and 23, which correspond to Prairie Potholes, the Eastern Tallgrass Prairie and the Prairie Hardwood Transition, respectively (Figure 1). This set of BCRs spans a gradient of forest to prairie from east to west. The Prairie Hardwood Transition (BCR 23) captures the prairie-to-forest ecotone (Riffell et al. 2008). The Eastern Tallgrass Prairie (BCR 22) is dominated by grassland in the west and becomes more heavily forested in the east. The Prairie Potholes (BCR 11) is grassland, though with heavy agricultural land use.

### *Bird Data*

The North American Breeding Bird Survey (BBS) has been conducted since 1966, and is designed to characterize breeding bird abundance in natural areas across the conterminous US (Keller and Scallan 1999). Each route covers 39.4 km of secondary road, and all birds seen and heard during each 3-minute stop (spaced every 0.8 km along the route) are counted. I excluded route runs that did not meet quality standards, as indicated in the dataset. I also only used standard BBS route runs, and did not include resampling efforts or non-standard protocols. The timing of the BBS is designed to capture adult birds on breeding territories, meaning that hypothetically, species have already made decisions to defend a territory where they are recorded (Thogmartin et al. 2004).

We first examined the 100 most common species in BCRs 11, 22 and 23 by total number of counts. I categorized each species by habitat affiliation in order to compare the results of our modelled tree cover responses (see below) to existing knowledge (Cornell Lab of Ornithology 2011). I excluded wetland species from our analysis, since wetlands were not within our habitat gradient of interest. In total, I analyzed the 58 most common species meeting our criteria. I retained species classified as grassland, town (obviously a modern classification not reflecting native habitat associations), open woodland, scrub, and forest (Appendix 1).

Spatial analysis was based on a dataset of digitized BBS route paths (cite the source- website?). I split routes into fifths in order to match the finest scale of BBS count data available. Due to digitization limitations, I was not always able to fully discern the paths of complex routes, since stop-level spatial data are not yet available. Thus, routes that I could not confidently split into fifths were excluded from our analysis.

### *Weather Data*

We analyzed weather data from the Maurer historical dataset (Maurer et al. 2002), which spans the contiguous U.S. at 1/8th degree spatial resolution from 1949-2010. I used weather data from 1966 through 2010 to match the temporal record of BBS data, and extracted values from the route centroid of each BBS route per year. To characterize precipitation, I calculated the Standardized Precipitation Index (SPI) as an indicator of the degree to which a given years' precipitation differed from the long term mean. This was accomplished by fitting a Pearson-III distribution to total precipitation for the 90-day time period leading up to June 1, and converted precipitation values to percentiles. I then transformed the percentiles to standard deviations from a standard normal distribution to aid in interpretability. The time window within each year for which I calculated SPI was designed to characterize precipitation conditions that would have influenced habitat conditions at the time when birds made decisions about location of settlement each year.

Similarly, I calculated the standardized temperature index (STI) as a measure of extremity of temperature for the month of June in each year of our analysis. Temperature was well-represented by a standard normal distribution, so standard deviations were readily calculated and did not require transformation. The time window for STI was chosen to represent temperature of the early breeding season.

### *Vegetation Data*

In order to measure percent tree cover within the landscape influencing bird abundance on BBS routes, I used the Moderate-resolution Imaging Spectroradiometer (MODIS) product MOD44B, Vegetation Continuous Fields (VCF). The VCF product is derived from remote sensing imagery, producing estimates of percent tree cover at 250m resolution (Hansen et al. 2005). I averaged percent tree cover within a 400m buffer of each fifth of a BBS route, to match the approximate area relevant to detection at stops along the route. I tested for spatial autocorrelation using global Moran's I.

*Statistical Analysis*

To allow for multiple levels of variance in nuisance variables that are likely to affect BBS data, I developed models in a Bayesian hierarchical framework (Sauer and Link 2002). I modeled BBS data with an over-dispersed Poisson distribution, using a log-link function to relate the mean predicted count to linear predictors (Wilson et al. 2011). I modeled nuisance effects such as year, route and observer as independent random variables, and assigned non-informative priors via the half-Cauchy distribution to the hyper-parameters. I also incorporated a linear trend and a binary indicator variable for an observer's first year.

The basic (null) model follows:

$$\log \mu = \beta_0 + \beta_1 year + \beta_2 firstyear + (route \,\&\, observer) + year \tag{1}$$

The candidate models included both additive and interactive (i.e. pairwise-product) combinations of weather and tree cover variables, added to the null model (Table 1). I fit the set of candidate models for each species using integrated nested Laplace approximations (INLA) via the R-INLA package (Blangiardo et al. 2013). I ranked our models based on the deviance information criterion (WAIC). For the best model, I examined the 95% credible intervals (CI) of the posterior distribution of parameter estimates, and assumed that parameters for which the credible intervals did not include zero were statistically significant. This ultimately resulted in a best model for each species, for which I examined the presence and significance of included weather and/or tree cover variables.

## Results

### *Characterization of tree cover associations per species*

In total, I considered 14 grassland bird species, 22 open woodland species, 5 scrub species, and 16 forest species. Of the 58 total species considered, 55 species responded significantly to percent tree cover. Percent tree cover was highly auto-correlated across our landscape ($p < 0.001$), which is unsurprising given that tree cover roughly decreases from east to west. Thus, percent tree cover was an important explanatory variable for most species considered, indicating the utility of VCF as a product to quantify habitat. Further, the effect sizes and directionality of species' response to percent tree cover were mostly in accordance with known preferences for tree cover (Figure 2). Modelled response to tree cover also elucidated nuanced habitat associations. For example, brown-headed cowbird, which was historically restricted to grasslands, had a slightly positive response to percent tree cover, which highlights this species' current use of forest edge. Similarly, eastern bluebird, classified as a grassland species (Cornell Lab of Ornithology 2011), showed stronger affinity with open woodland in our breeding season study, likely because of its dependence on tree cavities for nesting. The two species that were originally classified as "town" affiliates were ranked in accordance with known native habitat associations; our results showed that Brewer's blackbird is a grassland species (Martin 2002) and had a substantively negative response to percent tree cover, whereas northern mockingbird is a scrub species (Farnsworth, George Londono et al. 2011) and had a very small positive response to percent tree cover.

In contrast to our hypothesis that open woodland and shrub species would not exhibit a significant response to percent tree cover, species of these habitat associations did mostly respond linearly to percent tree cover. Yet, since I also only included routes where a given species was found at least once, I limited the potential habitat types considered per species, which also likely allowed subtle responses to tree cover to be detected in our model framework. This may explain the relatively large positive responses of Carolina wren and field sparrow to percent tree cover (Fig. 2), though these species are classified as open woodland/scrub species (Cornell Lab of Ornithology 2011). The abundances of 3 species were not significantly associated with percent tree cover, according to our models. These species were orchard oriole, eastern kingbird and brown thrasher. The best model for orchard oriole still incorporated the variable, but the parameter estimate was insignificant. Thus, our modelled response to tree cover overall allowed for a finer-grained habitat preference classification than the general literature-based categorizations (see Fig. 5).

### *Species' Inter-annual Variability*

The counts of grassland species were consistently more variable on routes year-to-year than the counts of forest species (Figure 3). A simple linear regression between CV of counts of each species and the percent tree cover parameter estimate (Figure 4) revealed a significant effect of percent tree cover as a predictor of CV ($p < 0.0001$) and a substantial amount of variation explained ($R^2 = 0.455$).

### *Responses to Weather and Habitat*

Species' response to percent tree cover and weather varied with habitat-community associations (Figure 2). Percent tree cover interacting with a weather variable was a term in the models of most (10 of 16) species for which response to tree cover was negative (i.e. grassland-to-scrub species). Thus, though the response to tree cover was in line with expectations regarding habitat use by the grassland species, as indicated by the direction and rank of the tree cover parameter estimates, the response to tree cover was part of a dependent relationship with weather in most cases. Conversely, 24 of the 41 species with positive responses to percent tree cover responded independently of weather. Of the 17 species that exhibited an interaction with weather and positive response to percent tree cover, 10 were open woodland/scrub species (Table 3).

For most species (46 of 58), a weather parameter was included in their best model, but only 26 species had a significant weather parameter estimate. Of the 26 species that responded to weather, 9 were grassland birds, 11 were open woodland/scrub species, and 6 were forest species. Thus, in proportion to the total number of species modelled per habitat guild, 64% (9 of 14) of grassland bird species considered responded significantly to weather, compared to 41% of open woodland/scrub species (11 of 27) and 38% of forest species (6 of 16). The best models for savannah sparrow and horned lark included a significant negative response to percent tree cover and a weather parameter. In the case of savannah sparrow, the best model included an interaction of percent tree cover with STI, and for horned lark, the best model was the additive model of percent tree cover and SPI (model 7). Though the weather parameter was insignificant in both cases, the best model still included weather and was selected above a model including percent tree cover alone.

Most (8 of the 14) grassland bird species considered were best modelled as responding to an interaction of percent tree cover and weather in their best fit model, and 6 of the 8 interactions exhibited strong hierarchy. Hierarchy in an interaction can be strong (i.e. both terms are independently significant) or weak (i.e. only one term is significant). Hierarchical support of an interaction lends credibility to the effect of the interaction (Cortina 1993). All models including interactions of land cover and weather achieved weak hierarchy, because percent tree cover was always significant except in one case (orchard oriole). Thus, there is evidence that for the majority of grassland birds considered, the interaction between land cover and weather was important in predicting the annual abundance index. Of species that responded significantly negatively to STI (dickcissel, bobolink, song sparrow, common yellowthroat, yellow warbler, cedar waxwing and least flycatcher), all but dickcissel responded to an interaction of percent tree cover and STI (Figure 5). Further, only one species, least flycatcher is a forest species; the remainder are grassland-to-open woodland species. Those that responded positively to STI mostly (4 of 5) responded linearly to STI and percent tree cover.

### *Species' Modelled Response to Precipitation and Temperature*

Of the 14 species considered, the abundances of Upland Sandpiper (*Bartramia longicauda*), Vesper Sparrow, Baird's Sparrow, Grasshopper Sparrow (*Ammodramus savannarum*) and Eastern Kingbird (*Tyrannus tyrannus*) were significantly associated with weather (Table 4). It appears that weather metrics capturing deviation from normal (SPI and STI) were informative predictors for these 5 species. Grasshopper Sparrow responded to the interaction between within-year SPI and STI and time-lagged STI (model 8), whereas Vesper Sparrow and Eastern Kingbird responded to both within-year SPI and the prior year's SPI (model 12). Upland Sandpiper responded to within-year STI. Baird's Sparrow responded linearly to within-year SPI and STI.

Hierarchy in an interaction can be strong (i.e. both terms are independently significant) or weak (i.e. only one term is significant). Strong hierarchy in the terms of interaction suggests especially high credibility for the effect of the interaction on bird abundance. The weather interaction included in the best-fit model for Grasshopper Sparrow achieved strong hierarchy. The remaining 9 species did not respond significantly to weather. Yet, though the parameter estimates were insignificant, all but one of the best-fit models for these species included a measure of SPI (Table 4). Thus, even though none of the aforementioned species responded to weather in a way that could be substantively interpreted, the best-fit models as determined by

WAIC mostly included a measure of SPI, suggesting that weather may be important for these species but I was not able to capture its effects with our datasets and framework.

## Discussion

At the broad scale of BCRs and using population-level data, I found evidence of differential site fidelity tendencies and weather response of avian communities across a gradient of woody cover. The broad-scale patterns of species' abundance variability are consistent with our hypotheses, and with previous studies investigating site fidelity phenomena at finer scales (Jones et al. 2007). Negative response to percent tree cover reflects aversion to woody cover, and species that exhibited this response were largely those classified as grassland birds (Peterjohn and Sauer 1999). Conversely, positive response to percent tree cover reflects use of woody cover, and the effect size (as indicated by parameter estimates for percent tree cover) corresponds roughly to preference for tree canopy cover (Boulinier et al. 1998). Further, the CV of species' counts shows the opposite pattern, demonstrating an increase in variability of species' abundance with decreasing tree cover. Species classified as open woodland affiliates exhibited variability in abundance among years that was intermediate between grassland and forest species, yet intergrading with scrub and forest species. The pattern over decades and broad regions is suggestive of life history characteristics that vary by habitat type (Schlossberg 2009). Thus, the relative variability in abundance on BBS routes of grassland birds compared to forest birds may be reflective of general trends toward low vs. high site fidelity (Igl and Johnson 1997).

Grassland species appeared to respond more strongly and consistently to weather than forest species, and to have a dependent response based on presence and amount of woody cover. By the time of the BBS survey each year, birds have already assessed conditions at the breeding ground either upon return to the area from migration, or in the case of residents, throughout the spring

(Morris et al. 2003). Bird response to weather could be the result of either movement or behavior that causes them to be less easily detectable (Rollfinke and Yahner 1990). Migratory nomadism is a term used to describe the mechanism driving low site fidelity (Dean 1997). Thus, the responses to weather in our models may reflect grassland bird shifts in concentration on BBS routes among years based on where suitable weather has provided suitable habitat (Ahlering et al. 2009). Since an interaction between weather and land cover was observed for most grassland species I modeled, and given prior knowledge that grassland birds are nomadic, I infer that an interactive response to weather and land cover may be due to migratory nomadism (Jones et al. 2010). Further, in grassland systems, weather is the preeminent driver of grassland structure year-to-year, so species may actually be responding to habitat condition rather than the weather variables themselves (Yang et al. 2008).

An interaction between land cover and weather in a model could have different interpretations based on assignment of the moderating variable (Jaccard and Turrisi 2003), and the relationship could in actuality be driven by different ecological phenomena. It is possible that weather may be the moderating variable for species that are not averse to woody cover, whereas woody cover may be the moderating variable for species that avoid woody cover (Graves et al. 2010). Species that are not averse to woody cover may seek woody cover as shelter in times of extremes, whereas species that avoid woody cover are restricted to herbaceous landscapes, no matter the weather conditions (Ribic and Sample 2001). Most of the species (5 of 6) that responded to an interaction of percent tree cover and temperature, and responded negatively to increasing deviation in temperature above the norm, were shrub-to-woodland species. For these species, it is plausible that the degree of woody cover they use is moderated by weather. The grassland species that was the exception, bobolink, is averse to woody cover and thus is likely limited by suitable habitat (i.e. weather response is constrained by woody cover).

With projected climate change, understanding how species are likely to respond can inform management implications. The Midwestern US has already become overall warmer compared to historic climate (O'Neal et al. 2005). Future climate change is projected to be most dramatic in the southwestern portion of our study area (Wuebbles and Hayhoe 2004). Thus, in conjunction with heavy land use and historic change in the region, BCR 22 and the southern portion of BCR 11 may be most imminently affected by changing climate. To determine best approaches, it is important to consider both climate change projections and the target species of management efforts. It is well known that extreme weather affects adult survival, condition and nesting success (Nice 1957). Further, there is evidence that population density is influenced by weather for some of the species that had significant responses in our analyses (Chase et al. 2005). The notion that changes in density may be due to changing habitat use in times of extremes has been noted in field studies, though the linkage is often not explicit (Mazerolle and Dufour 2005). Thus, a two-pronged approach, along with finer-scale investigation of the patterns I observed in our analysis, is likely necessary in considering adaptive management for species along the gradient of forest-to-grassland in the central US. For species that change their use of woody cover during extremes, adaptive management could incorporate climate refugia in the form of landscape heterogeneity. For species that are averse to woody cover, maintaining large tracts of available grassland habitat in order to best allow for movement in times of extremes could facilitate dispersal to avoid extreme conditions (Thogmartin et al. 2006). Consideration of long-range movements should be given for species that disperse widely in times of extremes. Considering that the eastern tallgrass prairie and the southern prairie potholes are currently the most at-risk areas of our study region (Wuebbles and Hayhoe 2004), species of conservation concern in these areas should be given priority in evaluating adaptive management strategies in the region.

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Table 2-1: Weather effects in candidate models. The null model was described in Eq. 1, and the following weather and land cover effects were built upon that basic model for selection. The best model was selected per species based on lowest WAIC score. Significance of the weather or woody vegetation effect was determined by whether or not the credible interval of the parameter estimate crossed zero.

| Model | Number | Effects |
|---|---|---|
| Null | 1 | (See Eqn. 1) |
| Precipitation | 2 | SPI |
| Temperature | 3 | STI |
| Weather Interaction | 4 | SPI*STI |
| Weather Additive | 5 | SPI + STI |
| Vegetation | 6 | VCF |
| Habitat and Weather | 7 | SPI + VCF |
|  | 8 | STI + VCF |
|  | 9 | SPI*STI + VCF |
|  | 10 | SPI + STI + VCF |
| Weather Interaction with Vegetative Cover (i.e. habitat plasticity depending on weather) | 11 | SPI + STI*VCF |
|  | 12 | SPI*VCF + STI |
|  | 13 | STI*VCF |
|  | 14 | SPI*VCF |

Table 2-2: Species that had a weather interaction in their best fit model. Species in bold have strong hierarchy for the interaction, and species in italics support weak hierarchy.

| Species | Model | SPI | STI | VCF |
|---|---|---|---|---|
| Eastern Kingbird | 4 | -0.006 (-0.018, 0.005) | -0.008 (-0.025, 0.009) | |
| Ovenbird | 9 | -0.005 (-0.034, 0.023) | 0.005 (-0.03, 0.041) | 0.07 (0.067, 0.073) |
| Rose-Breasted Grosbeak | 9 | 0.014 (-0.004, 0.031) | 0.005 (-0.023, 0.034) | 0.037 (0.035, 0.039) |
| Northern Cardinal | 9 | -0.002 (-0.011, 0.008) | 0.001 (-0.013, 0.015) | 0.028 (0.026, 0.029) |
| *American Goldfinch* | *9* | *-0.02 (-0.031, -0.009)* | *0.015 (-0.002, 0.033)* | *0.02 (0.019, 0.022)* |

Table 2-3: Species that had a weather interaction with land cover in their best fit model. Species with strong hierarchy in the interaction are in bold.

| Species | Model | Weather | SPI | STI | VCF |
|---|---|---|---|---|---|
| **Red-bellied Woodpecker** | **12** | **SPI** | **-0.024 (-0.047, -0.001)** | **0.009 (-0.015, 0.034)** | **0.039 (0.036, 0.041)** |
| Northern Flicker | 12 | SPI | -0.016 (-0.035, 0.003) | -0.007 (-0.028, 0.014) | 0.019 (0.017, 0.021) |
| Orchard Oriole | 12 | SPI | -0.043 (-0.073, -0.013) | 0.019 (-0.011, 0.048) | 0.002 (-0.004, 0.007) |
| **Dickcissel** | **12** | **SPI** | **0.064 (0.049, 0.078)** | **-0.034 (-0.053, -0.016)** | **-0.046 (-0.049, -0.044)** |
| **White-breasted Nuthatch** | **12** | **SPI** | **-0.058 (-0.09, -0.026)** | **-0.021 (-0.054, 0.012)** | **0.051 (0.049, 0.054)** |
| **Blue Jay** | **14** | **SPI** | **-0.019 (-0.034, -0.004)** | | **0.031 (0.03, 0.033)** |
| **Western Meadowlark** | **14** | **SPI** | **0.018 (0.004, 0.032)** | | **-0.079 (-0.083, -0.076)** |
| **Vesper Sparrow** | **14** | **SPI** | **-0.028 (-0.042, -0.013)** | | **-0.035 (-0.038, -0.033)** |
| Indigo Bunting | 14 | SPI | -0.003 (-0.016, 0.009) | | 0.033 (0.032, 0.034) |
| **Lark Bunting** | **14** | **SPI** | **0.454 (0.336, 0.572)** | | **-0.259 (-0.31, -0.208)** |
| Scarlet Tanager | 14 | SPI | 0.042 (-0.013, 0.096) | | 0.065 (0.062, 0.069) |
| Gray Catbird | 14 | SPI | 0.001 (-0.017, 0.018) | | 0.031 (0.029, 0.033) |
| **American Robin** | **14** | **SPI** | **-0.009 (-0.018, -0.001)** | | **-0.007 (-0.008, -0.006)** |
| Red-headed Woodpecker | 11 | STI | -0.021 (-0.038, -0.004) | 0.019 (-0.011, 0.049) | 0.011 (0.008, 0.013) |
| **Least Flycatcher** | **11** | **STI** | **0.03 (0.001, 0.06)** | **-0.057 (-0.108, -0.005)** | **0.051 (0.047, 0.055)** |
| **Bobolink** | **11** | **STI** | **0.036 (0.021, 0.052)** | **-0.06 (-0.088, -0.032)** | **-0.032 (-0.034, -0.029)** |
| Eastern Meadowlark | 11 | STI | 0.01 (0, 0.02) | 0.007 (-0.011, 0.026) | -0.026 (-0.028, -0.025) |
| Eastern Towhee | 11 | STI | 0.025 (0.001, 0.049) | 0.013 (-0.035, 0.061) | 0.057 (0.054, 0.06) |
| **Yellow Warbler** | **11** | **STI** | **0.011 (-0.004, 0.027)** | **-0.053 (-0.082, -0.024)** | **0.032 (0.03, 0.034)** |
| **Common Yellowthroat** | **11** | **STI** | **0.01 (0.002, 0.019)** | **-0.026 (-0.042, -0.011)** | **0.007 (0.005, 0.008)** |
| **Western Kingbird** | **13** | **STI** | | **0.083 (0.024, 0.143)** | **-0.071 (-0.088, -0.054)** |
| Baltimore Oriole | 13 | STI | | -0.01 (-0.032, 0.012) | 0.026 (0.024, 0.028) |
| Savannah Sparrow | 13 | STI | | -0.008 (-0.032, 0.015) | -0.054 (-0.056, -0.052) |
| Field Sparrow | 13 | STI | | 0.002 (-0.022, 0.025) | 0.041 (0.039, 0.042) |
| **Song Sparrow** | **13** | **STI** | | **-0.034 (-0.048, -0.02)** | **-0.009 (-0.01, -0.008)** |
| **Cedar Waxwing** | **13** | **STI** | | **-0.043 (-0.086, -0.001)** | **0.032 (0.029, 0.035)** |
| Blue-Gray Gnatcatcher | 13 | STI | | -0.042 (-0.108, 0.024) | 0.086 (0.08, 0.092) |
| Eastern Bluebird | 13 | STI | | -0.027 (-0.064, 0.009) | 0.026 (0.024, 0.029) |

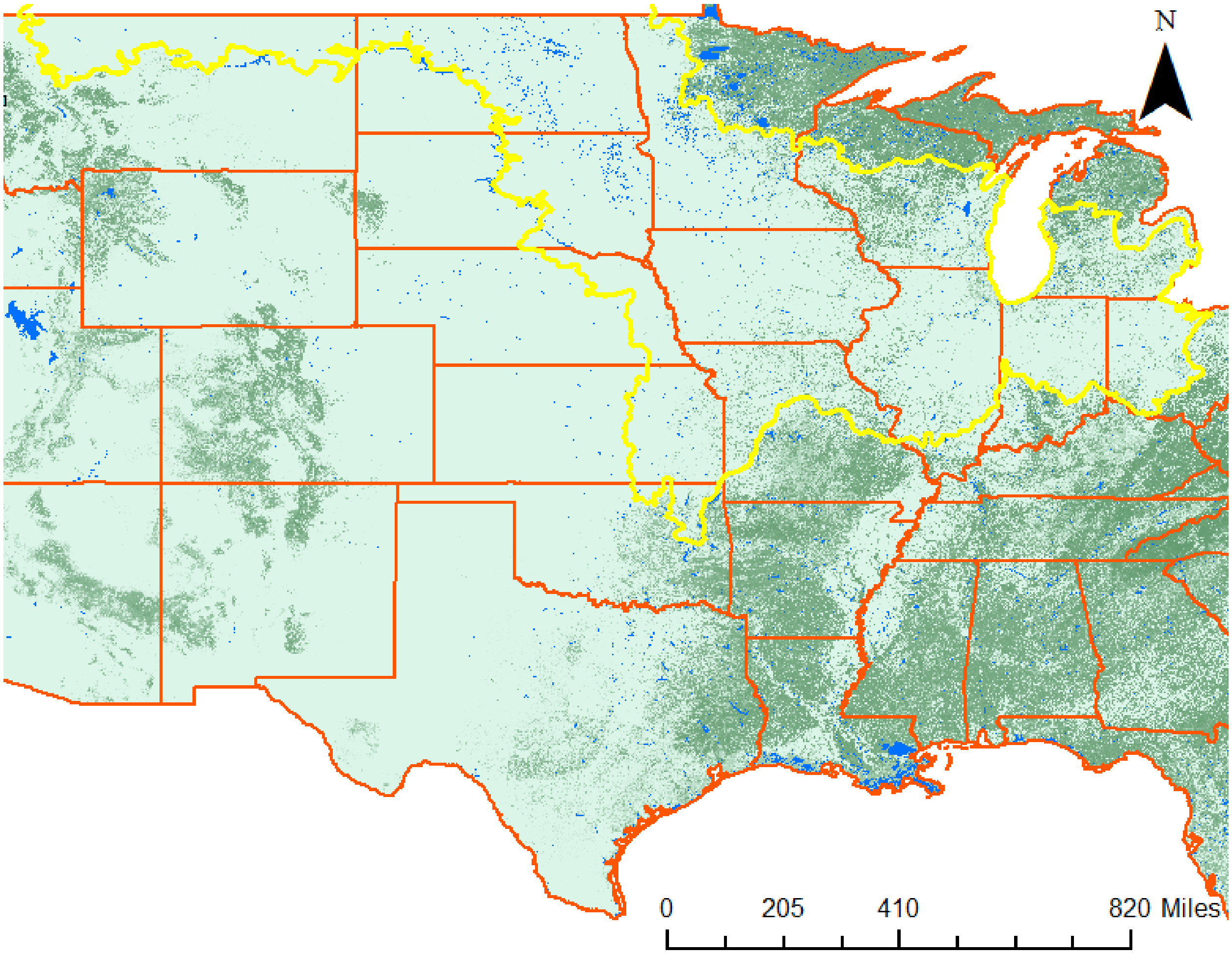

Figure 2-1: Example of LANDSAT imagery from 2005 within the study area. Boundaries of the study area are drawn in yellow. U.S. states are outlined in orange. U.S. states are outlined in orange.

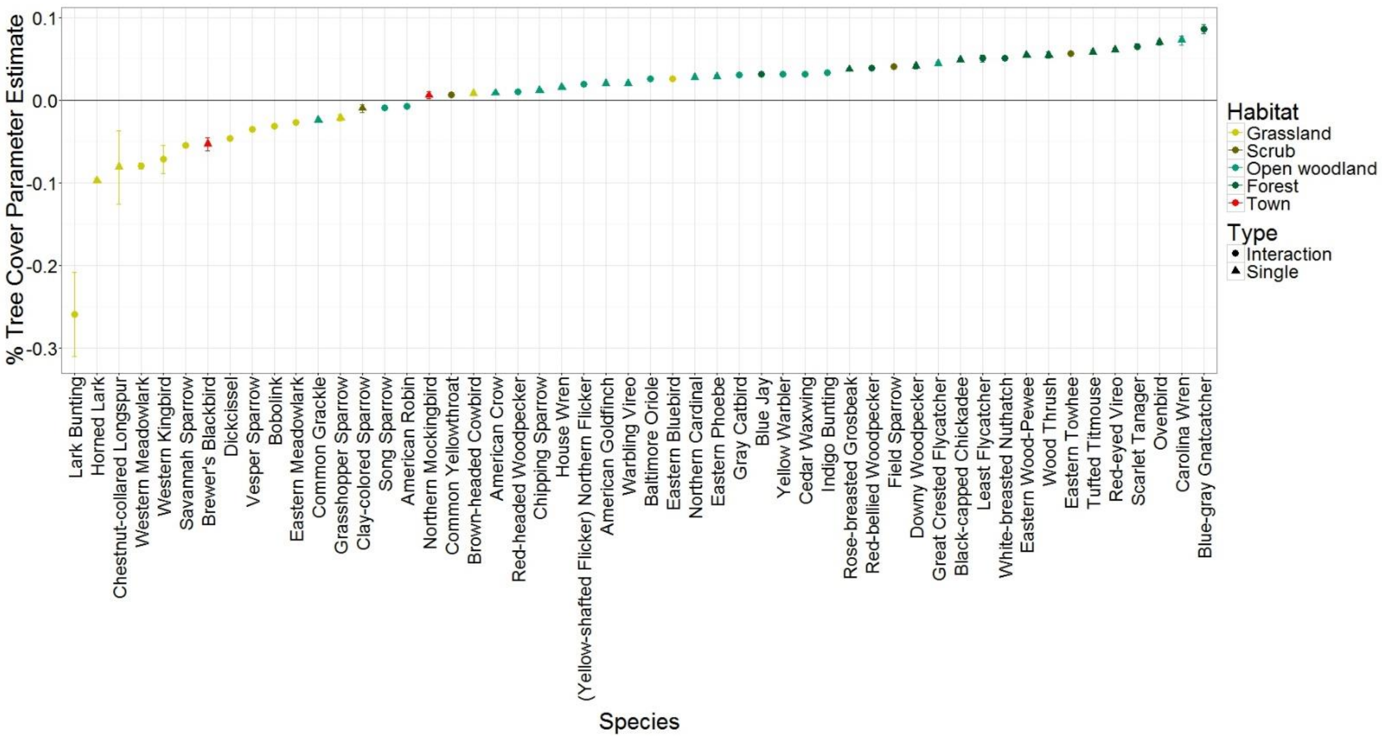

Figure 2-2: Parameter estimate for percent tree cover, for species that included percent tree cover in the best fit model. Species' response to percent tree cover is ranked in ascending order, in order to elucidate patterns among categorized habitat guilds. Type indicates whether the parameter was included additively, or as part of an interaction term.

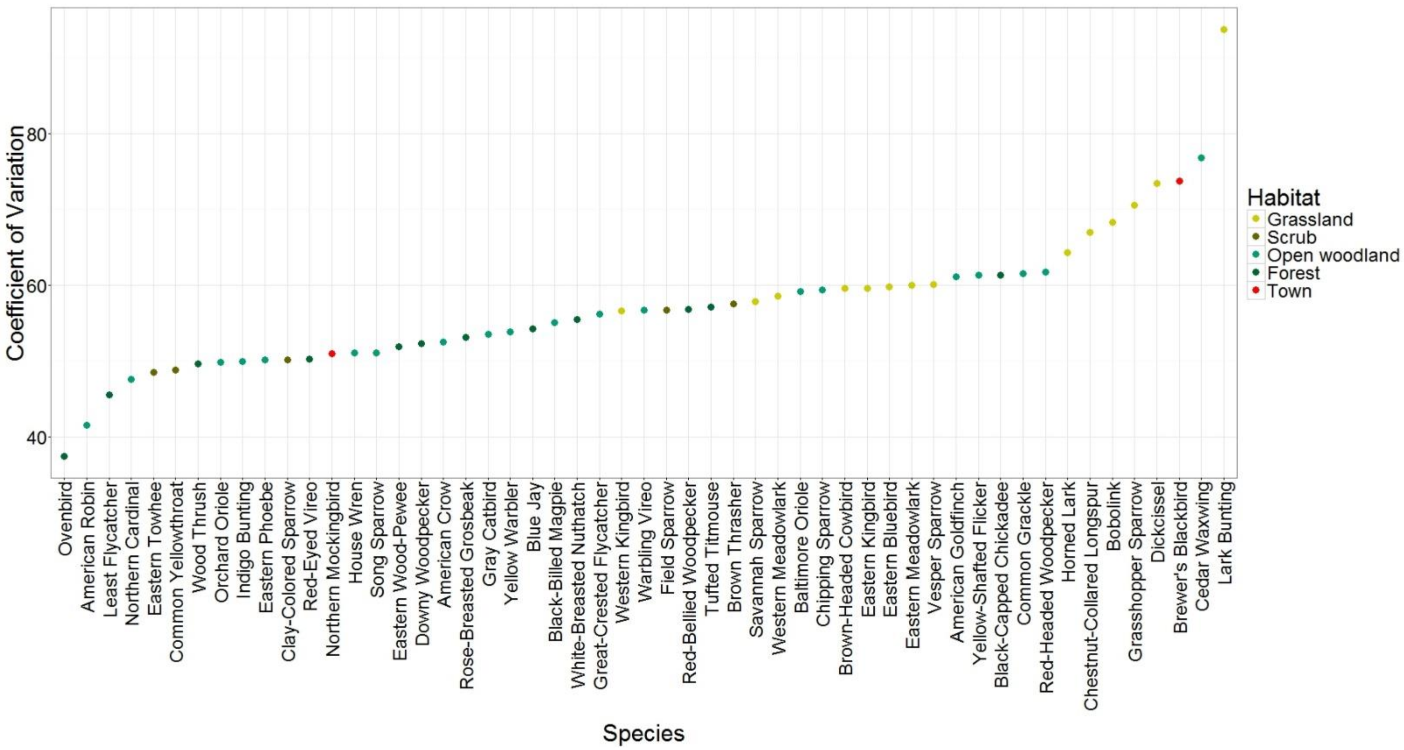

Figure 2-3: Coefficient of variation (CV) in species' counts computed per route across years, and then averaged per species. Thus, the value plotted is the average CV per species.

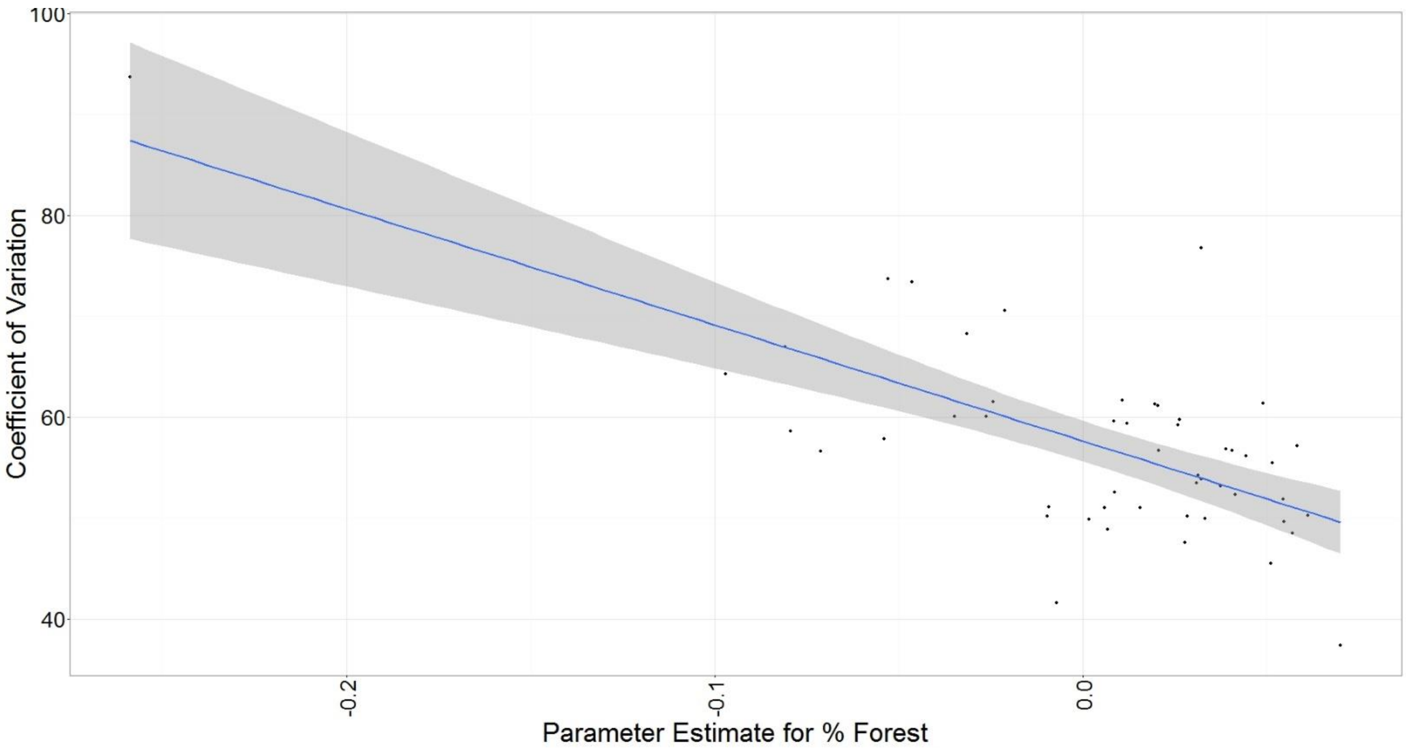

Figure 2-4: regression between CV of counts and percent forest cover, with confidence interval (CI) shaded in gray.

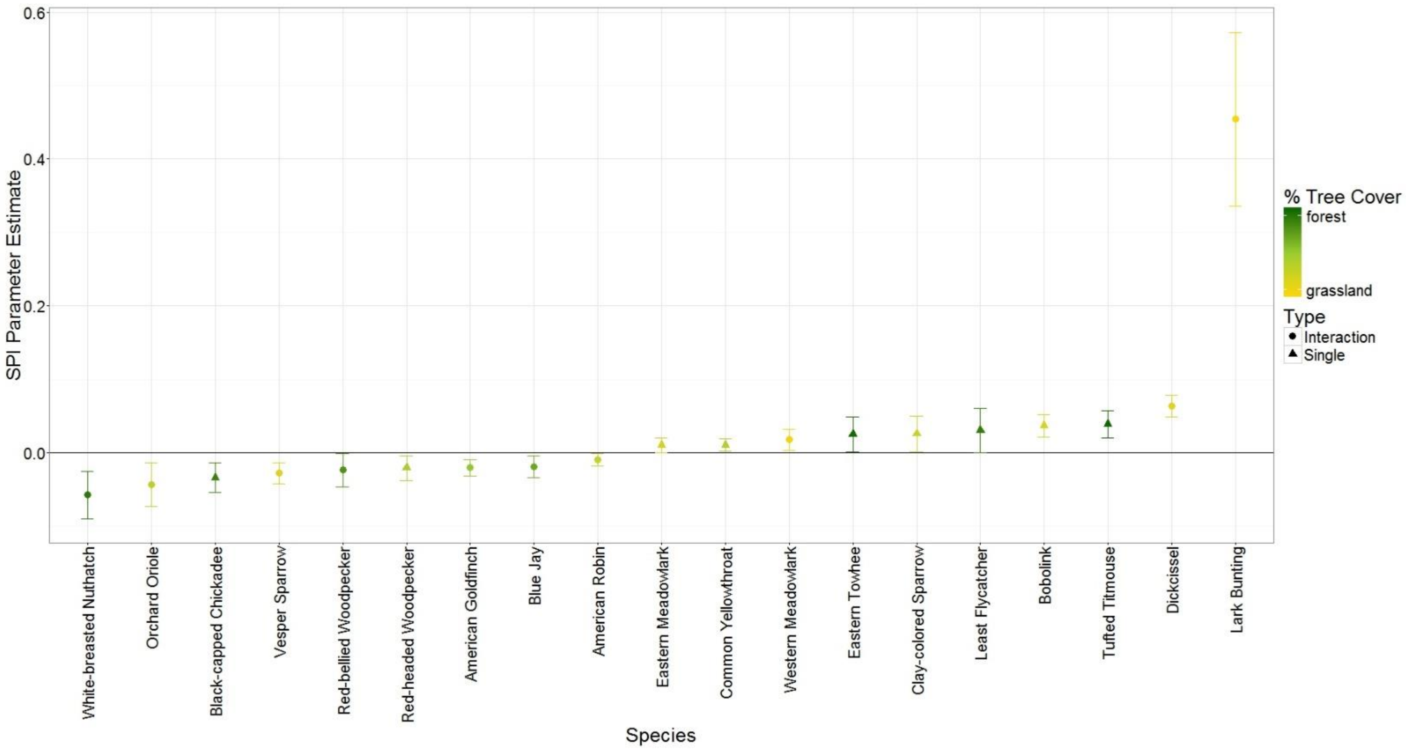

Figure 2-5: Species' response to STI, where STI was included as a significant parameter in the best-fit model. Species are color-coded according to their ranked parameter estimate of percent tree cover, on the gradient from yellow (negative) to dark green (positive), as a reflection of habitat preference. If percent tree cover was not included in the species' best-fit model, it is assigned to blue (or "No VCF"). The parameter symbol indicates whether or not STI was included linearly, or as part of an interaction term. If the parameter is included in an interaction, the estimate should be cautiously interpreted.

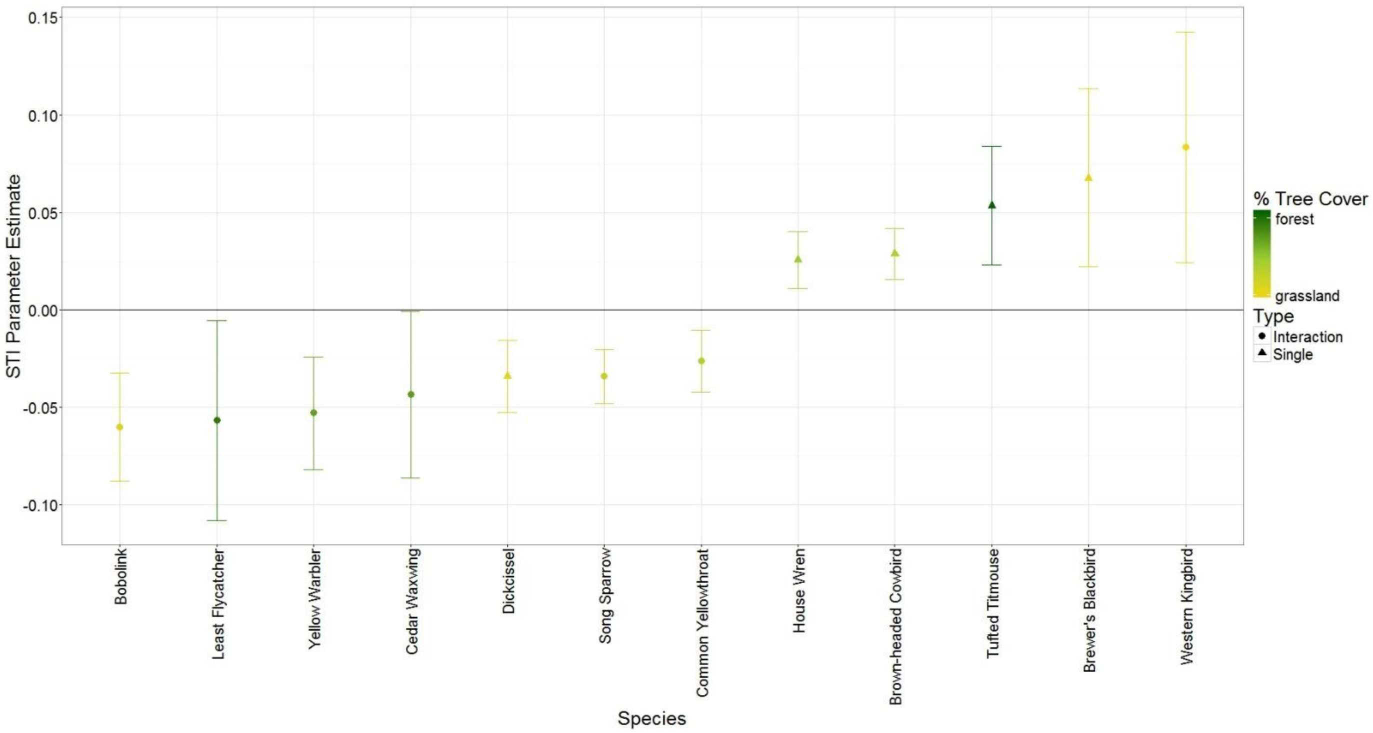

Figure 2-6: response to SPI, where SPI was included as a significant parameter in the best-fit model. Species are color-coded according to their ranked parameter estimate of percent tree cover, on the gradient from yellow (negative) to dark green (positive), as a reflection of habitat preference. If percent tree cover was not included in the species' best-fit model, it is assigned to blue (or “No VCF”). The parameter symbol indicates whether or not SPI was included linearly in the model, or as part of an interaction term. If the parameter is included in an interaction, the estimate should be cautiously interpreted.

Appendix 2-A. Species considered for analysis.

| AOU | Common Name | Total Counts | Habitat | IUCN |
|---|---|---|---|---|
| 5110 | Common Grackle | 1053769 | open woodland | Least concern |
| 7610 | American Robin | 732088 | open woodland | Least concern |
| 4950 | Brown-Headed Cowbird | 361022 | Grassland | Least concern |
| 4880 | American Crow | 355973 | open woodland | Least concern |
| 5810 | Song Sparrow | 333756 | open woodland | Least concern |
| 5011 | Western Meadowlark | 325420 | Grassland | Least concern |
| 4740 | Horned Lark | 319274 | Grassland | Least concern |
| 6040 | Dickcissel | 287201 | Grassland | Least concern |
| 5010 | Eastern Meadowlark | 268830 | Grassland | Least concern |
| 6810 | Common Yellowthroat | 199184 | Scrub | Least concern |
| 5930 | Northern Cardinal | 196601 | open woodland | Least concern |
| 5290 | American Goldfinch | 173951 | open woodland | Least concern |
| 5980 | Indigo Bunting | 173584 | open woodland | Least concern |
| 7210 | House Wren | 158750 | open woodland | Least concern |
| 5600 | Chipping Sparrow | 149057 | open woodland | Least concern |
| 5420 | Savannah Sparrow | 147361 | Grassland | Least concern |
| 5400 | Vesper Sparrow | 132730 | Grassland | Least concern |
| 4770 | Blue Jay | 119976 | Forest | Least concern |
| 4940 | Bobolink | 108648 | Grassland | Least concern |
| 4440 | Eastern Kingbird | 91341 | Grassland | Least concern |
| 5630 | Field Sparrow | 85990 | Scrub | Least concern |
| 7040 | Gray Catbird | 74789 | open woodland | Least concern |
| 7050 | Brown Thrasher | 71792 | scrub | Least concern |

| | | | | |
|---|---|---|---|---|
| 5070 | Baltimore Oriole | 70274 | open woodland | Least concern |
| 5460 | Grasshopper Sparrow | 69314 | grassland | Least concern |
| 6190 | Cedar Waxwing | 54411 | open woodland | Least concern |
| 6520 | Yellow Warbler | 53954 | open woodland | Least concern |
| 4120 | Northern Flicker | 45902 | open woodland | Least concern |
| 6270 | Warbling Vireo | 45819 | open woodland | Least concern |
| 4060 | Red-Headed Woodpecker | 45545 | open woodland | Near threatened |
| 6050 | Lark Bunting | 42596 | grassland | Least concern |
| 7310 | Tufted Titmouse | 42420 | forest | Least concern |
| 7660 | Eastern Bluebird | 42165 | grassland | Least concern |
| 4610 | Eastern Wood-Pewee | 40404 | forest | Least concern |
| 4090 | Red-Bellied Woodpecker | 39963 | forest | Least concern |
| 4520 | Great-Crested Flycatcher | 39303 | open woodland | Least concern |
| 6240 | Red-Eyed Vireo | 38648 | forest | Least concern |
| 5950 | Rose-Breasted Grosbeak | 38458 | forest | Least concern |
| 7030 | Northern Mockingbird | 36225 | town | Least concern |
| 7350 | Black-Capped Chickadee | 34672 | forest | Least concern |
| 5610 | Clay-Colored Sparrow | 34408 | scrub | Least concern |
| 4470 | Western Kingbird | 30049 | grassland | Least concern |
| 5100 | Brewer's Blackbird | 28486 | town | Least concern |
| 5380 | Chestnut-Collared Longspur | 26173 | grassland | Near threatened |
| 7270 | White-Breasted Nuthatch | 22742 | forest | Least concern |
| 3940 | Downy Woodpecker | 22071 | forest | Least concern |
| 4560 | Eastern Phoebe | 20867 | open woodland | Least concern |
| 5870 | Eastern Towhee | 18592 | scrub | Least concern |
| 5060 | Orchard Oriole | 17087 | open woodland | Least concern |
| 6740 | Ovenbird | 17071 | forest | Least concern |

| | | | | |
|---|---|---|---|---|
| 7550 | Wood Thrush | 11650 | forest | Least concern |
| 4670 | Least Flycatcher | 11428 | forest | Least concern |
| 7180 | Carolina Wren | 9189 | open woodland | Least concern |
| 6080 | Scarlet Tanager | 8600 | forest | Least concern |
| 7510 | Blue-Gray Gnatcatcher | 8210 | forest | Least concern |
| 7560 | Veery | 7955 | forest | Least concern |
| 6280 | Yellow-Throated Vireo | 7659 | open woodland | Least concern |
| 6870 | American Redstart | 7251 | forest | Least concern |

# Chapter 3: Investigating the Response of Waterfowl to Land Cover and Weather, from the Local Scale to Range-Wide

## Abstract

Waterfowl depend on having sufficient wetland habitat in the landscape. Conditions within in the Prairie Potholes, a center of waterfowl production, may vary widely among years. Waterfowl species can only persist where there is sufficient available water in the landscape. Some species are known to make large-scale movements to avoid droughts, but all species can only persist where there is sufficient available water in the landscape. My aim was to determine the landscape and weather factors influencing inter-annual abundance of 9 waterfowl species within the Prairie Potholes Bird Conservation region (BCR 11), as well as detect large-scale movements in times of drought. I examined how spatial variation in waterfowl abundance is influenced by land cover and temporal variation in weather, within a Bayesian hierarchical modeling framework, using North American Breeding Bird Survey (BBS) data from 1966 to 2010. I performed model selection to determine which variables were most important per species, and the directionality and magnitude of response. I also tested relationships of route-level abundances in Alaska, a northerly range edge for many waterfowl species, to drought in the Prairie Potholes. Water, variously characterized as amount of water, wetland, wetland configuration and precipitation, was a strong predictor of most species' abundance. The metric most frequently included in models were proportion of open water within 400m of the route ($19.03 \leq \beta_{water} \leq 42.13$). All waterfowl species that responded significantly to weather responded positively to precipitation and negatively to temperature. Although waterfowl species' movements to range edges have been recorded in field studies, I was unable to detect them with our analyses. Thus, both amount of water and precipitation were the most important factors for

waterfowl as a community, though species-specific responses were nuanced. Strong responses to both static and temporal measures of water affirm the need to maintain surface water availability in light of climate change in the region, which is projected to cause drier conditions throughout.

## Introduction

Waterfowl populations are dynamic in a way that tracks conditions within their breeding region, in that large fluctuations in abundance can occur concurrent with prevailing weather (Ruwaldt Jr et al. 1979). Weather severity is known to mediate waterfowl migration (Schummer et al. 2010). Weather events can grow or shrink the extent of available habitat, alter food resources and cause physiological stress (Swanson 1984), affecting waterfowl mortality, productivity, and distribution (Studds et al. 2012). For example, aquatic macroinvertebrates change in abundance according to weather, which leads to changes in prey item distribution for waterfowl (Bataille and Baldassarre 1993). Both the landscape and waterfowl react to extreme deviation from normal conditions, such as droughts and floods (Johnson et al. 2004). Extreme weather events are so named because they are, by definition, rare. Waterfowl are highly mobile and thus able to respond to extreme weather by moving elsewhere (Henny 1973). Some species exhibit dramatic responses to extreme drought, such as the continental-scale movements to range edges exhibited by northern pintails from their core breeding range in the Prairie Potholes (Derksen and Eldridge 1980). Movements away from core breeding areas in response to lack of suitable nesting habitat result in notable changes in spatial distribution of abundance year-to-year, and changing densities therefore occur in response to water level conditions. Thus, waterfowl are able to cope by escaping extreme weather, but movements may have consequences for productivity (Krapu et al. 2006). Large-scale movements to range edges may result in significant decreases in productivity (Smith 1970).

The majority (> 50%) of North America's waterfowl populations breed in the Prairie Potholes Bird Conservation Region (BCR 11). Climate differs across the geographic expanse of the Prairie Potholes, which ranges from Canada to Iowa, leading to different precipitation and temperature norms, as well as weather patterns in different parts of the region (Feldman et al. 2015). From the viewpoint of waterfowl, in the most simplistic description, the landscape can be thought of as ponds and wetlands as habitat patches amidst a matrix of grassland (Voldseth et al. 2014). Yet, native grassland is also used by waterfowl as nesting habitat. Landscape composition in the region is relatively homogeneous, yet the landscape is temporally dynamic (Winter and Rosenberry 1998). Hydrology is highly dependent on weather, so some while some ponds are perennial, others only occur in wet years (Larson 1995). Weather leads to changes in landscape configuration and connectivity year-to-year by affecting surface water levels, which may ultimately bear on waterfowl habitat (van der Kamp and Hayashi 2009). Thus, the Prairie Potholes can be considered a naturally dynamic landscape (Markon and Derksen 1994).

Human land use has, however, altered the natural dynamics of the Prairie Potholes. Land use/land cover changes, including draining of wetlands and replacing grassland with cropland (Wright and Wimberly 2013), have translated to differences in water retention, with less groundwater storage in agricultural land than in native grassland (Van der Valk 1988). An estimated >50% of prairie potholes have been drained or altered by agriculture. Seasonal water-level fluctuations are likely reduced due to changes in topography due to filling of wetlands (Anteau 2012). Restoration efforts in the region, such as the Conservation Reserve Program (CRP) have been successful in boosting waterfowl productivity (Kantrud 1993). Yet, the hydrological dynamics of the eco-region and its implications for wildlife habitat remain significantly altered over decades of land use.

As climate has changed, the most extreme weather on record has been observed in recent time, meaning that current conditions are more reflective of a new climate regime than historic climate (World Meteorological Organization 2013). In previous studies, it has been difficult to adequately characterize biotic response to extreme weather because data relevant to extreme weather was restricted to few anomalous events, and perhaps opportunistic data collection during those times. Thus, while previous research has highlighted important responses and provided ideas of what to expect, quantification of biotic response to extreme weather has suffered from low sample size. Now, events that were rare are becoming more common, providing opportunities to collect both weather and biotic data in times of extremes (Hansen et al. 2010). This allows for comparison of baseline historic conditions to changes that may be representative of the expectable climate regime of the future. As data continue to be collected and improved, knowledge of waterfowl relationships to land cover and weather needs to be continually revised, especially in the face of changing conditions both in terms of land use/land cover and climate (Sorenson et al. 1998). Since there has been much research interest in waterfowl due to their designation as game species, large-scale analyses can be assisted in interpretation by available information about processes at the local scale. Further, there is a paucity of replication in ecology research, yet even “quasi-replication” can enhance knowledge of biological dynamics (Kelly 2006). I aimed to re-examine relationships of waterfowl species to updated land cover and weather datasets at a broad scale utilizing one of the latest available datasets for land cover (National Land Cover Dataset 2011), indices of weather anomaly calculated from a long-term dataset (Maurer et al. 2002), and long-term avian survey data (North American Breeding Bird Survey).

Our goal was to investigate response of breeding waterfowl to weather variability, in the context of landscape composition and configuration of the Prairie Potholes. Specifically, I aimed to examine spatial and temporal inter-annual variability of waterfowl abundance, and determine which landscape and weather variables were important to the most abundant species in Prairie Potholes. Concurrently, our objective was to determine the relative importance (i.e. strength of response) and directionality of species' responses to landscape factors and weather. I also aimed to detect large-scale movement of these species in response to drought. I hypothesized that the most important weather and landscape variables for waterfowl would be those reflecting amount, configuration and temporal availability of water. I also expected negative response of species to agricultural land in the vicinity of where birds were detected, since during the breeding season, this would represent less native land cover and potentially less suitable nesting sites. Regarding movement responses to weather, I hypothesized that waterfowl species would be more abundant in northerly portions of their ranges during drought years.

## Methods

### *Study Area*

To explain waterfowl abundance at the route level, I examined water bird data within the Prairie Potholes Bird Conservation Region (BCR 11) which was a glaciated landscape that is now comprised of pothole lakes and wetlands (Poiani et al. 1996). However, intensive agricultural pressure has heavily altered the hydrology, composition and configuration of the landscape, which has consequences for waterfowl (Wardlow and Egbert 2008). The region spans a wide latitudinal range (approximately 43 to 52°N) and a longitudinal range between approximately 96°W and113°W (Figure 3-1). The region supports approximately 5 to 8 million small wetlands in a given year (JOHNSON et al. 2005).

### *Bird Data*

The North American Breeding Bird Survey (BBS) is based on annual counts of birds along 39.4 km routes conducted by skilled volunteers (Keller and Scallan 1999). I used BBS data from 1966 through 2010, in accordance with the time record of an available weather dataset (Maurer et al. 2002), for the 11 most abundant waterfowl species in the Prairie Potholes (Table 1). The BBS has been used both as a standalone and a supplementary dataset for waterfowl (Zimmerman et al. 2015). For each species, I only considered routes on which the species occurred at least once. I excluded route runs that did not meet quality standards, as indicated in the dataset. I also only used standard BBS route runs, and did not include resampling efforts or non-standard protocols.

### *Land Cover Data*

We used a spatial dataset of digitized route paths from USGS. I considered land cover data from the 2011 National Land Cover Dataset (NLCD) to investigate the effects of landscape features on abundance indices (Forcey et al. 2014). Within a 400m buffer of each route, considered to match the estimated detection radius, I computed land cover percentages of coarse classifications hypothesized to influence water bird abundance. I thus summed classification types where necessary, resulting in the following land cover types: open water (NLCD class 11), development (a sum of NLCD classes 21-24), forest (a sum of NLCD classes 41-43), grassland (NLCD class 71), agricultural lands (a sum of NLCD classes 81-82) and emergent herbaceous wetlands (NLCD class 95).

In order to investigate the influence of landscape configuration at a broad scale, I computed metrics using FRAGSTATS within a 10 km buffer of each route. At the class level, I calculated wetland interspersion-juxtaposition index (IJI), water IJI, and water largest patch index (LPI). At the landscape level, I calculated CONTAGIONion and Simpson's diversity of land cover types (Forcey et al. 2011). I also considered spatial autocorrelation of all land cover data using global Moran's I.

### *Weather Data*

We analyzed gridded weather data which covers the contiguous U.S. at 1/8th degree spatial resolution from 1949-2010 (Maurer et al. 2002). I used data from 1965 through 2010 to match the temporal record of BBS data, and extracted values for the route centroid of each BBS route per year. I considered weather both leading up to a given year's breeding season, and weather from the previous year as potentially influential for avian abundance.

**Precipitation.** I used the Standardized Precipitation Index (SPI) to characterize inter-annual variation in precipitation totals preceding the breeding season. The SPI is standardized so that values can be compared among areas with different precipitation patterns (McKee et al. 1993). Our metric was the precipitation totals during the 90-day period ending June 1 (i.e. spring, March-May) in the same year as the BBS count. I fit annual totals to the Pearson-III distribution, and transformed each annual total to a standard deviation from a standard normal distribution. The data are available online (http://silvis.forest.wisc.edu/climate-averages-and-extremes). Some precipitation values were too extreme to fit the distribution, and those were recoded as 7 or -7 depending on whether the anomaly was positive or negative, respectively.

**Temperature.** I calculated the Standardized Temperature Index (STI) for the month of June, which is the first summer month in which extreme temperatures (i.e. record heat anomalies) are possible. Extreme temperatures could either have direct effects on survival or exacerbate an extant precipitation deficit. I standardized average daily maximum temperature into the Standardized Temperature Index (STI) to account for differences in temperature mean and inter-annual variability among locations.

### *Summary Statistics*

As a basic exploratory data analysis step, I identified the highest counts per species on a single route in a given year, as well as the minimum sum count within the region in a given year. I reported both summary statistics as potential responses to extreme conditions, the former to explore concentration on a route with adequate resources during extremes, and the latter to explore out-migration in times of extremes.

### *Statistical Analysis*

To allow for multiple levels of variance in nuisance variables that are likely to affect BBS data, I developed models in a Bayesian hierarchical framework (Sauer and Link 2002). I modeled BBS data with an over-dispersed Poisson distribution, using a log-link function to relate the mean predicted count to linear predictors (Wilson et al. 2011). I modeled nuisance effects such as year, route and observer as independent random variables, and assigned non-informative priors via the half-Cauchy distribution to the hyper-parameters. I also incorporated a linear trend and a binary indicator variable for an observer's first year.

The basic (null) model follows:

$$\log \mu = \beta_0 + \beta_1 year + \beta_2 firstyear + (route \,\&\, observer) + year \tag{1}$$

## Model Selection

The candidate models included first-order additive combinations of weather and land cover variables, added to the null model. I considered all possible combinations of the land cover and weather variables I calculated, resulting in 8191 models per species. I fit the set of candidate models for each species using integrated nested Laplace approximations (INLA) via the R-INLA package (Blangiardo et al. 2013). I ranked our models based on the deviance information criterion (WAIC). For the best model, I examined the 95% credible intervals (CI) of the posterior distribution of parameter estimates, and assumed that parameters for which the credible intervals did not include zero were statistically significant.

Upon reviewing the results of the model selection, I tested for possible interaction effects by incorporating a set of 42 models with hypothetical interactions based on the set of best selected models per species (Appendix 3-A). Model fit was examined via a linear regression using the lm function between values fitted by the model and the raw counts, with $R^2$ reported as a measure of goodness-of-fit.

### Movement to Range Edge

Alaska is the region farthest north for which BBS data is available, so I used Alaska BBS data to represent northern waterfowl range edge. Thus, I tested whether or not waterfowl abundance at the route level in Alaska was affected by drought in the Prairie Potholes. To define drought at a species-specific level, I used relative abundance grids derived from BBS data to calculate the average percentage of species' relative abundance represented by each grid cell. I weighted Standardized Precipitation-Evapotranspiration Index (SPEI) by the percentage of species' relative abundance per grid cell, and summed negative weighted SPEI over the Prairie Potholes to calculate regional drought severity for each species. Then, I examined the significance of the predictor for each species' abundance indices in Alaska.

## Results

### *Summary Statistics*

Abundances varied considerably among species in the Prairie Potholes, with mallard being the most abundant species and American wigeon being the least (Table 2). Both maximum on a route and minimum in the region varied widely across species, in both number and year of occurrence. The highest count on a single route and lowest summed counts over the region occurred with the second-most abundant species, Canada goose.

The waterfowl species varied in total range size within North America (Table 2). All species considered had a core breeding range within the Prairie Potholes, but not all species occurred throughout the region, whereas some were distributed widely throughout the continent (e.g., mallard). For all species considered, average counts on routes were higher within the Prairie Potholes, indicating the significance of the region for waterfowl. Most standard deviations of counts within and outside of the region were larger than the averages, which is an indicator of over-dispersion. Thus, I modelled counts using the generalized Poisson distribution to account for over-dispersion.

### *Model Selection for Species in the Prairie Potholes*

In the top 15 models for each species, the most commonly included variables were % water and wetland interspersion-juxtaposition index (Table 3). The most commonly included variables in species' best models were % water and % grassland at the local (400m buffer) scale (Table 4), and Shannon's diversity index at the landscape (10 km buffer) scale (Table 5). All of these variables were significantly auto-correlated across the landscape ($p < 0.05$), as well as all the other 10 km buffer land cover configuration variables. The 10 km land cover configuration spatial auto-correlation may be due to overlapping buffers within this range. However, while response to % grassland and Shannon’s diversity varied in significance, magnitude and direction, % water responses were strongly positive and all significant (Table 4). Therefore, amount of water appears to be the most influential variable of those I considered for the dominant waterfowl species as a guild in the Prairie Potholes.

Upon examination of the best fit models and development of a candidate set of models including interaction terms, blue-winged teal and northern shoveler included interactions of weather and % crop in their best-fit models. Hierarchy of the interaction was weak for northern shoveler, but strong for blue-winged teal, indicating that an interaction of % crop and temperature was likely significant in determining species’ abundance at a given location.

## Land Cover

### Composition at the local scale

Species’ abundance was overall strongly (largest parameter estimates of any variable) positively related to proportion of water in the immediate surrounding landscape, both in terms of open water and herbaceous wetland. The only species that did not include % water in its best fit model was American wigeon. Similarly, two species included % wetland in their best fit models, and all of the wetland parameter estimates were strongly positive.

Response to non-water land cover variables was more variable per species, and less cohesive as a guild. The second-most included variable in species’ models was % grassland, though response varied per species. While 8 species included the variable in the best fit model, only 3 yielded significant parameter estimates. Northern pintail, blue-winged teal and lesser scaup responded positively to % grassland in the immediate landscape. Five species included %

cropland in their best model, but only two of the parameter estimates were significant; American wigeon responded negatively to crop, whereas northern pintail responded positively.

### Configuration at a broad scale

Interestingly, though parameter estimates were small compared to landscape composition responses, species' response to landscape configuration at the 10 km scale was largely coherent in direction and magnitude (Table 5). All but 3 species included wetland IJI in their best models, and all species responded significantly negatively in similar magnitude (ranging from -0.08 to -0.02). Similarly, 7 species included CONTAGIONion in their best models, but only 3 responses were significant and all were negative. Response to Shannon's diversity index (SIDI) was less generalizable. Only 4 species responded significantly to SIDI; northern pintail responded positively, but ruddy duck and Canada goose responded negatively. No species responded significantly to largest pond (i.e. water largest patch index) within 10 km of a route.

### Weather

We only considered weather within the year of the counts, because inter-annual waterfowl counts are influenced by harvest. Thus, though responses to previous year's weather may bear on productivity, I did not believe these were adequately separable from other drivers of abundances. While land cover was quantified statically for our analyses, weather was quantified annually, so modelled response to weather differed from land cover by representing annual variation with temporally-varying abiotic conditions. As a general trend, waterfowl responded positively to SPI and negatively to STI in our models (Table 6). The only exceptions were species where weather was included as part of an interaction (blue-winged teal and northern shoveler). Most (7 of 9) waterfowl species considered included SPI in their best fit model, and all linear term parameter estimates were positive (though only 5 were significant). Similarly, all species that included STI linearly in their best fit model responded negatively, though 2 STI parameter estimates were insignificant. Thus, weather appeared to be an overall important predictor of inter-annual abundance at the route level of waterfowl in the Prairie Potholes, with strength of response varying by species. The species with the largest magnitude parameter estimates for both weather metrics was ruddy duck, and the second-largest magnitude response for both weather metrics was exhibited by northern pintail. Thus, it appears these species are especially influenced by weather of the waterfowl species considered.

### *Long-Distance Movements in Response to Weather*

None of the species considered showed significant response at the route level to weather conditions in the Prairie Potholes by the drought metric I calculated (Table 7). Thus, it is likely that distribution of abundance of waterfowl species in Alaska is determined by several other factors, or our metrics were not adequate to detect the response. Though the record of extreme weather is currently longer than in the past centuries, the climate-change driven increases in extremes are still restricted to the past decade, and a notable shortcoming of our weather data is the exclusion of the 2012 drought in the central U.S. It is possible that the record of severe enough droughts in the Prairie Potholes to trigger large-scale movements is still small and thus difficult to model with our broad-scale datasets.

## Discussion

Waterfowl species' cohesive response to weather was evident in model selection, and possibly also in summary statistics. Maximum occurrence on a single route may be reflective of species concentrating there in a given year, whereas minimum summed counts may reflect species settling outside the region in a given year (Cowardin et al. 1995). For the 3 most abundant species, their maximum count on a single route coincided with severe drought years in parts of their range (Table 2). The highest maximum count for mallard on a single route in occurred in 1988, while there was an extreme drought in the Prairie Potholes (Dai et al. 2004). The highest maximum count for Canada goose occurred in 2012, when drought conditions were especially dire in the central U.S. and southern Prairie Potholes region (Mallya et al. 2013). Blue-winged teal showed the highest maximum count in 2009, when there was an intense drought in southern Texas (McRoberts and Nielsen-Gammon 2012). While much of the severely drought-affected region was south of the resident and breeding range of blue-winged teal, there were still drier than normal conditions in the southerly part of its range (Anderson and Walker 2011). Thus, concentrations may occur due to waterfowl moving away from drought conditions.

By contrast, minimum counts within a year in a region may be due to movement of individuals out of the U.S. portion of the Prairie Potholes during times of drought. Minimum count is harder to assess with the summary metric chosen, because the response of sample to number of routes may be nonlinear, as suggested by the idea that species concentrate on routes with more resources in times of drought. Nonetheless, as an example of a species known to undertake large movements in times of drought, northern pintail showed lowest counts with respect to number of routes sampled in 1988 (Hestbeck et al. 1991).

Weather influences landscape composition and configuration dramatically in the Prairie Potholes, so response to weather likely also reflected temporal response to landscape dynamics (Bethke and Nudds 1995). The general trend of positive response to increasing precipitation and negative response to increasing temperature is sensible for waterfowl, given the need for ephemeral wetlands and ponds during the breeding season. Increasing precipitation translates to more ponds, while increasing temperatures increase evaporation rates (Erwin 2009). Thus, increasing temperatures could reduce habitat for waterfowl by reducing availability of open water, and also by decreasing soil moisture.

Though large-scale movement to range edges was not detected in our analyses, they are known to occur in times of extremes, at least for some species. Therefore, our analytical design or datasets may not have been specific enough or tailored to detect this type of response. Alaska BBS data may be notably inadequate because of the paucity of roads in the state. Specific bird data collection programs, such as the Off-Road Breeding Bird Survey, have been developed for the state, but they focus on land birds and have only been operational since the last decade. So, there is a relative scarcity of terrestrial survey data for waterfowl in Alaska, and where BBS routes exist, they may not sample waterfowl habitat well. Thus, spatial coverage of waterfowl habitat and thus waterfowl sampling may be lacking for the Alaska BBS as compared to the Prairie Potholes.

In our analysis, landscape was a static factor, whereas weather varied temporally (Forcey et al. 2011). Waterfowl as a group responded strongly to landscape composition and configuration, indicating that our measures of land cover were useful in describing important components of the landscape for birds breeding in the Prairie Potholes (Table 3). While the significant response of most waterfowl species to the amount of water is sensible, the non-water land cover responses are more nuanced (Table 3). Grassland would have been the native land cover in the region (Evans and Black 1956). Species’ response to agricultural land was varied, which is somewhat in keeping with the literature (Duebbert and Kantrud 1974). On the whole, proportion of crop land in the Prairie Potholes region represents large-scale conversion of native grassland and wetland to agricultural land.

The coherent negative response of the waterfowl species considered to wetland IJI and CONTAGIONion highlights potential sensitivities at the landscape scale. The slight negative response of most waterfowl species to increasing interspersion, both of wetlands (wetland IJI) and all class types (CONTAGIONion), may reflect a negative response to small wetlands and/or small patches of habitat in a matrix of habitat. In other words, larger, contiguous wetlands may be more favorable than several small, disconnected ones. Wetlands have been lost or reduced in size due to agricultural pressure in the region.

Thus, management strategies should incorporate both landscape configuration and composition requirements at broad spatial scales, as well as response to temporally-varying conditions such as weather. Seventeen of the years 1993-2013 were above average annual temperatures for 1901-1960 in the Great Plains, and temperatures across the region are projected to increase (Kunkel et al. 2013). The Great Plains are projected to experience more frequent and more intense droughts and heat waves (Georgakakos et al. 2014). Since the Prairie Potholes region spans a large and geographically diverse area, climate change projections differ across the region (Dibike et al. 2012). Spring precipitation is projected to increase in the northern Great Plains, along with rapid spring warming, which could lead to flooding (Georgakakos et al. 2014). Thus, increasing precipitation in the Prairie Potholes region may not directly translate to greater water availability, but instead runoff. Also, it is not apparent that waterfowl are able to plan for extreme conditions by adjusting body condition (Lovvorn 1994). Since agriculture has already drastically affected landscape composition and configuration, reclamation opportunities should consider restoration to native habitat in terms of vegetation, topography and hydrology. Recreating depressions on reclaimed agricultural land may allow water to collect into ponds needed for waterfowl. Habitat restoration and conservation-oriented agricultural practices could aid in mitigating the effects of climate change, and thus provide critical habitat for waterfowl in a changing landscape.

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Table 3-1. Nest initiation dates of the most common waterfowl species in the U.S. Prairie Potholes, in chronological order. Dates and time ranges are adapted from the Birds of North America (BNA), with notes on origin from each species' account.

| Species | Timing of nesting | Notes on date/time range |
|---|---|---|
| Canada Goose | mid- to late March | Egg-laying for *B. c. maxima, moffitti* |
| Northern Pintail | mid-Apr-late Jun | N. Dakota initiation |
| Blue-winged Teal | 1–13 May | nesting onset in N. Dakota |
| Mallard | Early to mid-May | Peak initiation in mid-latitudes |
| American Wigeon | May 28 | Average initiation date in N. Dakota |
| Northern Shoveler | Late May | Initiation peaks in southern Canada |
| Lesser Scaup | Late May-late Aug | Nest initiation in N. Dakota |
| Ruddy Duck | 1-15 June | NW Iowa peak, beginning mid-May |
| Gadwall | June 29 | 50% of nests initiated by in N. Dakota |

Table 3-2: Summary statistics for waterfowl species considered. Count is the raw sum for each species on routes in the U.S. portion of the Prairie Potholes. The maximum (Max.) is the highest count observed for each species on a single route within the Prairie Potholes over the period of the survey. The minimum (Min.) is the total count and year when the lowest count-to-route ratio was observed. The standard deviation (S.D.) was calculated over all routes within the region over all years of the survey. North American range size is approximated from BBS gridded data, and is the total area of grid cells where the species has a non-zero projected count. Averages were calculated for species' counts on routes outside and within the U.S. Prairie Potholes.

| Species | Count | Maximum | | Minimum | | Range (km$^2$) | Average | |
|---|---|---|---|---|---|---|---|---|
| | | Highest | Year | Sum | Year | | Outside | Within |
| Mallard | 119008 | 703 | 1988 | 459 | 1967 | 9025216.414 | 3.256 | 24.032 |
| Canada Goose | 66085 | 938 | 2012 | 2 | 1971 | 8419039.386 | 5.961 | 13.733 |
| Blue-winged Teal | 40701 | 604 | 2009 | 431 | 1992 | 3166724.908 | 0.768 | 8.3454 |
| Gadwall | 27241 | 299 | 2006 | 165 | 1987 | 3407472.881 | 3.005 | 6.706 |
| Northern Pintail | 21135 | 720 | 1970 | 127 | 1988 | 2250756.931 | 1.314 | 4.875 |
| Northern Shoveler | 17581 | 128 | 1993 | 46 | 1967 | 2668055.403 | 1.2 | 4.106 |
| Lesser Scaup | 13959 | 112 | 2008 | 16 | 1967 | 2125155.087 | 2.54 | 3.911 |
| Ruddy Duck | 9933 | 303 | 2008 | 39 | 1976 | 2075862.958 | 1.708 | 2.966 |
| American Wigeon | 6189 | 86 | 2002 | 31 | 1968 | 2499458.996 | 1.696 | 1.806 |

Table 3-3: Prevalence of occurrence (sum of counts) of variables considered in the top 15 models for each species.

| Species | STI | SPI | Forest | Water | Grass | Crop | Developed | Wetland | Wetland IJI | LPI | Contagion | SIDI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mallard | 11 | 12 | 11 | 15 | 9 | 9 | 8 | 4 | 15 | 11 | 12 | 12 |
| Gadwall | 13 | 7 | 8 | 12 | 11 | 7 | 7 | 5 | 14 | 7 | 12 | 7 |
| American Wigeon | 6 | 13 | 6 | 7 | 9 | 13 | 7 | 5 | 14 | 3 | 5 | 12 |
| Blue-winged Teal | 15 | 15 | 8 | 15 | 10 | 10 | 8 | 7 | 15 | 7 | 11 | 11 |
| Northern Shoveler | 6 | 15 | 7 | 15 | 10 | 5 | 4 | 3 | 14 | 1 | 15 | 10 |
| Northern Pintail | 11 | 15 | 3 | 15 | 11 | 12 | 6 | 8 | 15 | 7 | 10 | 8 |
| Lesser Scaup | 14 | 0 | 2 | 15 | 11 | 6 | 6 | 14 | 15 | 5 | 5 | 3 |
| Ruddy Duck | 15 | 15 | 15 | 15 | 8 | 5 | 6 | 1 | 12 | 8 | 6 | 5 |
| Canada Goose | 5 | 2 | 14 | 15 | 13 | 13 | 1 | 5 | 9 | 8 | 15 | 15 |

| **Species** | **Water** | **Grassland** | **Crop** | **Wetland** | **R²** |
|---|---|---|---|---|---|
| Mallard | 19.38 (14.48, 24.27) | -1.14 (-3.27, 0.99) | -0.04 (-2.2, 2.11) |  | 0.53 |
| Gadwall | 33.14 (23.48, 42.78) | 3.81 (-0.76, 8.38) | 2.04 (-2.51, 6.6) |  | 0.59 |
| American Wigeon |  |  | -2.89 (-4.01, -1.79) |  | 0.32 |
| Blue-winged Teal | 42.35 (36.89, 47.91) | 7.51 (5.18, 9.89) | 8.14 (5.84, 10.48) | 9.89 (5.97, 13.81) | 0.71 |
| Northern Shoveler | 25.27 (18.32, 32.29) | 4.02 (1.35, 6.74) | 3.27 (0.59, 5.98) |  | 0.58 |
| Northern Pintail | 35.04 (27.73, 42.49) | 10.82 (7.49, 14.37) | 9.69 (6.48, 13.11) | 15.23 (10.04, 20.54) | 0.15 |
| Lesser Scaup | 42.13 (31.58, 52.91) | 4 (2.71, 5.31) |  | 11.31 (5.74, 16.85) | 0.68 |
| Ruddy Duck | 41.84 (33.48, 50.38) | 0.43 (-0.68, 1.54) |  |  | 0.25 |
| Canada Goose | 19.03 (11.87, 26.19) | -2.9 (-5.93, 0.13) | -2.51 (-5.52, 0.49) |  | 0.21 |

Table 3-5: Waterfowl response to landscape characteristics and configuration.

| **Species** | **Wetland IJI** | **Contagion** | **Shannon's Diversity** | **Size of Largest Pond** | **$R^2$** |
|---|---|---|---|---|---|
| Mallard | -0.02 (-0.03, -0.01) | -0.02 (-0.07, 0.03) | 1.24 (-1.11, 3.59) | 0.02 (-0.02, 0.07) | 0.53 |
| Gadwall |  | -0.03 (-0.14, 0.07) | 2.49 (-2.56, 7.52) | 0 (-0.09, 0.08) | 0.59 |
| American Wigeon | -0.03 (-0.06, 0) |  | 1.33 (-0.97, 3.64) |  | 0.32 |
| Blue-winged Teal | -0.05 (-0.06, -0.04) | -0.05 (-0.11, 0.01) | 1.22 (-1.5, 3.93) |  | 0.71 |
| Northern Shoveler | -0.07 (-0.09, -0.05) | -0.11 (-0.18, -0.03) | -1.19 (-4.77, 2.35) |  | 0.58 |
| Northern Pintail | -0.07 (-0.09, -0.05) | 0.05 (-0.03, 0.12) | 5.1 (1.79, 8.4) |  | 0.15 |
| Lesser Scaup | -0.07 (-0.12, -0.03) |  |  |  | 0.68 |
| Ruddy Duck |  | -0.16 (-0.25, -0.07) | -6.38 (-10.73, -2.1) |  | 0.25 |
| Canada Goose |  | -0.14 (-0.21, -0.06) | -6.52 (-10.17, -2.92) |  | 0.21 |

Table 3-6: Waterfowl response to weather.

| Species | SPI | STI | $R^2$ |
|---|---|---|---|
| Mallard | 0.1 (0.06, 0.15) | -0.09 (-0.16, -0.02) | 0.53 |
| Gadwall | 0.04 (-0.03, 0.1) | -0.15 (-0.24, -0.05) | 0.59 |
| American Wigeon | 0.07 (-0.04, 0.18) | -0.01 (-0.14, 0.11) | 0.32 |
| Blue-winged Teal | 0.18 (0.12, 0.24) | 0.25 (0.09, 0.42) | 0.71 |
| Northern Shoveler | -0.17 (-0.36, 0.02) | -0.11 (-0.23, 0.01) | 0.58 |
| Northern Pintail | 0.19 (0.1, 0.27) | -0.12 (-0.24, 0) | 0.15 |
| Lesser Scaup |  | -0.09 (-0.18, 0.01) | 0.68 |
| Ruddy Duck | 0.22 (0.12, 0.33) | -0.14 (-0.28, 0) | 0.25 |
| Canada Goose |  |  | 0.21 |

Table 3-7: Waterfowl response at the BBS route level in Alaska to drought in the Prairie Potholes.

| Species | Drought |
|---|---|
| Mallard | -0.06 (-1.26, 1.08) |
| Gadwall | -0.26 (-6.72, 4.84) |
| American Wigeon | -0.18 (-1.5, 1.08) |
| Blue-winged Teal | 0.78 (-5.41, 5.76) |
| Northern Shoveler | 1.08 (-1.02, 3.04) |
| Northern Pintail | -0.09 (-1.82, 1.53) |
| Lesser Scaup | 0.29 (-1.58, 1.98) |
| Canada Goose | 0.82 (-0.34, 1.93) |

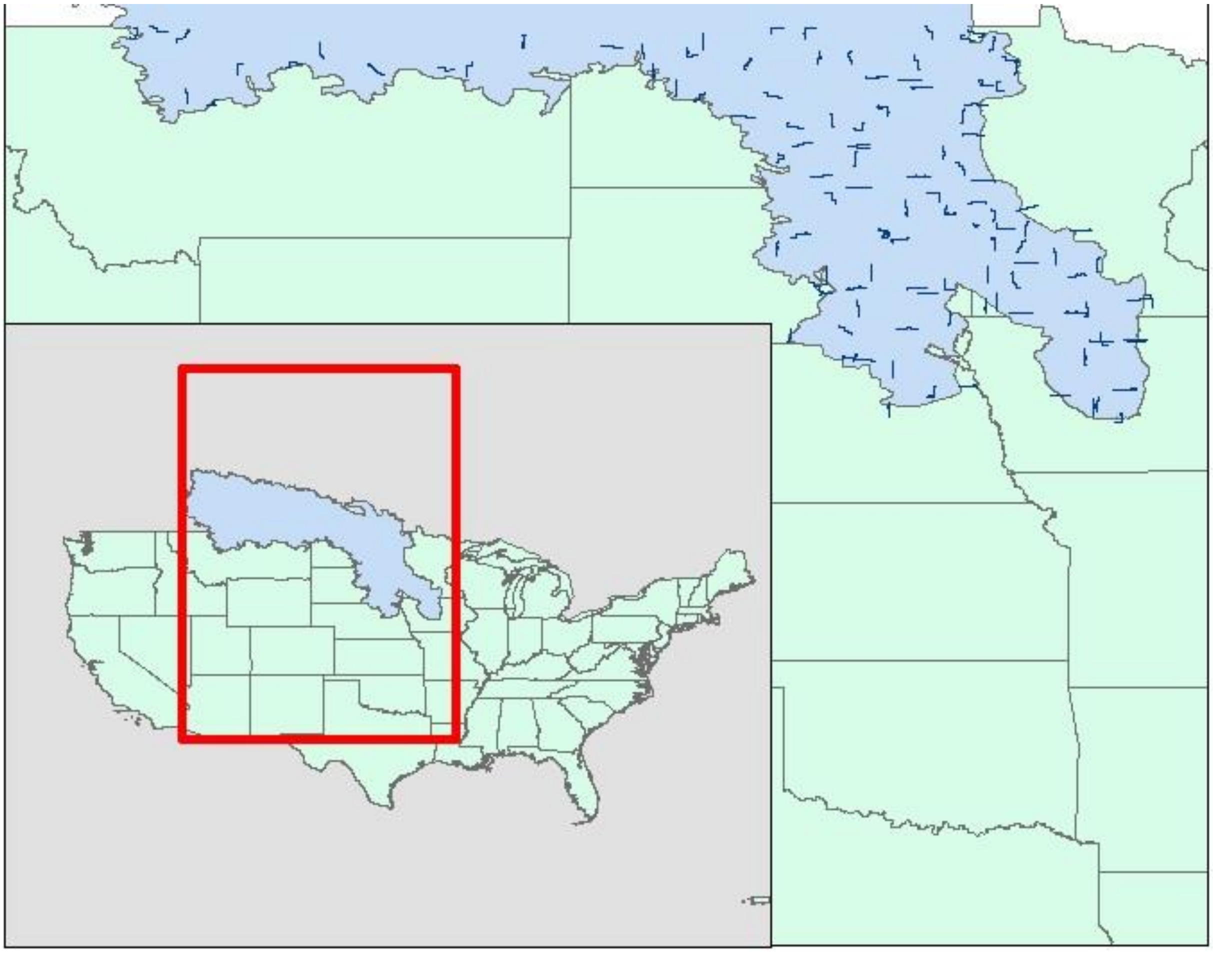

Figure 3-1: The U.S. portion of the Prairie Potholes (BCR 11), and locations of BBS routes therein.

Appendix 3-A. Parameters of interest in models considered containing an interaction between land cover and weather.

WATER + GRASSLAND*SPI
WATER + GRASSLAND*STI
GRASSLAND*SPI
GRASSLAND*STI
CROP*SPI
CROP*STI
WATER + GRASSLAND*SPI + IJI
WATER + GRASSLAND*STI + IJI
WATER + GRASSLAND + IJI*SPI
WATER + GRASSLAND + IJI*STI
WATER + GRASSLAND + IJI*SPI + CONTAGION
WATER + GRASSLAND + IJI*STI + CONTAGION
WATER + GRASSLAND + IJI + CONTAGION*SPI
WATER + GRASSLAND + IJI + CONTAGION*STI
WATER + GRASSLAND + IJI + CONTAGION*SPI + SIDI
WATER + GRASSLAND + IJI + CONTAGION*STI + SIDI
WATER + GRASSLAND + IJI + CONTAGION + SIDI*SPI
WATER + GRASSLAND + IJI + CONTAGION + SIDI*STI
WATER + GRASSLAND + IJI + CONTAGION + SIDI*SPI + STI
WATER + GRASSLAND + IJI + CONTAGION + SIDI*STI + SPI
WATER + GRASSLAND + IJI + CONTAGION*SPI + SIDI + STI
WATER + GRASSLAND + IJI + CONTAGION*STI + SIDI + SPI
WATER + GRASSLAND + IJI*SPI + CONTAGION + SIDI + STI
WATER + GRASSLAND + IJI*STI + CONTAGION + SIDI + SPI
WATER + GRASSLAND*SPI + IJI + CONTAGION + SIDI + STI
WATER + GRASSLAND*STI + IJI + CONTAGION + SIDI + SPI
WATER + GRASSLAND + IJI + CONTAGION + SIDI*SPI + STI
WATER + GRASSLAND + IJI + CONTAGION + SIDI*STI + SPI
WATER + GRASSLAND + CROP + IJI + CONTAGION + SIDI*SPI + STI
WATER + GRASSLAND + CROP + IJI + CONTAGION + SIDI*STI + SPI
WATER + GRASSLAND + CROP*SPI + wetland + IJI + CONTAGION + SIDI + STI
WATER + GRASSLAND + CROP*STI + wetland + IJI + CONTAGION + SIDI + SPI
WATER + GRASSLAND + CROP*SPI + IJI + CONTAGION + SIDI + STI
WATER + GRASSLAND + CROP*STI + IJI + CONTAGION + SIDI + SPI
WATER + GRASSLAND + CONTAGION*SPI + SIDI + STI
WATER + GRASSLAND + CONTAGION*STI + SIDI + SPI
WATER + GRASSLAND + CONTAGION + SIDI*SPI + STI
WATER + GRASSLAND + CONTAGION + SIDI*STI + SPI
WATER + CONTAGION*SPI + SIDI + STI
WATER + CONTAGION*STI + SIDI + SPI
WATER + CONTAGION + SIDI*SPI + STI
WATER + CONTAGION + SIDI*STI + SPI

## Conclusions

### *Contributions to scientific understanding*

Overall, avian communities of the north-central grasslands, from of the moderate tree cover Prairie Hardwood Transition region through the shortgrass prairie-dominated Badlands and Prairies region, responded strongly to weather. The response to recent and current weather is one indicator of how these grassland bird species will respond to climate change. Though climate projections at local scales throughout the region are accompanied by a great deal of uncertainty, the central grasslands overall are projected to become warmer, likely contributing to increasingly dry conditions, especially in the summer months (Morgan et al. 2008). Precipitation projections vary across the geographic expanse of the region, and also seasonally (Cubasch et al. 2001). Northern portions of the grasslands are projected to experience increasing precipitation in the summer, but southward projections suggest minimal change in precipitation (Garbrecht et al. 2004). Temperature increases are expected to offset precipitation, resulting in drier conditions across the region (Loehman 2009). This is likely to have negative consequences for birds that rely on water (i.e. the waterfowl of the Prairie Potholes) and grassland birds that depend on lush tallgrass vegetation (i.e. Baird's and grasshopper sparrows).

Also due to increasing temperature, the climate space currently occupied by grasslands is projected to shift northwest, such that the grasslands could expand farther north in Canada and be lost in the southeastern portions of the U.S. Thus, the northwestern regions of potential grassland expansion are likely to become more productive with warmer temperatures (due to a longer growing season and more summer precipitation), while grassland productivity in the southeast may decline. The most imminent effects of climate change will thus be felt in on the southeast edge of U.S. grasslands, the Eastern Tallgrass Prairie region, and by the grassland bird community there. The obligate grassland species included in my chapter 2 analysis, in order of lack of tolerance for woody cover (as indicated by the magnitude of modelled negative response to woody cover) include lark bunting, horned lark, chestnut-collared longspur, western meadowlark, western kingbird, savannah sparrow, Brewer's blackbird, dickcissel, vesper sparrow, bobolink, eastern meadowlark and grasshopper sparrow. These species are thus imminently at risk of changes in habitat suitability in their current range, due to climate change. Grasshopper sparrow was likewise identified in my first chapter analysis as being sensitive to increasingly dry, warm conditions, along with Baird's sparrow.

The shift in climate space also bears on where suitable wetlands for waterfowl breeding will occur (Larson 1995). The Prairie Potholes is likely to suffer loss of existing wetlands, which is problematic in the context of a shifting climate space (Covich et al. 1997). Wetlands suitable for waterfowl breeding are expected to likewise shift northwest, which is problematic because of the removal of wetlands and alteration of topography in this portion of the Prairie Potholes (Murkin 1998). Given that in my 3rd chapter results, waterfowl respond to within-year precipitation and temperature, as well as water on the landscape, it is possible that waterfowl will track weather conditions and climatic shifts. What remains to be seen is if there will be sufficient available places for water to collect in future land use/land cover change scenarios.

Weather is likely to become more variable across the region, with more observations of extremes in precipitation and temperature (Meehl et al. 2000). A drier climate with more variable precipitation and increasingly intense storms also favors wildfires, which may be altered in dynamics across the landscape (McKenzie et al. 2004). As a potential positive effect for woody cover avoiders, an increasing amount of area affected by wildfire would inhibit woody vegetation (McLaughlin and Bowers 1982). The aforementioned woody cover avoiders from my

2nd chapter thus may be less inhibited by breeding site availability if future climate increases wildfire in grassland habitats. It remains to be seen, though, if more available habitat will also host a suitable climate for these species. Thus, increasing weather variability has significant consequences for the central U.S. grasslands (Katz and Brown 1992).

### *Contributions to analytical methods*

I built upon the Bayesian hierarchical framework developed to analyze BBS data (Link and Sauer 2002) by interpreting potential influences to the count data into models, re-examining the prior assumptions governing hyper-parameters, and fitting models via the INLA approach (Martins et al. 2013). I considered trend to simply be a linear function of year, such that I fit a slope to year as a predictor, which would translate to a change in abundance annually. By examining the influence of annual weather on counts, I attempted to better explain annual variation in counts (i.e. explain variation that otherwise would be accounted for in the random year effect incorporated in my models). I used the half-Cauchy distribution for hyper-parameters over more often-used distributions because it allows hyper-parameters to be “less informative” than e.g., if one of the inverse-gamma family of distributions was used (Gelman 2006).

Predictive models, including weather and for 2 of 3 chapters, land cover, generally approximated counts well, which is an indicator of fit and applicability of these models. Modelled counts from these chapters incorporate influences known to affect counts (e.g., route, observer, whether or not it was an observer’s first year, and year). Thus, the use of modelled counts may provide more accurate abundance indices at the route level, which can be scaled up for regional assessments.

### *Contributions to management applications*.

The avian species, or groups thereof, identified in this dissertation that may be most imminently threatened by climate change on breeding grounds are Baird’s and grasshopper sparrows, and waterfowl. All of the species therein responded positively to precipitation and negatively to temperature, indicating that drier, warmer conditions will negatively affect them. Thus, they should be focal species in adaptive management strategies, in order to maintain population levels in future climate scenarios.

There are several possible hypothetical adaptive management strategies for grasslands, but many of them are as-of-yet untested in efficacy. The most immediately relevant strategies are those that are in line with our current understanding of restoration needs, and which promote resilience of the native habitat. For instance, in order to facilitate dispersal by birds to track climate, fragmentation should be reduced to increase habitat connectivity within the central grasslands. This translates to restoration of human altered areas to native grassland and oak savanna, to achieve habitat patches large enough to function as population sources rather than as sinks, which is the role of many small patches.

Thus, this dissertation highlights the need for grassland restoration and preservation perhaps most urgently in the northern portions of species’ current ranges, as projected climate space shifts may mean species that are able to track climate will become more abundant in the northerly edges of their ranges. This is sensible both because it doesn’t require management for habitat in novel locations before projected changes occur, and yet is appropriate to effectively manage species with consideration to climate change. The chapters of this dissertation support other literary findings that grassland birds exhibit migratory nomadism, so there is hope that species of the central grasslands will indeed be able to adapt by moving northward. Facilitation of adaptation in breeding range should thus be a focus in management for future climate scenarios.

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