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RESEARCH ARTICLE

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

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ABSTRACT

Avian populations can respond dramatically to extreme weather such as droughts and heat waves, yet 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. We 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. We 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 ($\beta = 0.101$), and 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 -0.02, respectively), although for Vesper Sparrow the lag effect was insignificant. With projected warmer, drier weather during summer in the Badlands and Prairies BCR, Baird's and Grasshopper sparrows may be especially threatened by future climate change.

Keywords: drought, Bayesian, climate, weather, breeding, STI, SPI, INLA

Uso del Conteo de Aves Reproductivas de América del Norte para evaluar la respuesta a gran escala de la comunidad de aves más amenazada del continente, las aves de pastizal, a la variabilidad climática

RESUMEN

Las poblaciones de aves pueden responder de modo dramático al clima extremo como las sequías y las olas de calor. Sin embrago, los patrones de respuesta al clima a escalas más amplias permanecen en gran medida desconocidos. Nuestro objetivo fue evaluar la variación anual en la abundancia de 14 especies de aves de pastizal que se reproducen en la pradera mixta de pastizales del norte, en relación a la variación anual de la precipitación y la temperatura. Modelamos la abundancia de aves durante la estación reproductiva usando los datos del Conteo de Aves Reproductivas de América del Norte para la Región de Conservación de Aves de EEUU de Páramos y Praderas (BCR – por sus siglas en inglés– 17) desde 1980 a 2012. Usamos métodos jerárquicos bayesianos para ajustar modelos y estimar los correspondientes parámetros del clima para el índice de precipitación estandarizado (SPI por sus siglas en inglés) y el índice de temperatura estandarizado (STI por sus siglas en inglés) para el mismo año y para el año anterior. *Bartramia longicauda* respondió positivamente al STI del mismo año ($\beta = 0.101$). *Ammodramus bairdii* respondió negativamente al STI del mismo año ($\beta = -0.161$) y positivamente al SPI del mismo año ($\beta = 0.195$). Las estimaciones de los parámetros fueron superficialmente similares (STI $\beta = -0.075$, SPI $\beta = 0.11$) para *Ammodramus savannarum*, pero el modelo mejor seleccionado incluyó una interacción entre SPI y STI. El mejor modelo para *Tyrannus tyrannus* y *Pooecetes gramineus* incluyó los efectos aditivos de SPI del mismo año ($\beta = -0.032$ y $\beta = -0.054$, respectivamente) y de SPI del año previo ($\beta = -0.057$ y -0.02, respectivamente), aunque para *P. gramineus* el efecto de demora fue insignificante. Ante la proyección de un clima más cálido y seco durante el verano en los Páramos y las Praderas, *A. bairdii* y *A. savannarum* pueden verse especialmente amenazadas por el futuro cambio climático.

Palabras clave: bayesiano, clima, cría, sequía, tiempo

INTRODUCTION

Birds experience and respond to a variety of weather conditions during the breeding season, governed in part by regional climate. Climate is defined by both averages and variability of precipitation and temperature over a 30-year or longer time period, whereas 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, although 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) by exceeding physiological thresholds. In drought conditions, birds may abandon nests or forgo breeding altogether, as was the case for Bridled Titmouse (*Baeolophus wollweberi*) in the southwestern U.S. (Christman 2002). Thus, avian settlement and productivity may depend heavily on interannual variation in weather.

Droughts are common in temperate semiarid 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). Because 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 semiarid 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 stressed many sectors, including human food production, and breeding birds were also affected (Krapu et al. 2006). For example, during the drought, breeding bird density in June 1988 was 61% lower than in June 1987 in North Dakota (George et al. 1992). Furthermore, Horned Lark (*Eremophila alpestris*), Western Meadowlark (*Sturnella neglecta*), and Vesper Sparrow (*Pooecetes gramineus*) stopped nesting in mid-June 1988 (George et al. 1992). Prior empirical evidence on the effects of extreme weather on grassland bird communities, however, 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 to determine if weather is an important driver of species-specific annual abundance. We 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, we 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 >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). We used BBS data from 1966 through 2010, in accordance with the time record of an available weather dataset (Maurer et al. 2002). We 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 that had adequate representation in the BBS dataset; thus, we excluded Sharp-tailed Grouse (*Tympanuchus phasianellus*), leaving 14 grassland bird species (Table 1). For each species, we considered only routes where the species had occurred at least once. The Badlands and Prairies BCR includes 117 routes, but the number of routes on which each species was detected differed. We excluded route runs that did not meet quality standards, as indicated in the dataset. We also used only standard BBS route runs and did not include resampling efforts or nonstandard protocols.
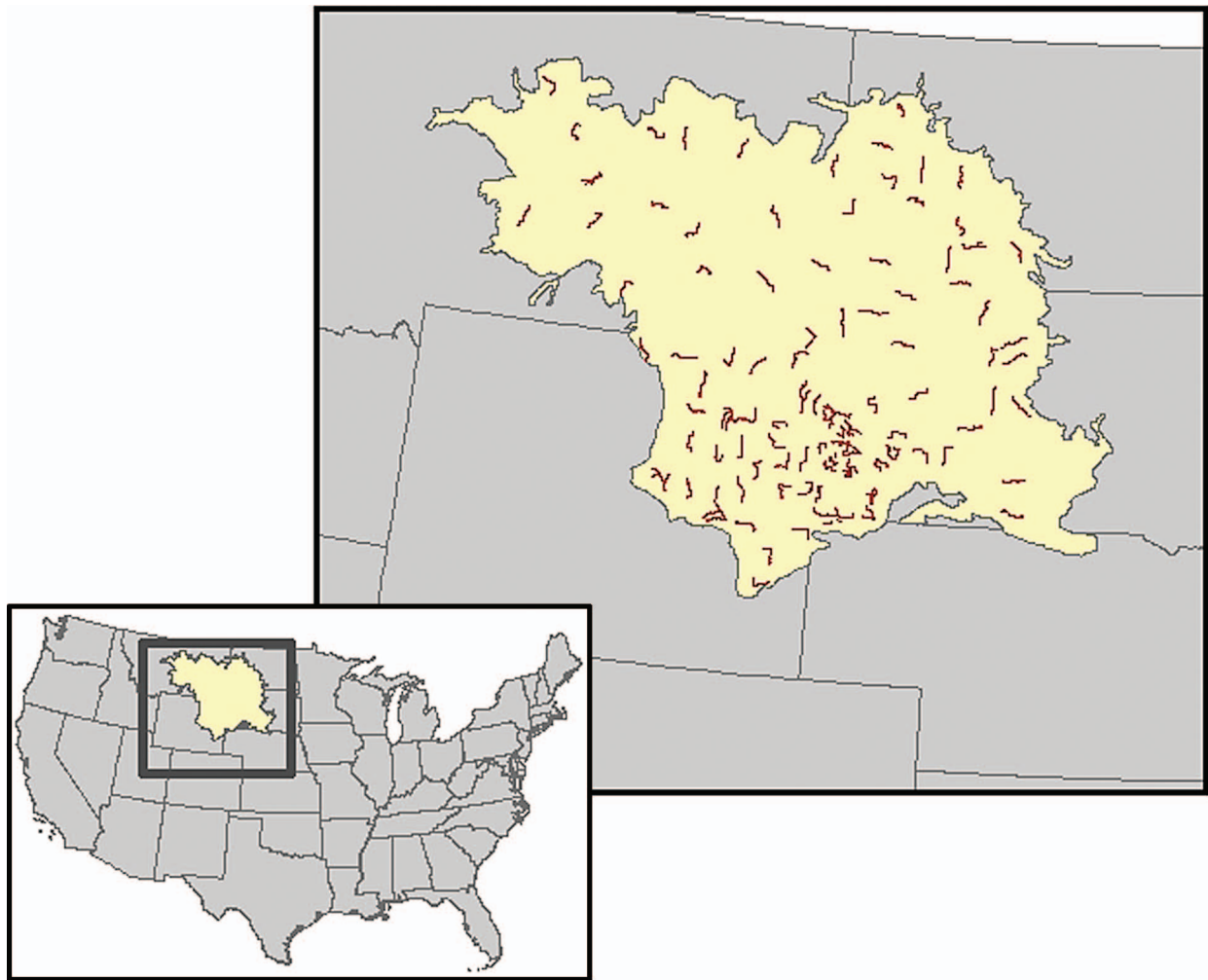
FIGURE 1. Location of Bird Conservation Region 17 within North America. Lines represent BBS routes.

TABLE 1. Life history characteristics of the 14 grassland birds considered for this analysis, adapted from VerCauteren and Gillahan (2004) and Birds of North America (BNA) accounts for Clay-colored and Field Sparrows. Species in bold are considered to be indicator species for the Northern Plains (VerCauteren and Gillahan 2004).

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)

Weather Data

We analyzed weather data from the gridded meteorological dataset produced by the Maurer et al. (2002) algorithm, which covers the contiguous U.S. at one-eighth degree spatial resolution (∼140 km^2 per grid cell) from 1949 to 2010 (Maurer et al. 2002). We 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. We considered weather leading up to a given year's breeding season and weather from the previous year as potentially influential for avian abundance.

Precipitation. We used the Standardized Precipitation Index (SPI) to characterize interannual 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, we used the summer (i.e. June–August) SPI. We fit annual totals to the Pearson Type III distribution and transformed each annual total to a standard deviation from a standard normal distribution. Full details of these calculations are available online (http://silvis.forest.wisc.edu/climate-averages-and-extremes). In some cases, anomalous precipitation values that did not fit the distribution were recoded as 7 or −7, depending on whether or not the anomaly was positive or negative, respectively.

Temperature. We calculated the Standardized Temperature Index (STI) for June, 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. We standardized average daily maximum temperature into the STI to account for differences in temperature mean and interannual variability among locations. 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, we 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). Vegeta-

tion indices are designed to measure vegetative vigor (Ji and Peters 2003). We averaged and calculated standard deviations per pixel of June EVI from 2003 through 2012 and then subtracted the mean and divided by the standard deviation for each pixel, yielding a standard score per pixel for each June from 2003 through 2012. We averaged the pixels of the SSG image within 400 m of each BBS route to characterize vegetative anomaly for each route per year from 2003 through 2012. We 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 multiple levels of variance in nuisance variables 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 run by different observers influence the detection, and ultimately the tally, of species' abundances recorded. Bayesian methods allow 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). We 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). We modeled nuisance effects such as year, route, and observer as independent random variables and assigned standard noninformative priors via the half-Cauchy distribution to the hyperparameters (Gelman 2006). We 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 and their additive and interactive combinations (Table 2). We performed model selection for each species with the goal of selecting the best model explaining each species' variation in abundance index. We ranked our models based on the Watanabe-Akaike information criterion (WAIC), a Bayesian information criterion (Watanabe 2010). If the model best explaining a species' abundance patterns included a weather variable, we assessed its significance by examining the 95% credible interval (CI) of the posterior distribution. If the CI did not include zero, we considered the weather variable to have a statistically significant effect on species' abundance.

TABLE 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.

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

RESULTS

Our analysis included 109 BBS routes across the Badlands and Prairies BCR surveyed from 1966 to 2010 between May 15 and August 4, although 99% of routes were surveyed in June or later. The number of routes considered per species ranged from 30 to 103 (Table 3). The 14 species under consideration had total counts ranging from 614 for Sprague's Pipit (*Anthus spragueii*) to 368,814 for Western Meadowlark across all routes from 1966 to 2010 (Table 3). 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 BCR. 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 were 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 used to derive spring and summer SPI 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 1967–1969, 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 1970–1971, 1973–1974, 1976, 1979, 1985, 1987–1988, 1990–1991, 1994, 1996, 2002, and 2006–2007. Thus, of the spring SPI drought years, 43% were also summer SPI drought years. Year 1980 produced 22% of the most severe spring SPI values, including the overall most extreme drought value on a route that could not be placed within the distribution. Summer SPI included 4 values too extremely negative to be modeled in the distribution, occurring in 1970, 1994, and 2006–2007. The 50 highest spring SPI values observed on a route (i.e. the wettest conditions) occurred in 1970–1971, 1975, 1977–1978, 1981–1982, 1986, 1991, 1995, 1998, 2005–2007, 2008, and 2010. The 50 highest summer SPI values occurred in 1968–1969, 1972, 1976–1982, 1984, 1992–1993, 1995, 1997–1999, 2001, 2004, 2008, and 2009–2010. 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

A significant positive linear relationship between SPI and SSG (RSE = 0.49, $P < 0.001$) seemed 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, the routes with highest mean seasonal greenness seemed the most consistent in vegetative condition year-to-year across a gradient of weather conditions, whereas

TABLE 3. Summary statistics for bird species included in this analysis on BBS routes in BCR 17 from 1980 to 2012. For each species, the total number of birds detected over all routes during the 32 year period is presented, and average annual count (Average), Minimum, and Maximum 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 was found on per year, and the associated standard deviation.

				Frequency				
Common name	Total	Average	Standard deviation	Minimum	Maximum	Average	Standard deviation	No. routes
Upland Sandpiper	14,790	8.3	15.7	8	39	24.6	9.6	80
Mourning Dove	78,378	36.6	35.8	12	66	42.6	13.4	103
Eastern Kingbird	14,918	7.5	8.3	9	52	34.8	11.3	92
Horned Lark	94,781	48.3	64.2	10	57	36.2	11.1	92
Sprague's Pipit	614	0.8	2.8	0	9	3.5	2.2	30
Brown-headed Cowbird	53,203	25.0	37.0	9	62	37.6	14.6	100
Western Meadowlark	368,814	173.2	145.2	12	67	42.2	12.9	102
Brewer's Blackbird	24,640	12.3	24.1	4	50	29.6	11.3	92
Vesper Sparrow	31,603	15.5	24.1	7	55	32.6	11.7	96
Baird's Sparrow	1,311	1.3	3.7	0	12	6.1	2.5	39
Grasshopper Sparrow	23,427	11.6	18.2	9	47	29.2	9.7	94
Lark Sparrow	10,543	5.1	12.6	8	45	25.1	9.7	95
Clay-colored Sparrow	1,896	1.5	3.7	2	15	8.5	2.8	53
Field Sparrow	3,313	2.8	7.0	1	17	9.1	3.8	54

routes of lower mean seasonal greenness varied interannually 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, because of the nature of extremes, more bird surveys occurred in average or near-average weather years than in years when extreme weather events occurred.

Species' Modeled 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). Weather metrics capturing deviation from normal (SPI and STI) seemed to be 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, and 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, and, although the parameter estimates were insignificant, all but one of the best-fit models for these species included a measure of SPI (Table 4). Thus, although none of the aforementioned species' responses to weather 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 the effects were not captured by 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 (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 relatively few years represented the hottest and coldest observations. This pattern reflects the annual spatial variability in precipitation in this region 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, although
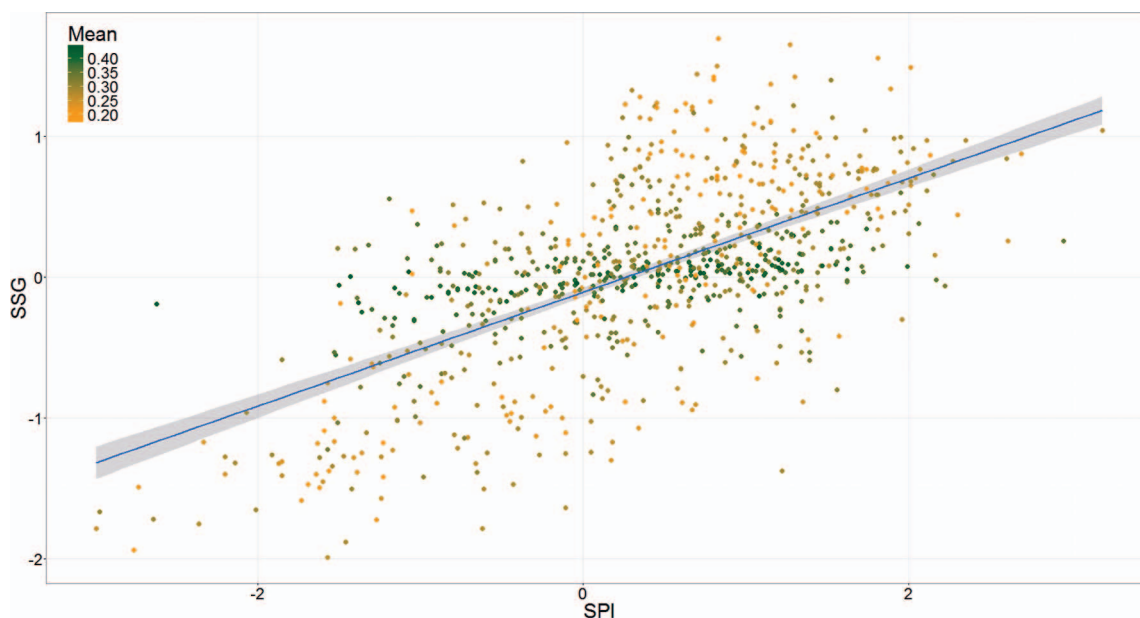
FIGURE 2. The relationship between standardized precipitation index (SPI) and standardized seasonal greenness (SSG) in BCR 17. Dots are observations of both variables (SPI and SSG) along a route in a given year. Color codes are the average EVI for the route from 2003 to 2012. The residual standard error 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.

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. 1987–1988, 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, most (32 of 50) of the coolest route observations occurred in 1998, and although 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 5 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, but 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 5 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' responses 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 interannual 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 be due to a significant decrease or increase in the population based on weather during the prior year's breeding season, although 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
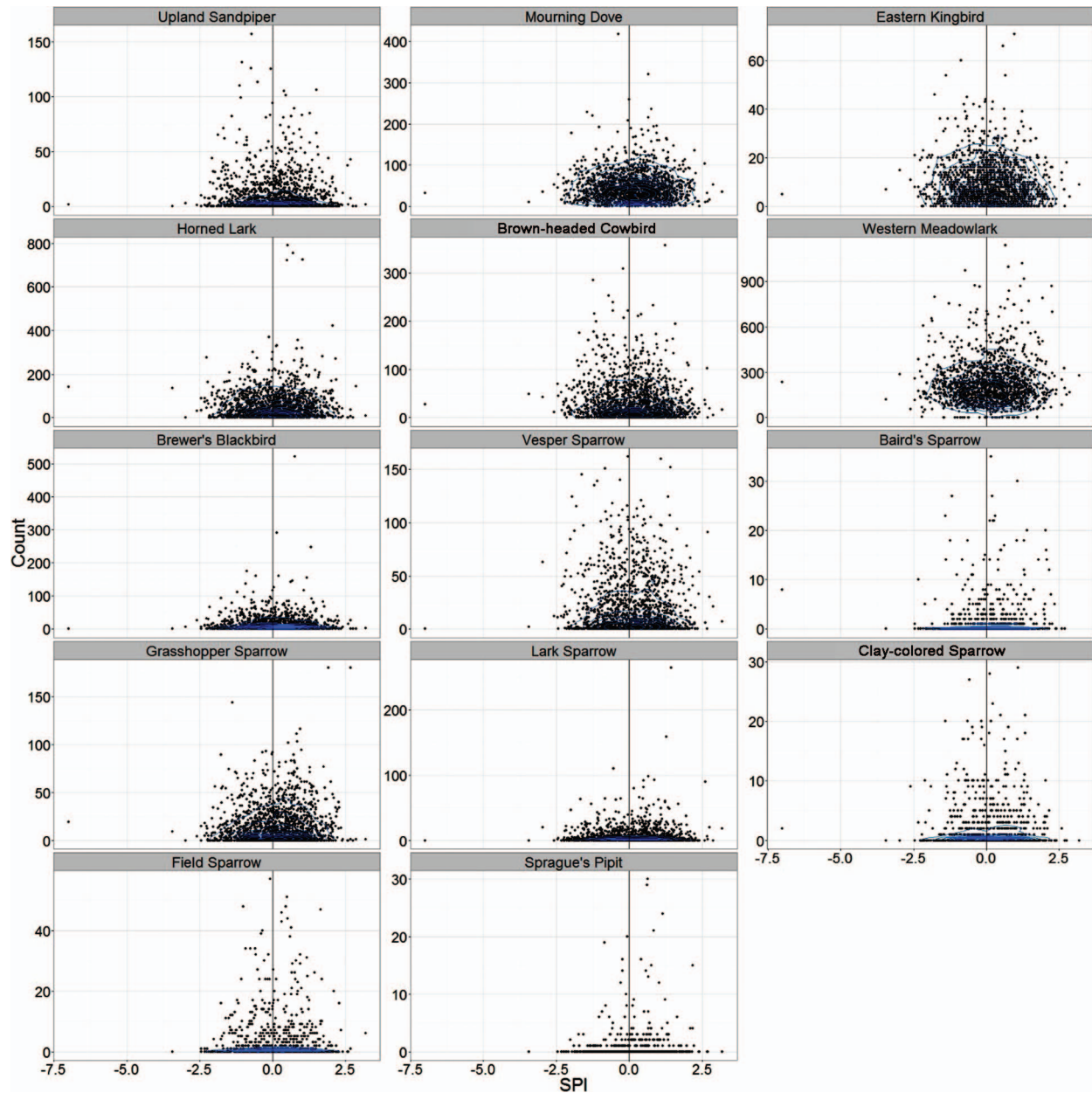
FIGURE 3. Species' raw counts in relation to SPI, with density contours overlain on the point cloud.

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 (*Zenaida macroura*), Horned Lark, Western Meadowlark, Brewer's Blackbird (*Euphagus cyanocephalus*), Brown-headed Cowbird (*Molothrus ater*), Lark Sparrow (*Chondestes grammacus*), Clay-colored Sparrow (*Spizella pallida*), Field Sparrow (*S. pusilla*), and Sprague's Pipit. Although 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 Lark and Western Meadowlark 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
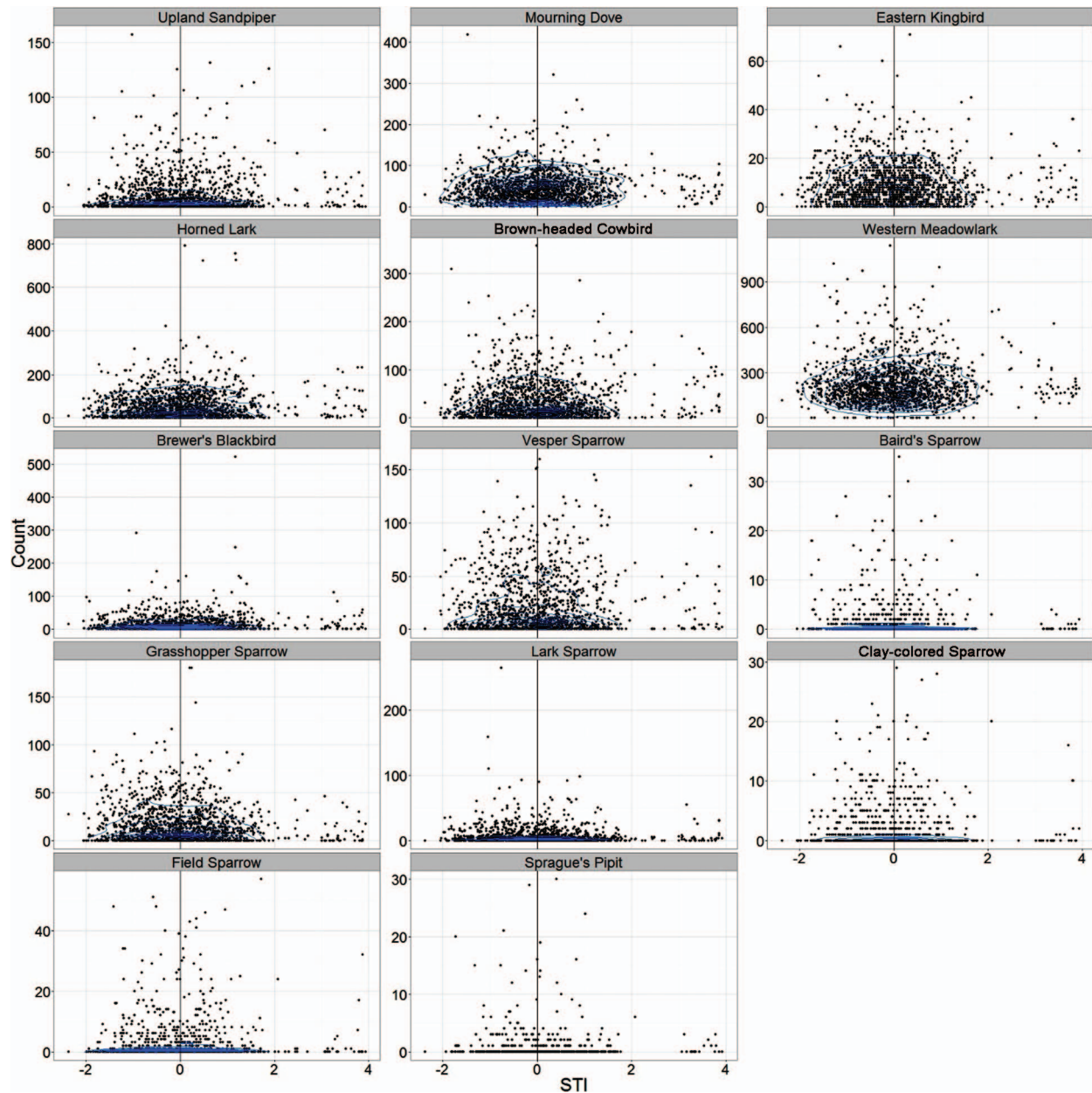
FIGURE 4. Species' raw counts in relation to STI, with density contours overlain on the point cloud.

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 because of the loss of grassland habitat as agricultural

land use has expanded (Vickery and Herkert 2001). Several bird species of semiarid 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

TABLE 4. Modeled response of species' abundance index to weather. The model number corresponds to the list of candidate models provided in Table 2. 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	SPI$_{lag}$	STI	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	−0.034 (−0.082, 0.014)	−0.001 (−0.015, 0.013)		0.018 (−0.006, 0.043)
Brewer's Blackbird	10			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)**	**−0.161 (−0.297, −0.029)**	
Baird's Sparrow	**5**	**0.195 (0.079, 0.311)**			
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)		

be conducted to assess further risks posed by climate change and guide adaptive management strategies.

ACKNOWLEGDMENTS

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